Plant Pathology in the 21st Century

Maria Lodovica Gullino
Ramon Albajes
Philippe C. Nicot *Editors*

Integrated Pest and Disease Management in Greenhouse Crops

Second Edition

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Introduction

Crops are grown in greenhouses to extend their growing season and protect them from adverse environmental conditions, diseases and pests. Greenhouse structures vary significantly in the different geographic areas and depending on the crops grown, consisting essentially of a light scaffolding covered by sheet glass, fibreglass, or plastic. Crops may be grown in ground beds, usually amended with different types of substrates; on benches; in pots containing soil, soil mixtures or soil substitutes; and in hydroponic systems, such as sand or rockwool cultures and flowing nutrient systems, without a matrix for the roots. Generally, value-added crops are grown under protected conditions, most of which are labour-intensive with high energy demands in cold weather. Quality is a high priority for greenhouse crops, requiring much care in pest and disease management, not only to secure yields but also to obtain a high aesthetic standard. Although technological changes are ultimately intended to reduce production costs and maximise profits, precise environmental and nutritional control has pushed plants to new limits of growth and productivity. These changes modify biotic and abiotic environments of crop plants and generate chronic stress conditions that are conducive to some pests and diseases, including Fusarium wilts. For example, short or no rotations of greenhouse crops can allow build-up of many soil-borne pathogens such as *Fusarium oxysporum* or *Verticillium dahliae* if the soil is not properly treated; they can also allow the increase of some insect or mite pest populations, free of natural enemies, if those are not released by augmentative biocontrol.

Growing crops in greenhouses presents both options and limitations with respect to disease and pest development and management. On the plus side, contamination with pathogens or colonisation by herbivore insects can be reduced in the greenhouse, in contrast to field environments. Moreover, it is easier to manipulate agricultural practices, for example fertilisation and irrigation, to favour crop growth over disease development or pest population enhancement. On the other hand, some cultural practices are conducive to more incidence of diseases and pests; for example, the high density of plants in greenhouse production favours disease development and spread, especially via the irrigation water, or high temperatures may limit the efficacy of some insect or mite predators. Once greenhouses are contaminated with pathogens or infested by pests, highly effective sanitation measures are needed. Increased yield and higher market prices justify the more intensive cropping and high investments in greenhouse production and the use of more expensive measures than those used in field cropping, for example soil disinfestation, but the economic risks are also high. This book is, at least partially, adjourning a previous one, edited 20 years ago by two of the authors. In 20 years many things changed, in terms of greenhouse structures, crops grown, and tools available for pest and disease management. The book, with its 23 chapters, tries to focus on the many advancements and improvements as well as the many constraints.

In the first part, more general chapters take into consideration the main pathogens and pests affecting greenhouse crops (Chaps. 1, 2, 3, 4 and 5). The situation described clearly indicates that in the case of dynamic systems such as greenhouse crops, new problems arise continuously, mostly due to the international exchange of seeds, planting material, and people that permit a very quick spread of new pests and diseases (Chaps. 6, 7 and 10). Fortunately, the diagnostic process, particularly in the case of pathogens, takes advantage of new effective and rapid tools, which permit early detection, with the adoption of effective management strategies (Chap. 8). Host resistance helps the management of many problems in various crops (Chap. 9), and cultural techniques often permit, particularly in the most sophisticated structures, to prevent many problems (Chap. 10). With the ability of many pathogens to be spread through infected seeds and propagative material, the use of healthy material is fundamental (Chap. 11), as well as the adoption of all possible methods to maintain soil (and substrate) health (Chap. 12). Biocontrol agents are much more intensively used now than in the past, responding to the increasing demand of markets for safer food that is mostly consumed fresh (Chaps. 13 and 14), while effective chemical pesticides are less numerous now than before and more and more replaced by biostimulants and natural products (Chap. 15). The second part of the book takes into consideration the implementation of IPM, from general concepts (Chap. 16) to practical cases on a number of crops (Chaps. 17, 18, 19, 20, 21 and 22) with a final Chap. 23 dealing with implementation of IPM in practice.

Hopefully this book will be helpful not only to students and researchers but also to the extension services, dealing daily with the not easy task to protect crops from pests and diseases.

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Part I
Major Diseases and Pests in Greenhouse Crops

Chapter 1
Viral Diseases

Enrique Moriones and Eric Verdin

Abstract Viruses cause many important plant diseases and are responsible for yield and quality losses in crops in all parts of the world. No curative methods are available for infected plants and the main control strategies are cultural practices including prophylactic measures to prevent virus arrival, installation and spread into the crop or use genetic resistance to limit disease damage. Factors driving viral emergence include genetic variability of plant viruses, changes in agricultural practices, exchanges of plant material and new introduction or increase in the population of insect vectors in the environnent of the crops. In this review, we briefly describe the most important viruses emerging in economically important vegetable greenhouse crops including pepper, tomato and cucurbit species.

Keywords Virus · Emergence · Vector · Diversity · Resistance · Tomato · Pepper · Melon · Zuchini · Cucurbit

1.1 General Aspects

Viral diseases are a major limiting factor in many crop production systems. Plant viruses cause the largest fraction of emerging plant diseases (Anderson et al. 2004) mostly because of their ability to adapt to changing environmental conditions and to

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their easy dissemination frequently associated to vector transmission. Virus control is difficult because antiviral products are not available and control strategies are limited to a set of hygienic measures to prevent virus arrival, installation and spread into the crop or rely on genetic resistance to limit disease damage. Increasing international trade of plant materials and intensive production systems characterized by frequent cultural practices and rapid turnover of cultivars could enhance the risk of introducing new viruses and their vectors and foster the emergence of viral diseases. Thus, whitefly-transmitted viruses are an example of emergent viruses mostly resulting from global emergence of their whitefly (Hemiptera: Aleyrodidae) vectors. *Bemisia tabaci* whitefly populations have drastically increased worldwide since the early 1980s, especially in tropical and subtropical areas (De Barro et al. 2011). Even populations of the whitefly *Trialeurodes vaporariorum*, that have long been restricted to greenhouses, have been emerging in open-field vegetable production over the last 20 years, with large populations in summer crops and weed reservoirs (Wintermantel 2004). Virus emergence is a complex phenomenon that involves multiple ecological and genetic factors acting either during the first phase when the virus encounters the new host, the second phase that involves virus adaptation to the new host, or during the third phase in which the virus adapts to the new environment (Elena et al. 2014). Factors driving the emergence and establishment of viral diseases include the ability of viruses to evolve, changes in the vector populations, climate change, and human activities that promote emergence (Moreno-Pérez et al. 2014; Navas-Castillo et al. 2011).

In this review, we briefly describe the most important viruses emerging in economically important vegetable greenhouse crops including pepper, tomato and cucurbit species.

1.2 Emerging Viral Diseases in Pepper

Viral diseases are a major constraints on pepper (*Capsicum annuum*) production throughout the world (Florini and Zitter 1987; Green and Kim 1991). Among the 49 virus species described to infect pepper (Hanssen et al. 2010), 20 of them belonging to 15 different taxonomic groups have been reported to cause serious damage in pepper cultivation, especially in greenhouses. The most predominant are mechanically- and seed-transmitted viruses like tobamoviruses and insect-transmitted viruses like potyviruses, cucumoviruses, orthotospoviruses and begomoviruses. These threats are still relevant today but over the past 20–30 years, it has been noted that the incidence of viral diseases differed markedly between the Mediterranean basin, where only few emergences have been mentioned in pepper crops (Moury and Verdin 2012), and the tropical and subtropical areas with a significant increase of viral incidences (Kenyon et al. 2014a). In this chapter, we describe the biological characteristics of the most important viruses which affect pepper crops.

1.2.1 Potyviruses

Potyviruses are responsible for important diseases in a wide range of plant species all over the world. The *Potyvirus* genus of the family *Potyviridae* is among the largest group of plant virus species. Virions are 680–900 nm long and 11–13 nm wide flexuous particles possessing a helical symmetry with a pitch of about 3.4 nm. Particles encapsidate a monopartite single-stranded positive-sense RNA genome of about 9.7 kb in size with the VPg viral protein covalently-linked at the 5′ end and a poly-adenylated tail at the 3′ end. The genome encodes a single polyprotein which is cleaved into 10 proteins by viral proteinases and a frameshift during translation allows the synthesis of an additional 11th protein (Chung et al. 2008).

All potyviruses are transmitted in nature by aphid vectors in a non-persistent manner. Some of them are transmitted by seeds and occasionally by direct contact between leaves. The species that infect solanaceous plants belong to three clades. The largest clade includes the type member of the genus, *Potato virus Y* (PVY), which is subdivided in five major groups named C, N, O, Chile and Y^u. Only strains from groups C and Chile can infect pepper crops efficiently (Moury 2010; Janzac et al. 2015). PVY, which is the most prevalent potyvirus in pepper crops, was first reported in the 1930s in potato and is now distributed worldwide. Symptoms associated with PVY include generally systemic vein clearing, progressing into a mosaic (Fig. 1.1c). Vein necrosis of petioles and leaf blades can also occur, depending on the pepper cultivar and PVY strains, and can lead to plant death in some extreme cases (Dogimont et al. 1996). The most spectacular symptoms on fruits consist of mosaic patterns, necrotic spots and distortions; but these symptoms do not always occur. Economic losses depend on the earliness of infection and can reach 100% (Avilla et al. 1997a). *Myzus persicae* is one of the most efficient PVY aphid vector, that has a particular tropism toward warm climate conditions and proliferates at high densities in greenhouses or plastic tunnels.

Isolates of *Pepper veinal mottle virus* (PVMV) have been reported as causing epidemics in solanaceous crops, including pepper. They were mainly found in several West African countries (Thottappilly 1992), although the virus also affects pepper crops in Afghanistan (Lal and Singh 1988) and India (Nagaraju and Reddy 1980). PVMV-infected plants exhibit leaf chlorosis of the veins, followed by systemic interveinal chlorosis, mottle, and small distortion of leaves and sometimes leaf abscission and fruit distortion (Brunt et al. 1978). There have been various reports about the devastating effect of PVMV in Africa, contributing to low yield and reduced fruit quality and leading to great economic loss (54.5–64.3%) in chili and sweet pepper (Alegbejo and Abo 2002; Fajinmi 2011).

Chilli veinal mottle virus (ChiVMV) includes isolates that cause mottling, dark vein banding, narrowing and distorsion of leaves and stunted growth. ChiVMV is the most important pepper virus in Asia. Field surveys conducted in several Asian countries showed that the incidence of ChiVMV infection may reach 30–50% and may cause yield loss up to 95%, mainly in sweet chili pepper (Shah et al. 2009;

Fig. 1.1 Symptoms of cucumber mosaic virus, strain I17F (a), alfalfa mosaic virus (b), potato virus Y (c) and tomato spotted wilt virus (d) in pepper

Hidayat et al. 2012). ChiVMV can also infect other solanaceaous crops, including tomato, tobacco and weeds (*Physalis* and *Datura sp*.).

The *Tobacco etch virus* (TEV) species, which belong to a *Potyvirus* clade distinct from that of PVY, comprise isolates often associated with foliar vein banding and vein clearing, mosaic, mottle and distortion on leaves and fruits. The vein banding is distinct from that caused by PVY, consisting of pronounced dark-green mosaic and mottled areas which are usually associated with the larger veins. The growth of pepper plants is affected. If the plants are infected during the early growth stages, TEV can induce abortion of floral buds. Root necrosis and severe wilting symptoms followed by death of plants have also been described in some cultivars (Chu et al. 1997). TEV was found primarily in the North and Central America. In the Mediterranean basin, TEV was reported in pepper plants only in Turkey where yield reduction can reach 70% (Pernezny et al. 2003).

Prophylactic measures and genetic resistance of pepper cultivars are the main control methods to reduce potyvirus epidemics. Prophylactic methods targeting the aphid vectors are often unsuccessful because of the non-persistent transmission of potyviruses. As a matter of fact, insecticide treatment have a limited effect against aphid transmission, because the vectors can acquire and inoculate viruses during superficial and brief probes in the plant epidermal cells (Raccah 1986; Collar et al. 1997). The use of barrier crops, mineral oil sprays, polypropylene floating rowcovers have been assessed more recently or are under investigation at a local/regional scale to reduce the aphid population size and partially decrease secondary infections and inoculum pressure (Avilla et al. 1997b; Fereres 2000; Anandam and Doraiswamy 2002; Hooks and Fereres 2006). Successful breeding programmes for resistant cultivars have been used for more than 50 years, relying on monogenic resistances. This is the case for two recessive resistance alleles at the *pvr*2 locus (mapping on chromosome P4), *pvr2*^{1} and *pvr2*^{2}, that confer efficient resistance against PVY. Allele *pvr2*^{2} is also effective toward TEV (Ruffel et al. 2002). The dominant resistance gene *Pvr4* (chromosome 10) related to hypersensitive reactions is also widely used in pepper cultivars because of its high durability. In addition, *Pvr4* confers resistance not only to PVY but also to five additional potyvirus species that are present in the Americas (Janzac et al. 2009). The effect of polygenic resistance to PVY was assessed after the mapping of resistance QTLs (Caranta et al. 1997a). It was shown that quantitative trait loci (QTLs) have minor effects on resistance by themselves but increase the durability of the major *pvr2*^{3} gene, which is rapidly overcome when present alone in pepper varieties (Palloix et al. 2009).

1.2.2 Cucumoviruses

Cucumber mosaic virus (CMV), the type species of the genus *Cucumovirus* of the family *Bromoviridae*, infects more than 1200 plant species in 100 families (Edwardson and Christie 1991) including dicots and monocots. Consequently, large numbers of weeds or wild plant species can act as reservoirs between growing periods making it one of the most economically important pepper viruses (Tomlinson 1987). Cucumoviruses are transmitted by aphid vectors in a non-persistent manner. Virions are 28–30 nm icosahedrical particles that have electron dense centers. The genomic RNAs are single-stranded positive-sense RNAs with 5′ terminal cap, tRNA-like structures at 3′ ends and containing at least five open reading frames. The viral genome consists of three genomic RNAs, RNA 1 (3.3 kb), RNA 2 (3.0 kb) and RNA 3 (2.2 kb) (Mochizuki and Ohki 2012). Virions encapsidate the three genomic RNAs separately and occasionally two subgenomic RNAs, RNA 4 (1.0 kb) and RNA 4A (0.7 kb) and satellite RNAs which are able to modulate the symptoms induced by CMV (Palukaitis et al. 1992).

CMV is distributed worldwide, predominantly in temperate regions but with increasing importance in tropical countries. Considering their nucleotide identity, CMV isolates are classified into two major subgroups named I and II (Palukaitis and Garcia-Arenal 2003). Subgroup I can be phylogenetically subdivided in two clades: IA and IB. (Roossinck et al. 1999). The geographical prevalence of the members of each subgroup depends on the climate conditions: isolates from subgroup I are more widely found under warm climate and isolates from subgroup II under cold climate (Marchoux et al. 1976; Quiot et al. 1979). The pepper crops that are more widely cultivated in regions with a hot climate are therefore probably more frequently affected by subgroup I isolates.

CMV is transmitted in nature by aphid vectors in a non-persistent manner and experimentally by mechanical inoculation. CMV is not considered a seed-borne virus in pepper since no sanitary problems linked to CMV transmission have been reported. Nevertheless some authors have reported a seed transmission rate ranging from 10% to 14% for CMV isolates from the subgroup IA (Ali and Kobayashi 2010). In pepper, CMV induces yield reduction, mainly due to stunting and sometimes plant sterility, and the production of non-marketable fruits because of reduced size, distortion and irregular maturation. CMV infections in pepper cause symptoms in leaves including mosaics (Fig. 1.1a). Some CMV isolates are associated with a filiform morphology of young leaves, and necrotic symptoms in older leaves. Stem necrosis and death of plants can occur after early infections. Yield losses greatly depend on the earliness of infection and can reach 80% (Avilla et al. 1997b).

Control of CMV is difficult because of its wide host range and its rapid natural transmission by aphids. Integrated control measures are recommended in protected crops to reduce CMV incidence: (i) elimination of infected plants, (ii) avoidance of aphid entrance in the greenhouse by covering entrances with aphid-proof nets, (iii) reduction of aphid populations and (iv) elimination of alternative spontaneous hosts present in and around the crop. Resistance to CMV has been largely exploited in pepper. However, in most cases resistance or tolerance is not absolute and is overcome by some CMV species (Caranta et al. 1997b; Palloix et al. 1997) although a major-effect resistance associated with the dominant resistance gene *CmrI* has been described in a Korean cultivar of pepper (Kang et al. 2010).

1.2.3 Alfamoviruses

Alfalfa mosaic virus (AMV), the type species of the genus *Alfamovirus* (family *Bromoviridae*), comprises isolates distributed worldwide (especially under temperate climate conditions). It infects over 250 plant species belonging to 48 families, mostly herbaceous plants. AMV is generally considered to be a minor threat to pepper. Infected peppers exhibit bright yellow to white mosaic that sometimes covers large areas of interveinal leaf tissue and bleaching on fruits. If infected at a young stage, the plants may be stunted, foliar necrosis appears (Fig. 1.1b) and the fruits will be deformed. AMV is transmitted by more than 20 aphid species (Marchoux et al. 2008). Seed transmission has been reported at a rate of 2% in pepper (Edwardson and Christie 1997) but there is no evidence for an impact of this mode of transmission on the natural spread of AMV in cultivated crops.

1.2.4 Fabaviruses

Broad bean wilt virus (BBWV), the type species of the genus *Fabavirus* (family *Comoviridae*), has a worldwide distribution. BBWV isolates are transmitted by aphids, mostly *Aphis gossypii* and *Myzus persicae*, in a non-persistent manner and infect naturally more than 200 plant species in 41 families (Brunt et al. 1996; Marchoux et al. 2008). BBWV comprises two distinct viral clades recognizable by the divergence of their genome: BBWV-1 and BBWV-2 (van Regenmortel et al. 2000). BBWV is frequently found in pepper plants, especially in the Mediterranean area or in Asia (Moury and Verdin 2012; Kwak et al. 2013). Infected pepper plants display mosaic and concentric rings on leaves and fruits followed sometimes by necrotic spots on leaves and streaks on stems which may lead to the death of the plants. BBWV can also cause partial to general bleaching of pepper fruits reducing their commercial value. However, in pepper crops, BBWV shows a rather low prevalence and has a limited economic impact.

1.2.5 Poleroviruses

Unlike viruses mentioned above, viruses belonging to the genus *Polerovirus,* family *Luteoviridae,* are vectored by phloem-feeding insects in a persistent, circulative and non-propagative manner (Dietzgen et al. 2016). Virions are composed of a single-stranded positive-sense RNA, 5.3–5.7 kb in size, encapsidated in an icosahedral shell. Poleroviruses are often associated with interveinal yellowing, leaf discoloration, leafroll, and stunting symptoms. Discoloration and size reduction of fruits is also observed in symptomatic plants. *Beet western yellows virus* (BWYV) was the first described polerovirus species that infects pepper crops (Duffus 1960; Timmerman et al. 1985). Since then, other poleroviruses including *Pepper vein yellows virus* (PeVYV), *Pepper yellow leaf curl virus* (PYLCV) and *Pepper yellows virus* (PYV), were observed in several Asian countries, Africa, Europe, and North America (Dombrovsky et al. 2010; Knierim et al. 2013; Murakami et al. 2011; Buzkan et al. 2013; Villanueva et al. 2013; Alabi et al. 2015). A recent study highlights the existence of high genetic diversity within the poleroviruses, which could be associated with the emergence of new viral diseases in various crops worldwide, including pepper (Lotos et al. 2017).

1.2.6 Orthotospoviruses

Viruses belonging to the *Orthotospovirus* genus *(*family *Tospoviridae*), previoulsy named *Tospovirus*, cause serious diseases worldwide in economically important crops including pepper. Its main features (genome organisation, morphology, transmission) are mentioned in the Sect. 1.3.5 below.

Orthotospovirus includes numerous species that infect *C. annuum*, such as *Capsicum chlorosis virus* (CaCV), *Chrysanthemum stem necrosis virus* (CSNV), *Groundnut bud necrosis virus* (GBNV), *Impatiens necrotic spot virus* (INSV), *Tomato necrotic ring virus* (TNRV), *Tomato spotted wilt virus* (TSWV), *Tomato yellow ring spot virus* (TYRV), *Watermelon bud necrosis virus* (WBNV) and *Watermelon silver mottle virus* (WSMoV). Some of them are geographically restricted to a continent, such as GBNV, TNRV, WBNV and WSMoV in Asia, or TCSV in South and North America. Others, on the contrary, are globally spread around the world (especially in temperate and subtropical areas), such as INSV and above all TSWV, the type member of *Orthotospovirus*. TSWV has one of the largest host ranges among plant viruses, equivalent to that of CMV (Parrella et al. 2003). In pepper, TSWV is more prevalent than INSV, which infects mainly ornamentals (Daughtrey et al. 1997). TSWV symptoms in *C. annuum* include stunting and yellowing of the whole plant, mosaic or necrotic spots and curling of the leaves. Infected fruits often show deformations, necrotic ring patterns and arabesque-like discolorations (Fig. 1.1d).

Control of TSWV is difficult because of the wide host ranges of both the virus and the vector, the efficient natural transmission by thrips combined with high fecundity and their capacity to develop resistance to insecticides. The application of sanitation measures must be intensified in glasshouses: eradication of infected plants and weeds and use of sticky cards to identify the presence of thrips. Biological control of thrips relies on the use of predatory mites or predatory bugs to decrease the virus inoculum pressure (Hatala Zseller and Kiss 1999; Maisonneuve and Marrec 1999). Genetic resistance to TSWV has been characterize and incorporated into commercial pepper cultivars. This is the case of the monogenic resistance conferred by the *Tsw* gene (Boiteux 1995; Moury et al. 1997). *Tsw* controls a hypersensitive reaction against most TSWV isolates and prevents virus movement from cell to cell (Soler et al. 1999), but is not efficient against other orthotospovirus species, like INSV. Breakdown of the resistance was described in *Tsw*-carrying cultivars rapidly after their deployment (Garcia-Arenal and McDonald 2003).

1.2.7 Begomoviruses

Begomoviruses (genus *Begomovirus*, family *Geminiviridae*) are transmitted by the whitefly *Bemisia tabaci* in a persistent and circulative manner. Seed transmission of begomoviruses in several hosts, including sweet pepper, has also been reported (Kil et al. 2017). Diseases caused by begomoviruses have emerged to be important constraints to the production of solanaceous crops, including peppers, in many tropical and subtropical regions of the world. The most studied so far is *Tomato yellow leaf curl virus* (TYLCV) which has spread from its likely origin in the Mediterranean basin region to the rest of the world. TYLCV was reported for the first time on *C. annuum* plants in Europe (Reina et al. 1999), later in North Africa (Gorsane et al. 2004), America (Quinones et al. 2002; Salati et al. 2002) and Asia (Tahir and Haider 2005). TYLCV-infected pepper plants are frequently symptomless, a fact that suggests that economic incidence of TYLCV on pepper production is probably low. It is presumed that pepper could be a dead-end host in the epidemiological cycle of TYLCV (Morilla et al. 2005). However, a potential role of pepper is also suggested in the epidemiology of TYLCV: pepper plants could act as reservoirs for TYLCV dissemination, particularly among plants showing more severe symptoms as is the case for tomato, a crop often grown in close vicinity to pepper (Polston et al. 2006).

Other *Begomovirus* species infecting peppers can cause outbreaks in areas limited to a few countries. Beginning in the late 1980s, epidemics of begomovirus diseases of pepper occurred in Southwestern United States, Mexico, and Central America (Brown and Poulos 1990; Stenger et al. 1990). *Pepper golden mosaic virus* (initially named *Texas pepper virus*) isolates causing leaf distortion and mosaic symptoms were isolated from whitefly-infested greenhouses in Texas. Over the same period other begomoviruses, like *Pepper huasteco yellow vein virus*, were recovered from pepper during severe epidemics of « rizado amarillo » disease occurring in Mexico with yellow mosaics, interveinal chlorosis, wrinkling and stunting (Garzon-Tiznado et al. 1993). Since the late 1990s in Asia, epidemics of *Pepper yellow leaf curl Indonesia virus* have been noticed in many pepper producing regions especially from East Asia and cause major damage to pepper crop production (Rusli et al. 1999; Trisno et al. 2009). Although limited to a restricted geographical area, the dissemination of all these devastating begomoviruses at a larger scale on other countries or continents must be monitored.

1.2.8 Criniviruses

Phloem-restricted viruses belonging to the genus *Crinivirus* (family Closteroviridae) are transmitted by whiteflies including *B. tabaci*, *T. vaporariorum* and *T. abutilonea. Tomato chlorosis virus* (ToCV) is the only crinivirus described so far on pepper crops. ToCV is emerging as a problem worldwide on tomato plants since its first description in Florida in 1989 (Wisler et al. 1998). ToCV infected peppers have been reported in southeastern Spain in 1997 (Lozano et al. 2004). Since then, ToCV has also been found in greenhouses in Brazil and Costa Rica on sweet pepper (Barbosa et al. 2010; Vargas et al. 2011). Infected pepper plants exhibit stunting and symptoms of interveinal yellowing and mild upward leaf curling. ToCV causes significant yield losses that could severely limit pepper production in areas of high prevalence, favored mainly if whitefly vectors are present and tomato and pepper crops overlap (Fortes et al. 2012).

1.2.9 Tobamoviruses

The genus *Tobamovirus* (family *Virgaviridae*) includes particularly stable viruses distributed worldwide that cause devastating diseases in protected crops, mostly vegetables and ornamentals. Particles are elongated rigid and rod-shaped, about 18 nm in diameter and 300–310 nm long, that encapsidate a monopartite linear positive-sense single-stranded RNA, from 6.3 to 6.6 kb in size, with a methylated nucleotide cap structure at the 5′ end and a tRNA-like structure at the 3′ end. The genome encodes at least four proteins that have been associated with replication, encapsidation, movement and symptom induction.

The most predominant tobamoviruses affecting *Capsicum* species are *Tobacco mosaic virus* (TMV), *Tomato mosaic virus* (ToMV), *Tobacco mild green mosaic virus* (TMGMV) and *Pepper mild mottle virus* (PMMoV). PMMoV is considered as the most destructive tobamovirus of protected pepper crops, with infections reaching up to 100% of the plants and drastic reduction in the yield of marketable fruit. ToMV can also cause severe losses on susceptible pepper cultivars (Brunt 1986). Symptom severity varies with virus strains and pepper genotypes and generally affect both quantity and quality of production. Tobamoviruses induce leaf chlorotic mosaic or mottling, leaf distortion and surface reduction, irregular shapes and colours associated with a reduction of size of fruits. Necroses can also be observed on leaves and fruits (Moury and Verdin 2012; Kenyon et al. 2014a). In nature, tobamoviruses are transmitted and easily spread between plants by contact, and during cultural operations, through contaminated instruments. Due to their high stability, the viruses can survive over months/years in plant debris and greenhouse structures. Most tobamoviruses are easily disseminated via infected seeds although tobamoviruses rarely reach the seed embryo or albumen. The virus is mostly carried in the external seed surface, allowing infection of seedlings during germination, and sometimes in maternal tissues such as seed coat or residual perisperm, which can remain infected for years (Johansen et al. 1994; Genda et al. 2011). No natural insect vectors are known for tobamoviruses.

To avoid primary infections, control methods involve prophylaxis, including seed sanitation by soaking in different solutions of active reagents (trisodium phosphate, hydrochloric acid, sodium hypochlorite) or by dry heat treatment (Rast and Stijger 1987), implementation of cautionary measures during handling of plants (since the viruses can be transmitted by physical contact between plants), removal of plant debris from previous susceptible crops and steam treatment of the soil and greenhouse structures. Cross protection was featured to control the tobamovirus-associated diseases in pepper (Goto et al. 1984; Hagiwara et al. 2002; Ichiki et al. 2009; Yoon et al. 1989). Its basis is that prior infection of a plant with one mild virus strain affords protection against secondary infection by severe strains that are closely genetically related (Pennazio et al. 2001; Zhou and Zhou 2012). This process has not been largely used in commercial conditions due to the widespread deployment of resistant cultivars. Different dominant alleles at the *L* locus have been identified in different *Capsicum* species. These alleles differ by their specificity towards tobamovirus pathotypes (called P_0, P_1, $P_{1.2}$, $P_{1.2.3}$, $P_{1.2.3.4}$) and by their efficiency under temperature stresses (Moury and Verdin 2012). Breakdown of resistance by PMMoV variants has been observed and mutations involved in these events identified (Tsuda et al. 1998; Hamada et al. 2002; Genda et al. 2007; Antignus et al. 2008).

1.2.10 Tombusviruses

Tombusviruses (genus *Tombusvirus*, family *Tombusviridae*) have a 30 nm icosahedral particles that encapsidate a monopartite, linear, positive-sense single-stranded RNA genome from 4 to 5.4 kb which lacks a cap structure and a poly-A tail. Particularly stable, tombusviruses are primarily soil-borne and are transmitted by contact and by seed. No invertebrate vector is known.

Moroccan pepper virus (MPV) and *Tomato bushy stunt virus* (TBSV) are the main tombusviruses described on *C. annuum*. Isolates of MPV cause leaf deformation, leaf and flower abscission, stunting and lethal systemic necrosis, while those of TBSV cause leaf mottling, leaf deformation and lack of fruit production. MPV was first described in Morocco in 1977 (Gallitelli and Russo 1987). Since then, no further observation in pepper crops has been reported. *Lettuce necrotic stunt virus*, a virus that takes increasing importance in lettuce crops in Asia and North America, was recently reclassified as MPV (Wintermantel and Hladky 2013). Thus, it should be appropriate to remain vigilant to ensure that MPV could not emerge into pepper crops. TBSV is not generally considered as an economically important plant pathogen in pepper production, with the possible exception of North Africa and Spain (Cherif and Spire 1983; Luis-Arteaga et al. 1996).

1.2.11 Ilarviruses

Ilarviruses (genus *Ilarvirus*, family *Bromoviridae*) have 28–30 nm icosahedrical particles that encapsidate a segmented, linear positive sense, single-stranded genome composed of 3 RNAs. Each genomic segment possesses a 5′ cap and a 3’ tRNA-like structure. Transmission of ilarviruses occurs primarily through pollen, often enhanced by vectors visiting flowers. Transmission by seed has also been described in several studies (Mink 1993).

Pepper plants infected with illarviruses may be symptomless or they may show leaf mosaic and necrosis, stem and fruit necrosis and sometimes apical necrosis. Among ilarviruses infecting pepper, *Tobacco streak virus* (TSV, type member) and *Potato yellowing virus* (PYV) have a worldwide distribution while *Parietaria mottle virus* (PMoV) appears to be located only in southern Europe. TSV has a wide host range but infected peppers were only mentioned in Argentina and in India (Gracia and Feldman 1974; Jain et al. 2005). PYV infects only *Solanum* species and was reported causing disease in pepper in Ecuador (Sivaprasad et al. 2015). PMoV infects several plant families including *Solanaceae* with a high prevalence in the Mediterranean countries of Europe. PMoV has been identified in bell pepper plants grown in greenhouses in Spain, France and Italy (Janssen et al. 2005; Moury and Verdin 2012; Parrella et al. 2016)

1.3 Emerging Viral Diseases in Tomato

Tomato (*Solanum lycopersicum*) plants with edible fruits have tremendous popularity in the world diet. Economically, tomato is by far the most important vegetable crop worldwide and has a large number of viral species reported able to infect it. There are at least 140 characterized viral species that have been described infecting tomato, some of them causing emergent viral diseases. Some good reviews are available compiling information about viruses causing damage to tomato (Hanssen and Lapidot 2012; Hanssen et al. 2010). Over recent years, several viral diseases, including those caused by isolates of *Tomato yellow leaf curl virus* (TYLCV), the two criniviruses *Tomato infectious chlorosis virus* (TICV) and ToCV, *Pepino mosaic virus* (PepMV), *Tomato torrado virus* (ToTV), or by orthotospoviruses and tobamoviruses have emerged in greenhouse tomato crops and are presently impacting fresh-market tomato production in diverse geographic areas worldwide. Characteristics of major viruses causing emergent damage in tomato are provided below.

1.3.1 Begomoviruses

Begomoviruses rank among the top of the most important plant viruses causing diseases of severe consequences in economically and socially relevant crops (Scholthof et al. 2011). Begomoviruses have a circular single-stranded DNA genome either bipartite (comprising two components named DNA-A and DNA-B) or monopartite (one component similar to DNA-A of bipartite begomoviruses). In nature they are transmitted in a persistent and circulative manner by members of the *B. tabaci* species complex (De Barro et al. 2011). Over the past 25 years, begomoviruses have emerged as serious constraints to cultivation of important crops in various part of the world, especially in warm regions. Emergence has also been observed in temperate regions seriously affecting greenhouse crop production. Emergence of these viruses is associated with the global spread of their insect vector, the whitefly *B. tabaci* (De Barro et al. 2011; Navas-Castillo et al. 2011). Factors driving this emergence have been reviewed (Navas-Castillo et al. 2011; Moriones et al. 2011). Also, the ability of these viruses to recombine (Lefeuvre and Moriones 2015) seems to be relevant for their emergence and adaptation to novel ecological conditions. About 90 different begomovirus species have been reported infecting tomato, most of them emerging locally such as in the Americas (Fernandes et al. 2008; Ribeiro et al. 2003; Geraud-Pouey et al. 2016) or in Asia (Kenyon et al. 2014b). However, the most significant emergence corresponds to the global spread of begomoviruses associated with the tomato yellow leaf curl disease (TYLCD) and among them of TYLCV. Because of this relevance, it is specifically revised here.

TYLCD-associated viruses cause one of the most devastating and emergent diseases of tomato crops in tropical and warm regions worldwide (Moriones et al. 2011). The first reports of TYLCD date back to 1929 in the Jordan Valley, but from the late

1980s on, a rapid emergence and geographic spread of TYLCD has occurred worldwide; this disease is now widespread in many agricultural production areas of warm climate zones worldwide, while in temperate regions it is mostly associated with glasshouse tomato cultivations (Moriones and Navas-Castillo 2000). At least ten different begomovirus species have been associated with TYLCD (Brown et al. 2015), TYLCV being the most widespread worldwide. Thanks to the availability of a significant number of sequences for TYLCV, molecular epidemiology studies helped to establish that epidemics of TYLCVs most probably arose in the Middle East between the 1930s and 1950s and that the global spread began in the 1980s (Lefeuvre et al. 2010). This virus was the first monopartite begomovirus introduced in the New World where it rapidly emerged in different countries (Duffy and Holmes 2007). The worldwide dissemination of TYLCD is one of the best examples of human impact on begomovirus emergence and spread (Moriones et al. 2011). TYLCD infections in tomato result into severe stunting of plants, with virtually no yield when infections occur during early growth stages. Symptoms consist of upward curling of leaflet margins and reduced size of young leaflets that can exhibit a yellow chlorosis (Fig. 1.2a). Also, flower sterility occurs in infected plants, and although no symptoms are observed in set fruits, as infected plants are less vigorous, they produce fruits with reduced market value.

Management of tomato-affecting begomoviruses, as for other begomoviruses, requires adoption of integrated management measures. Although a specific management section is available in this volume, nice reviews about management alternatives for begomoviruses have been published that might help to design control strategies in specific cases (Antignus 2007; Lapidot et al. 2014b). During the past decades several effective resistance sources to the virus and to the vector have been reported, some of them highly effective in commercial tomato cultivars (Lapidot et al. 2014a; Rodríguez-Lopez et al. 2011).

1.3.2 Criniviruses

During the mid 1990s, severe outbreaks of yellowing occurred in tomato, threatening tomato production in the United States. The disease was shown to be transmitted by several whitefly species and to be caused by isolates of two crinivirus species (genus *Crinivirus*, family *Closteroviridae*), TICV and ToCV (Tzanetakis et al. 2013; Wintermantel 2010). Criniviruses have large bipartite single-stranded positive-sense RNA genomes with long flexuous virions averaging between 650 and 900 nm in length. Both TICV and ToCV are transmitted in a semipersistent manner but whereas TICV is transmitted solely by the greenhouse whitefly *T. vaporariorum*, ToCV is transmitted by *B. tabaci*, *T. vaporariorum*, and *T. abutilonea*. Symptoms induced by isolates of TICV and ToCV on tomato are almost identical, consisting of a yellowing of leaves that is frequently attributed to nutritional disorders or pesticide phytotoxicity. Symptoms develop from basal to apical leaves and include interveinal yellowing and thickening of mature leaves (Fig. 1.2b). Production

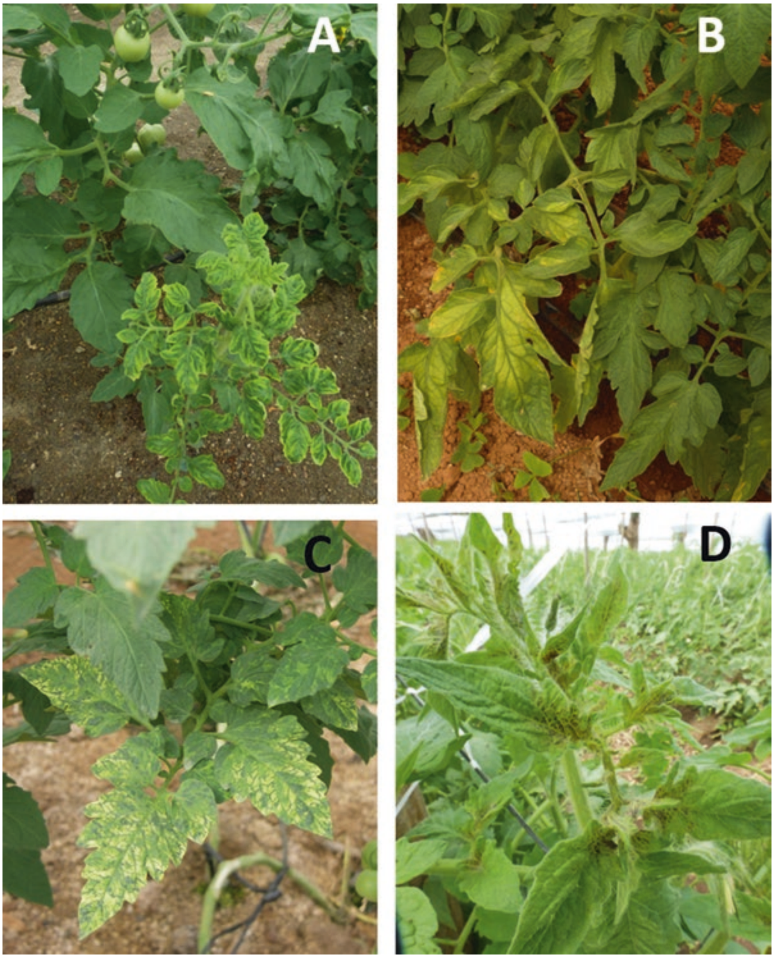

Fig. 1.2 Symptoms of tomato yellow leaf curl virus (healthy fruit on the left) (a), tomato chlorosis virus (b), pepino mosaic virus (c) and tomato torrado virus (d) in tomato

is reduced because of flower abortion, decreased fruit size and altered ripening that decrease commercial value of fruits. Early senescence also occurs. Both TICV and ToCV have a wide host range which complicates control because cultivars with resistance to these viruses are not yet commercially available. Control is mostly based on implementation of crop management measures to avoid whiteflies. These viruses are emerging over the last decades in association with the worldwide emergence of whiteflies. However, their pattern of distribution greatly differs. Whereas TICV exhibits a restricted geographic distribution, mainly in North America and in Europe, but with decreasing importance, ToCV shows a global distribution with increasing emergence worldwide (Navas-Castillo et al. 2011). Differences between ToCV and TICV incidence and geographical distribution are mostly associated with the differences in their whitefly vectors.

1.3.3 Potexviruses

Pepino mosaic virus (PepMV) (genus *Potexvirus*, family *Flexiviridae*) is a single-stranded positive-sense RNA virus with filamentous particles of around 510 nm in length that has been described recently as emerging in tomato. PepMV appears to affect mostly intensively-grown tomato crops, although the virus can infect other crop and weed species (Gómez et al. 2012b) that may act as reservoirs and/or virus sources. Initially identified in Peru affecting pepino (*Solanum muricatum*), it is thought that PepMV entered Europe from South America, resulting into multiple, geographically dispersed outbreaks between 2000 and 2002. The virus was first isolated from tomato in the Netherlands, in 1999 and then spread rapidly in tomato crops throughout the Northern hemisphere. Currently, it is present in many temperate regions in America, Africa, Asia, and Europe and is considered one of the most important epidemic viruses in agriculture (Gómez et al. 2012b; Hanssen et al. 2010). Ecological and genetic determinants seem to be involved in the emergence of this virus (Moreno-Perez et al. 2014). PepMV isolates seem to group in four main genetic types and mixtures of co-circulating genotypes might occur during epidemics (Gómez et al. 2012a). However, no strict correlation between the disease phenotype and genotype is observed. PepMV infections in tomato cause diverse symptoms in leaves, including more or less severe mosaics, chlorosis, blistering or bubbling and laminal distortions, and necrosis (Fig. 1.2c). Affected plants are often stunted. However, the major impact is on fruit quality and can result in great yield loss. Fruit marbling is the most typical and economically devastating symptom, but fruit discoloration and fruit splitting also occur. Importantly, fruit symptoms might arise without previous warning symptoms in the rest of the plant and they may even develop after harvest during ripening in commercialized fruit. Symptom expression is dependent on the cultivar, lighting and/or temperature within the greenhouse and on the PepMV isolate (Gomez et al. 2012a, b; Hanssen et al. 2009). Spread of PepMV is extremely effective during epidemics and mechanisms have been extensively reviewed (Gomez et al. 2012a, b; Hanssen et al. 2009). Initially, long-range PepMV dispersal probably occurs through contaminated seeds. Then, as mechanical transmission of PepMV is very efficient, the virus rapidly spreads and infects most plants if it is introduced into a tomato greenhouse. PepMV can also be transmitted by the soil fungus *Olpidium virulentus* in drainage water, a trait that may increase PepMV transmission by irrigation or the recirculation of contaminated water or solution in hydroponic crops. Moreover, PepMV can be vectored by bumble bees with enhanced risk of PepMV infection during pollination. The success of PepMV outbreaks may also reflect the stability of virion particles and persistence in soil and plant debris or contaminated tools and structures. Then, exhaustive hygiene measures to avoid transmission are essential, as there are currently no commercial tomato cultivars resistant to PepMV.

1.3.4 Torradoviruses

Torradoviruses (genus *Torradovirus*, family *Secoviridae*) belong to a group of emerging plant viruses that has been discovered recently in different parts of the world as a constraint to tomato production (van der Vlugt et al. 2015). ToTV, the type member of the genus, was first described in 2007 as the causal agent of a novel burn-like disease syndrome observed in tomato several years before. Symptoms of this disease initiate as necrotic spots surrounded by light green or yellow areas at the basal part of leaflets (Fig. 1.2d) that derive to leaf, stem, and fruit necrosis and plants exhibiting growth reduction. The virus exhibits isometric viral particles that contain a bipartite positive-sense ssRNA genome and is transmitted by whiteflies (either *B. tabaci*, *T. vaporariorum*, or *T. abutilonea*) in a stylet-borne semipersistent manner (Amari et al. 2008; Verbeek et al. 2014). Presence of this virus was reported in several countries of the world (e.g. Spain, France, Italy, Poland, Australia, Colombia, Hungary, Panama) and after the characterization of ToTV, other torradoviruses were reported causing similar symptoms to tomato in the Americas, such as isolates of *Tomato marchitez virus*, *Tomato chocolate virus*, *Tomato chocolate spot virus*, or of *Tomato necrotic dwarf virus* (van der Vlugt et al. 2015). The incidence of ToTV in commercial tomato crops can be significant (Gomez et al. 2010), and control is difficult through vector control. Efficient virus control depends heavily on the availability of healthy planting material as well as on timely recognition of infections. Deployment of plant genetic resistance might facilitate control and tomato cultivars that are not infected have been reported (Pospieszny et al. 2010).

1.3.5 Orthotospoviruses

Orthotospoviruses and tobamoviruses are the cause emergent and re-emergent viral diseases in tomato.

Orthotospoviruses are enveloped isometric viruses with a tripartite ssRNA ambisense genome that are emerging associated with increasing thrips populations, mostly related to the rapid expansion of the western flower thrips (*Frankliniella occidentalis*) (Prins and Goldbach 1998; Hanssen et al. 2010). They are transmitted by thrips in a persistent and propagative manner. Only larvae (and not adults) can acquire the virus but adults are epidemiologically the most important stage because they are more mobile and remain viruliferous for their entire life (German et al. 1992; Aramburu et al. 1997). No transovarial transmission has been reported. Viruses such as TSWV belonging to the orthotospovirus group are one of the most important plant viruses causing damage to a wide range of economically important crop plants all over the world. Orthotospoviruses have emerged in different parts of the world as a major constraint to production of important vegetable, legume and ornamental crops, among them tomato (Turina et al. 2016; Pappu et al. 2009; Mandal et al. 2011). Several new species have been reported causing increasing damage with at least 29 distinct orthotospoviruses identified as distinct or tentative species (Turina et al. 2016; Webster et al. 2014). The high incidence of new orthotospoviruses in tropical Asian regions suggests a “hot spot” of viral genetic diversity in this region, where they can be transmitted to commercial crops through increasing vector populations (Mandal et al. 2011; Dong et al. 2008). Owing to the difficulty in combating thrips vectors with insecticides, the best way to limit orthotospovirus damage is through crop management strategies that includes virus resistance. TSWV is by far the most widely spread orthotospovirus species in tomato worldwide and has been targeted for genetic resistance approaches in tomato. Symptoms of the disease vary depending on the cultivar and the TSWV isolate and can include necrotic spots and necrotic/bronzed areas in leaves and necrotic ringspots or ring discolorations in fruits with stunted plants showing severe necrosis if heavily infected. The search for natural resistance sources and resistance genes has been intense, and within the past three decades several resistance sources have been reported and incorporated into commercial tomato cultivars. The gene *Sw-5* originates from *Solanum peruvianum* (Stevens et al. 1995) and has been the most widely deployed resistance source because of its durability and the ability to provide stable resistance against several orthotospovirus species and isolates from different geographic locations. Nevertheless, resistance against orthotospoviruses is compromised by the continuous emergence of resistance-breaking strains and new species (Turina et al. 2016). In absence of resistance, control of orthotospoviruses is hampered by the rapid development of insecticide resistance within thrips populations. Therefore, alternatives to chemical thrips control are needed, primarily based on biological control in protected crops.

1.3.6 Tobamoviruses

Similar to orthotospoviruses, tobamoviruses (genus *Tobamovirus*, family *Virgaviridae*) cause emergent and re-emergent viral diseases in tomato. Tobamoviruses, mainly isolates of *Tomato mosaic virus* (ToMV), can cause significant yield losses to susceptible tomatoes (Broadbent 1976). The main features of tobamoviruses (genome organisation, morphology, transmission) are mentioned in the Sect. 1.2.9 above. Deformation, green mosaic, and/or necrotic symptoms are observed in leaves and fruits of infected plants. As described earlier in Sect. 1.2.9, tobamoviruses are transmitted by mechanical contact during crop operations and capable to preserve infectivity in seeds. Owing to these characteristics, control of infections is very difficult. However, the introgression in tomato of dominant resistance genes (*Tm-1*, *Tm-2*, and *Tm-2*^{2}), proved to be very effective to manage infections, especially the *Tm-2*^{2} gene that remained effective for more than 25 years (de Ronde et al. 2014; García-Arenal and McDonald 2003). However, concern for the future of the effectiveness of *Tm-2*^{2} exists as new tobamoviruses infecting tomatoes are identified that might overcome the resistance. In this sense in Jordan, isolates of a new tobamovirus species named *Tomato brown rugose fruit virus* (ToBRFV) have been reported from infected tomatoes, and were shown to overcome *Tm-2*^{2} resistance in Israel (Salem et al. 2016; Luria et al. 2017). The recent outbreaks of ToBRFV in Italy, Germany, Mexico, and United States of America (Menzel et al. 2019; European and Mediterranean Plant Protection Organization, EPPO, reports) suggests the dangerous spread of this virus to other tomato growing regions.

1.4 Emerging Viral Diseases in Cucurbits

Cucurbit crops (family *Cucurbitaceae*) are grown throughout the world for human consumption, with four major species being among the major vegetable crops cultivated worldwide: melon (*Cucumis melo*), cucumber (*Cucumis sativus*), watermelon (*Citrullus lanatus*) and squash/pumpkin (*Cucurbita pepo*, *Cucurbita maxima*, among others). Cucurbits are affected by a significant number of viruses belonging to several genera either possessing DNA or RNA genomes (Lecoq and Katis 2014). Some of these viruses cause significant economic damage and are typically emerging viruses that are becoming widely spread in relatively recent times. Virus infections in cucurbits result in major losses of marketable fruits. Flower abortion occurs and fruits develop abnormally exhibiting mosaic symptoms, necrosis, and/or growth alterations that depreciate them commercially (Fig. 1.3a, b). Severe yield loss might occur, especially when infections occur during early growth stages. Specific characteristics of the most prominent viruses emerging in cucurbit crops are summarized below. Control strategies to manage major cucurbit viruses have been comprehensively studied (Lecoq and Katis 2014). Characteristics of viral diseases/viruses emerging in cucurbit crops are provided below.

1.4.1 Criniviruses-Ipomoviruses-Poleroviruses-Carlavirus

There are a number of plant virus species with isolates causing emergent yellowing diseases in cucurbit crops worldwide. The most prominent among them are (i) the criniviruses (genus *Crinivirus*, family *Closteroviridae*) *Cucumber yellow stunting disorder virus* (CYSDV) and *Beets pseudoyellows virus* (BPYV), (ii) the ipomoviruses (genus *Ipomovirus*, family *Potyviridae*) *Squash vein yellowing virus* (SqVYV) and *Cucumber vein yellowing virus* (CVYV), and (iii) the polerovirus (genus *Polerovirus*, family *Luteoviridae*) *Cucurbit aphid–borne yellows virus* (CABYV). All these viruses have positive-sense single-stranded RNA and some of them are widely distributed in commercial crops (Kassem et al. 2007; Abrahamian and Abou-Jawdah 2014). The common aspect among most of these emergent viruses is that they are transmitted in nature by whiteflies in a semipersistent manner, either by *T. vaporariorum* (BPYV) or by *B. tabaci* (CYSDV, SqVYV and CVYV). In contrast, CABYV is transmitted by aphids in a persistent manner and it is more prevalent in open-field crops (Kassem et al. 2007). Emergence of CYSDV, SqVYV, and CVYV is a typical example of emergence associated with the global dissemination of the vector *B. tabaci* (De Barro et al. 2011). Characteristics of viruses transmitted

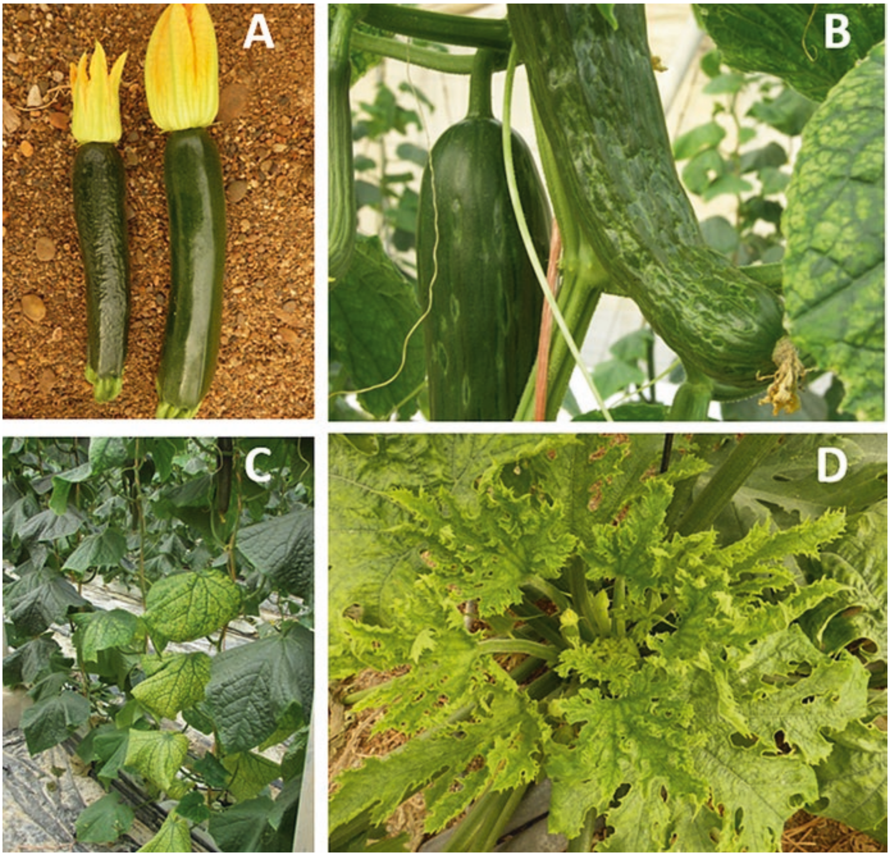

Fig. 1.3 Symptoms of tomato leaf curl New Delhi virus (healthy fruit on the right) (a) and cucumber green mottle mosaic virus (b) infections in zucchini squash and cucumber fruits (respectively), and of cucumber yellow stunting disorder virus (c) and tomato leaf curl New Delhi virus (d) in cucumber and zucchini squash plants (respectively)

by whiteflies have been reviewed by Navas-Castillo et al. (2011). Similar symptoms are induced in plants by CYSDV, BPYV, and CABYV, consisting on interveinal yellowing in older leaves that maintain green veins and are more brittle (Fig. 1.3c). These symptoms can be confused with nutritional or physiological disorders. In the case of CVYV, symptoms are more prominent in young leaves and consist of bright yellow veins and leaf deformation. Although the viruses considered previously are examples of viruses causing emerging yellowing diseases in cucurbits, in several production areas, more specific emergence cases occur that should also be taken into account. This can be the case of a novel flexivirus of the genus *Carlavirus* (family *Betaflexiviridae*) named melon yellowing-associated virus (MYaV) which is transmitted by the *B. tabaci* whitefly that has been reported as an emerging serious problem in Brazil causing a yellowing viral disease on melon plants (Costa et al. 2017; Nagata et al. 2005).

1.4.2 Tobamoviruses

Although *Cucumber green mottle mosaic virus* (CGMMV) (genus *Tobamovirus*, family *Virgaviridae*) is known from old times (Ainsworth 1935), global emergence of this tobamovirus is being observed recently as a problem in cucurbit crops, especially from 2007. An excellent review on this virus has been published recently, providing a compilation of what is known about CGMMV (Dombrovsky et al. 2017). Therefore, only the most relevant aspects are summarized here. Serious damage is caused in most grown cucurbits such as cucumber, squash, zucchini, pumpkin, melon, gourd species, or watermelon. The virus greatly affects yield and quality, especially of watermelon. CGMMV, as other tobamoviruses, is a positive sense single-stranded RNA virus with rod-shaped particles for which genetically diverse isolates have been reported that also can differ biologically (Dombrovsky et al. 2017; Crespo et al. 2017). Symptoms of CGMMV infection vary greatly depending on the cucurbit species, cultivar, plant growth stage at time of infection, environmental conditions, and virus pathotype/strain. However, in general, green or yellow mottling and mosaic could be observed in leaves of infected plants, and necrosis might occur in fruit peduncles and stems with a possible resulting collapse of the plant. Moreover, fruits develop different degrees of malformation, mottling, with internal discoloration and/or necrosis that render them unmarketable (Fig. 1.3b). Epidemics of this virus occur without the need of a vector. Where locally present, CGMMV can spread easily by contact with rapid disease progress (Li et al. 2015). Pollen transmission also occurs (Liu et al. 2014). An extremely efficient contact transmission occurs during cultural practices. As for other tobamoviruses, virion particles are highly stable and CGMMV remains infectious in contaminated roots and plant debris in soil, surfaces and tools for long periods that facilitate healthy plant infection when contact (through aerial parts or roots) occurs. The infection can also spread through contaminated irrigation water. Beneficial or pollinator insects can also participate in CGMMV spread after visiting an infected plant (Darzi et al. 2017). Moreover, transmission also occurs through seeds, with seed disinfection not being completely effective to eliminate infectivity (Liu et al. 2014; Reingold et al. 2015). This latter aspect is crucial in CGMMV emergence because it facilitates long distance worldwide dispersal through the international seed trade. Thus, an easy spread of CGMMV to healthy geographical areas can occur through contaminated seeds. Plants derived from infected seeds constitute the primary and major sources of infection in a crop, in which rapid secondary contagious spread of the disease from initial foci of infection is observed. Recent generalized seed trade for cucurbit production in warm and temperate regions has resulted in the rapid emergence worldwide of this seed-borne virus.

1.4.3 Begomoviruses

As indicated above, over the past years, begomoviruses have emerged as serious constraints to cultivation of important crops, among them cucurbits, associated with the emergence of their vector *B. tabaci* in various part of the world. Several important begomoviruses cause damage to cucurbit crops and emergence of some of them is being observed in recent times. Thus, during the last 10 years, isolates of two bipartite begomoviruses species have emerged as serious constraints to cucurbit crops in the eastern Mediterranean basin and Middle East. On one hand, *Squash leaf curl virus* (SLCV) originally reported in the New World (Brown et al. 2002) which is causing emerging damage in cucurbits in the Old World (Antignus et al. 2003). On the other hand, *Watermelon chlorotic stunt virus* (WmCSV), an Old World virus, is rapidly spreading among Middle East and the Western Mediterranean basin, inducing emergent damage to cucurbit crops (Sufrin-Ringwald and Lapidot 2011). It seems that both viruses may have entered the region only once and subsequently spread causing their emergence (Lapidot et al. 2014a). To date, SLCV is the only case of a New World virus establishing emergent damage in the Old World. Another relevant case of emergent begomovirus species causing damage to cucurbits is *Tomato leaf curl New Delhi virus* (ToLCNDV), a bipartite begomovirus originally from the Indian Subcontinent (Zaidi et al. 2016). ToLCNDV causes one of the most predominant and economically important diseases affecting tomato in the Indian sub-continent. However, in recent years, ToLCNDV has been extending rapidly its host range and spreading to new geographical regions with emergence in the Mediterranean basin as a severe constraint to cucurbit production (Moriones et al. 2017; Zaidi et al. 2016). Although WmCSV affects mostly watermelon (*C. lanatus*) and SLCV and ToLCNDV cause devastating damage to squash (*C. pepo*) crops, their host range includes all of the major cultivated cucurbit crops. Diseased plants can exhibit severely curled leaves with mottled areas and shorter petioles, vein yellowing, sterility, severe plant stunting, distortion of fruits and a drastic reduction of fruit yield (Fig. 1.3a, d). General management strategies to control begomoviruses affecting cucurbits have been discussed in a recent report (Lecoq and Katis 2014). It is important to note that resistance is being developed against ToLCNDV, which can help to reduce damage (Saez et al. 2016, 2017).

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Chapter 2
Bacterial Diseases

Vittoria Catara and Patrizia Bella

Abstract Bacterial plant pathogens under favourable environment conditions, as in protected cultivation, cause serious economic crop losses. In this chapter the symptomatology, causal agents and disease cycles of important bacterial diseases mainly of Solanaceae and Cucurbitaceae crops are described. Main bacterial genera included are: *Acidovorax*, *Clavibacter*, *Pectobacterium*, *Pseudomonas*, and *Ralstonia*. Bacteria can be introduced in a new cultivation area via water, wind and dust however the most probable means in greenhouses, nurseries and crops is via seeds, plant propagation materials or plantlets. Given that greenhouse conditions are favourable for all bacterial epidemics, healthy seeds and transplants are still the main goal to control most of the diseases. Noteworthy bacterial diseases are notoriously difficult to control and require an intensive integrated management approach to mitigate serious economic losses that are briefly discussed.

Keywords Plant pathogenic bacteria · Tomato · Pepper · Cucurbits · Ornamental plants · Bacterial wilts · Soft rot · Leaf spot · Fruit blotch · Pith necrosis

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2.1 Introduction

Bacterial plant pathogens have evolved to grow well in their plant hosts, both in specific hosts as well as in specific plant parts (Kado 2010). Most plant pathogenic bacteria are nutritionally non fastidious and cause many of the same kinds of diseases in plants as fungi do: cankers, galls, leaf spots, rot and vascular wilts (Schumann and D'Arcy 2006).

In this chapter, basic information on bacteria is outlined below and more details can be found in specialised books (e.g. Janse 2006; Kado 2010). Most of plant pathogenic bacteria do not form spores and are rod shaped. They are not able to actively penetrate the plant surface, as fungi do, and so they enter the plant through natural openings (stomata, hydathodes, lenticels, nectaria, etc.) and wounds. These impairing traits make bacteria responsible for devastating crop diseases which cause considerable economic losses. When they meet a compatible host plant and favourable environment conditions, they rapidly reproduce clonally, reaching high population concentrations and activate a wide range of weapons that allow them to accomplish plant colonization.

Bacterial diseases are notoriously difficult to control and require an intensive integrated management approach to mitigate serious economic losses.

The closed environment of a protected cultivation either under a greenhouse or tunnel are highly favourable for bacteria, and their populations can increase very rapidly (Vidaver and Lambrecht 2004). Due to the fact that they have an optimum growth temperature of around 23–28 °C (although a few pathogens can grow at 42 °C), they need high humidity to avoid dehydration, and use water on the host plant in order to reach the natural openings and be sucked in. Once inside the plant they most frequently colonise the intercellular spaces and the xylem vessel, and less frequently the phloem (e.g. phytoplasmas, spiroplasmas and liberibacters) (Kado 2010). In this chapter we deal with the bacteria that can survive as facultative saprophytes; we thus do not focus on fastidious bacteria.

Bacteria can be introduced in a new cultivation area via water, wind and dust however the most probable mean in greenhouses, nurseries and crops is via seeds, plant propagation materials or plantlets. Propagation materials influence the successful establishment of diseases in different production regions of the world. Both above- and below-ground plant parts can be colonised by plant pathogenic bacteria. Bacteria may be transient or reside on the plant surfaces as epiphytes on seeds, flowers, buds, pollen, fruits as well as vegetative cuttings and seed pieces and in the rhizosphere.

In this chapter we describe the symptomatology, causal agents and disease cycles of important bacterial diseases, mainly of Solanaceae and Cucurbitaceae crops. For the IPDM in the greenhouse environment, please refer to Part III of this book.

In the last few decades genetic and genomic analyses have led to the study of the diversity of bacteria using phylogenetic trees which also identify evolutionary groups below the bacterial species level. In some cases the subgroups coincide with previously defined species, genomospecies or pathovars, but in other cases they represent taxonomically different bacterial species (Vinatzer and Bull 2009). These may share the same phytopathogenic behaviour toward the host plants and may also cause phenotypically indistinguishable diseases. It is therefore not surprising if a disease that has already been known about for a long time is nowadays reported to be caused by multiple bacterial pathogens.

2.1.1 Bacterial Wilts

2.1.1.1 Tomato Bacterial Canker

Tomato bacterial canker is considered one of the most serious diseases of tomato and has been reported wherever tomatoes are grown. It occurs only occasionally, but often as sudden epidemics both in the open field and in the greenhouse, in soil and soilless cultivations, causing up to 80–100% yield loss (Jones et al. 2014). Bacterial canker can also occur in pepper, but only with a low economic impact on production.

The disease is caused by the Gram-positive actinobacterium *Clavibacter michiganensis* subsp. *michiganensis*. Recently strains isolated from pepper were included in a new subspecies *C. michiganensis* subspecies *capsici* (Oh et al. 2016).

Disease symptoms on tomato vary depending on the age of the plant, susceptibility of the cultivar, environmental factors, and the virulence of the strains (Gleason et al. 1993; de Leon et al. 2011; Bella et al. 2012; Sharabani et al. 2014; Ialacci et al. 2016). Wilting is the main disease symptom. Infections that originate from seeds or young infected seedlings give rise to systemic infections (primary infections) that typically lead to plant death. At the early stage of infection, unilateral wilting or withering of leaflets are observed on one side of the leaf (Fig. 2.1a). Pale yellow to brown discolorations may appear on the stems, petioles and peduncles. These tissues later darken and split open as typical cankers (Fig. 2.1b–c). When cut lengthwise, infected plants show reddish-brown discoloration of the vascular tissue. Cross-section at the insertion of the petiole to the stem reveals a characteristic browning of the vascular bundles, referred to as the ‘horse shoe track’ (Fig. 2.1d). The stem pith can appear hollow and discoloured.

The pulp of fruits reached through the xylem may be decayed and yellowed and sometimes with small dark cavities. Secondary infections, mainly due to wounds cause localized small white pustules on the fruits, called ‘bird’s eye’ (Fig. 2.1e), and through hydathodes, cause marginal necrosis of the leaves. On bell peppers, symptoms also include light brown and raised lesions on leaves and bird’s eye spots on fruits (Lewis-Ivey and Miller 2000).

Related to the tomato growing cycle, the bacterium may be present in: (a) seeds, in which the bacteria survive at low concentrations; (b) nurseries for the production of transplants; and (c) tomato production areas (de Leon et al. 2011; Sen et al. 2015).

C. michiganensis subsp. *michiganensis* can reach fruits and seeds through the xylem, fruit lesions and flower pedicels (Tancos et al. 2013). Although the rate of seed transmission is quite low (Chang et al. 1991), under favorable conditions (e.g. in nurseries and greenhouses), as few as one infected seed in 10,000 can give rise to devastating epidemics (Jones et al. 2014).

Fig. 2.1 Symptoms of tomato bacterial canker (*Clavibacter michiganenensis* subsp. *michiganensis*). (**a**) curling and wilting of the leaves; (**b**, **c**) typical canker on stem and peduncle with affected tissues split open lengthwise, (**d**) reddish-brown discoloration of vascular tissue at the insertion of the petiole referred as 'horse shoe track', (**e**) small raised white pustules with necrotic centre on the surface of fruits, called bird's eye-spot. (Felipe Siverio, Instituto Canario de Investigaciones Agrarias,Spain)

C. m. subsp. *michiganensis* can survive on the leaf surface in tomato and the main source of epiphytic populations and secondary inoculum originates from infected guttation droplets (Chang et al. 1991, 1992a; Sharabani et al. 2013).

Once the bacterium has been introduced into a cultivation area, it can survive for up to 314 days in tomato plant debris left on the ground, or 45–75 days on buried residues (Gleason et al. 1991; Fatmi and Schaad 2002). Its persistence in bare soil may range from a few months to years (Gleason et al. 1991). Genome analysis has highlighted a poor ability to survive in the soil due to the absence of genes involved in the acquisition of various elements (Gartemann et al. 2008).

The bacterium colonizes the host longitudinally through the spiral elements of the primary xylem, accompanied by the invasion of the perivasal parenchyma in both directions which is facilitated by the formation of biofilm-like structures (Chalupowicz et al. 2012; Nandi et al. 2018).

Disease severity decreases as the age of the plants increase, in temperatures below or higher than 25 °C, in moderately resistant cultivars, and with low initial inoculum concentrations (Chang et al. 1992b).

Following the transplant of seedlings with latent infections, *C. m.* subsp. *michiganensis* in the field or in the greenhouse spreads mainly through contact between healthy and infected plants, irrigation water, rainwater, and nutrient solutions in soil cultivation (Gitaitis et al. 1992; De Leon et al. 2011; Sharabani et al. 2013).

A rapid course of the disease is favoured by high environmental humidity and temperatures of 23–28 °C, with a more serious incidence when, before stabilization of the temperature at 28 °C, stress occurs due to particularly hot or cold periods (Sharabani et al. 2014).

Infections occurring within a tomato's "susceptibility window" (from transplant to the 16–18 leaf stage) and an optimal temperature of 28 °C in the early stages of infections promote the development of the disease and the virulence of the pathogen (Sharabani et al. 2013, 2014).

Pepper strains have shown reduced virulence in tomato and increased virulence in pepper (Yim et al. 2012). When inoculated in bell pepper seedlings, the tomato and pepper isolates caused similar symptoms as well as a reduction in shoot dry weight (Yim et al. 2012).

2.1.1.2 Ralstonia Bacterial Wilts

Bacterial wilt caused by *Ralstonia* spp. is one of the most widespread bacterial diseases (Elphinstone 2005; Peeters et al. 2013). The disease affects over 250 plant species, belonging to more than 50 botanical families, including tomato, tobacco, potato, eggplant, pepper, sunflower and other solanaceous plants, together with a wide range of ornamentals including hollyhock, nasturtium, zinnia, marigold, dahlia, geranium.

The taxonomy of the phytopathogenic *Ralstonia* species complex has changed considerably as a result of new acquisitions obtained through phylogenetic studies, the analysis of sequences of conserved genes, and comparisons of entire genome sequences. The *R. solanacearum* species complex is currently divided into three species, *Ralstonia solanacearum*, *R. pseudosolanacearum* and *R. sygzygii*, which includes three subspecies: *syzygii*, *celebesensis* and *indonesiensis* (Safni et al. 2014).

The division of the species is in line with the previous classification in four phylotypes which were correlated with the geographical origins of the strains (Janse 2012; Peeters et al. 2013). The present classification and phylotyping scheme have been compared to previous race and biovar classification systems (Peeters et al. 2013; Safni et al. 2014; Prior et al. 2016).

Strains of the *Ralstonia* complex occupy different ecological niches but share the same phenotypic potential, as they are all soil-borne and plant xylem-infecting bacteria (Peeters et al. 2013). Symptoms in tomatoes (and similarly in eggplant) affect the younger leaves, which initially lose turgidity during the hottest hours, followed by the collapse of all the leaves within a few days. Before shrivelling, the plant develops adventitious roots along the stem. In the case of high environmental humidity, the foliar petioles may show signs of rotting. The various different host plants show some varied symptoms on the epigeous part of the plant; in the pepper, there may be yellowing and leaf rolling, followed by phylloptosis; in potato, the symptoms include dwarfism and yellowing of the basal leaves. Stem vascular bundles have a yellowish-brown colour that darkens in an advanced stage of the disease. Light pressure exerted on the transverse cut of the base of the stem, produces whitish drops of bacterial exudate from the dark vascular bundles. Symptoms related to xylem invasions can be seen on other host plants, e.g. on geranium such as wilting and subsequent leaf chlorosis (often sectorial), and internally, vascular browning is often visible (EPPO 2018).

The start of the infectious process involves the bacterium moving towards the host plant, adhering to the roots, invading the cortical layers, and colonizing the xylem. Thanks to the flagella, it moves towards the roots initially attracted by chemotactic and aerotactic stimuli, then by radical exudates (Yao and Allen 2006, 2007; Alvarez et al. 2010). Penetration occurs through wounds or natural openings on the roots of the host on which it adheres thanks to the presence of membrane lipopolysaccharides and appendages such as fimbriae.

The sites of preferential penetration are the root tips and the points of emission of the secondary roots. Before reaching the xylem, the bacterium invades the cortical layers of the roots and the vascular parenchyma adjacent to the vascular bundles located in the intercellular spaces, and it degrades the cell walls thanks to hydrolytic enzymes. Within the xylematic vessels, the pathogen moves in an acropetal direction, reaching concentrations of 10^{10} cells per cm of stem in tomato plants (Saile et al. 1997; Alvarez et al. 2010). The high bacterial concentration and the production of exopolysaccharides (EPS) obstruct the vascular bundles which leads to wilting. The collapse of the plant leads to the release and spread of the bacterium into the environment.

The bacterium survives in moist soil, in deep layers (>75 cm) and in water which is an important source of inoculum. The type, humidity, and presence of crop residues influences the survival of the bacteria in the soil, while the pH levels, salt content, along with the presence of organic substances and antagonist microorganisms all play a role in survival in aquatic environments. *R. solanacearum* can survive in crop residues, in the rhizosphere of numerous spontaneous plants. This is true also in spontaneous semi-aquatic plants (*Solanum dulcamara*) which are a reservoir for the bacterium and from which *R. solanacearum* can be released into the environment by contaminating the water and soil (Caruso et al. 2005).

A temperature of 27 °C is optimal for the development of the disease. The bacterium in fact causes significant damage at temperatures of between 25 and 35 °C, while the virulence of the bacterium decreases above 35 °C and below 12 °C.

The bacterium is not seed transmitted. In the field the bacteria spread from plant to plant by moving from the roots of infected or spontaneous tomato plants to nearby healthy plants or through runoff water after irrigation or rain. Contaminated irrigation water plays a key role in spreading the bacterium. The bacterium can be transmitted during grafting and cultural practices using contaminated tools or through the sub-irrigation or ebb and flow systems (Swanson et al. 2005).

2.1.1.3 Bacterial Wilt of Cucurbits

Bacterial wilt disease is typically fatal once symptoms appear. It causes significant economic losses in cultivated cucurbit crops and infected plants rarely recover or yield marketable fruit. The disease affects two genera of Cucurbitaceae crop plants—*Cucumis* spp. (cucumber and muskmelon) and *Cucurbita* spp. (pumpkin, squash, and yellow-flowered gourds).

The causal agent of the disease is *Erwinia tracheiphila,* which is a xylem-limited bacterium transmitted from infected to healthy plants by several species of neotropicalluperine beetles (either dotted or striped). Pathogenicity assays using strains from the host of the different genus have highlighted that *E. tracheiphila* induces wilt symptoms more rapidly when inoculated into hosts within the genus of isolation, than when cross-inoculated into a plant of the other genera (Saalau Rojas et al. 2013). A phylogenomic analysis revealed three genetic clusters with effector virulence gene repertoires, host plant association patterns, and geographic distributions (Shapiro et al. 2018). Both in the field and greenhouse, cucumber is the most susceptible host plant species and the only species susceptible to isolates from all three lineages. Shapiro et al. (2018) suggest that the establishment of large agricultural populations of highly-susceptible *Cucumis sativus* in temperate eastern North America is now acting as a highly-susceptible reservoir host.

Symptoms are characterised by the typical wilting of leaves and stems, which in turn necrotise and the entire plant collapses. Symptoms begin from cucumber beetle damage and may occur in a wide range of time after infection (four to more than 21 days) (Saalau Rojas et al. 2015). The way symptoms are expressed and develop varies depending on the host and its phenological state – the youngest infected seedlings are the most susceptible.

Although wild Cucurbitaceae are hosts of *E. tracheiphila,* there is no evidence they might act as an inoculum reservoir. Moreover, the extent to which epiphytic populations of *E. tracheiphila* act as reservoirs of inoculum is uncertain and limited to days (Saalau Rojas and Gleason 2012). The beetle vector is therefore assumed to be the primary overwintering reservoir of *E. tracheiphila*, leading to infection from one cucurbit growing season to the next (Saalau Rojas et al. 2015). Infected beetles deposit frass containing the bacterial cells onto floral nectaries or fresh leaf wounds, from which they enter the xylem. The ability to obstruct a xylem flow suggests the presence of many *E. tracheiphila* cells in symptomatic tissues. *E. tracheiphila* can be seen oozing from multiple blocked xylem vessels in a cross-section of a symptomatic cucumber stem (Shapiro et al. 2018).

Beetles are attracted by infected plants and after brief exposure to them can transmit the pathogen probably as soon as the infected plant material moves through the beetle's gut. In addition, the bacterium is capable of establishing persistent colonization presumably throughout most or all of the life-span of the adult vector (Shapiro et al. 2014). In the United States, economic damage is the consequence of leaf herbivory wounds and bacterial infection as well as the indirect costs of controlling vector populations. Insecticide applications against cucumber beetles is the primary bacterial management programme since there are no commercially available disease-resistant cultivars.

2.1.2 Bacterial Soft Rots and Stem Pith Necrosis

2.1.2.1 *Pectobacterium* and *Dickeya* Soft Rots

Soft rot diseases are characterized by the dissolution of host tissues and the release of cellular fluids. Soft rotting agents rely mainly on the production and secretion of an arsenal of extracellular pectic enzymes and a wide range of other plant cell wall-degrading enzymes (Perombelon 2002; Charkowski 2018). Although these bacteria are more associated with post-harvest diseases, soft rot may also be observed during crop cultivation. The soft rot of crops, both in temperate and tropical areas, is mainly caused by bacteria previously in the genus *Erwinia* which are now found in the genera *Pectobacterium* and *Dickeya*, which can macerate the plant tissues of the host (Ma et al. 2007; Charkowski 2018). Other pathogenic causal agents of soft rot include *Pseudomonas* species, such as *P. viridiflava* or *P. marginalis*, which are generally considered more common as the post-harvest agents of fruit and vegetable soft rot although such agents have been reported in greenhouse-grown tomato and eggplants (Kado 2010).

Bacterial soft rot is a disease complex caused by multiple genera of bacteria, with *Dickeya* and *Pectobacterium* being the most widely studied soft-rot bacterial pathogens (Charkowski 2018). Such bacteria can affect the growing potato plant that causes blackleg and are responsible for tuber soft rot in storage, thereby reducing yield and quality (Czajkowski et al. 2015). Soft Rot Enterobacteriaceae (SRE) also cause diseases in vegetables and ornamentals. They include *P. carotovorum* subspecies, *P. atrosepticum, P. aroidearum* and *Dickeya* spp. (Ma et al. 2007; Charkowski 2018). Members of the genus *Dickeya* affect a wide range of plant hosts worldwide (Toth et al. 2011) and typically are soft rot organisms and can also necrotize the xylem.

The favorable conditions for soft rot include high humidity, abundant rain or irrigation, poor soil drainage, dry and warm temperatures. Plant tissue infection occurs when free water is present. In low humidity, the lesions dry and affected tissues wither. Bacteria penetrate through natural openings, such as hydathodes, lenticels or wounds also caused by insect damage. Infected plants and organs are sources of inoculum during cultivation, harvest and post-harvest.

Members of the genus *Pectobacterium* cause soft rot disease in plants of at least 16 dicotyledonous and 11 monocotyledonous angiosperm families (Ma et al. 2007). In greenhouse grown Solanaceae, *Pectobacterium* stem rot has been described above all in tomato but also in pepper and eggplant. Since the taxonomy and diagnostic techniques are continuously evolving, the number of species involved has increased. *P. atrospeticum*, *P. carotovorum* subp. *carotovorum* and susp. *brasiliensis* and *Dickeya chrysanthemi* have been involved in the soft rot of Solanaceae.

Reports are more frequent on grafted plants than on seedlings (Catara et al. 2001; Fiori et al. 2005; Caruso et al. 2016). Infected plants of all species show similar symptoms of soft rot dark brown longitudinal discoloration of the stem near the plant base, but also along the stem where it is often in contact with the plastic strings of the training system or near side shoot pruning scars (Fig. 2.2a–c). The plant may show wilting symptoms. Epidermis slip off and decay of the petioles at the insertions with the stem have also been observed. Lesions dry if the humidity decreases. Internally, the stem shows brown water-soaked to rotted pith tissues, also beyond the area affected externally.

Stem rot can also affect other crops, such as broccoli and cauliflower, where the stem becomes hollow. In salad crops (such as lettuce, endive and escarole) and other leafy vegetables, symptoms may appear at the leaf margins or affect the stem end and progress toward the midveins. Leaf decay often causes leaf or entire plant detachment at the head base. *P. carotovorum* subsp. *carotovorum* is responsible for most of these diseases, although *P. carotovorum* subsp. *odoriferum* is more frequent in soft-rotted chicory (Waleron et al. 2014).

On other plants or plant organs, initially lesions appear to be water-soaked and darker in color than the surrounding healthy tissue. *P. carotovorum* subsp. *carotovorum* has the widest host range. The fruit, tubers, fleshy roots, fleshy stems, and leaves are susceptible to soft rot. Subsequently a cloudy, whitish liquid can exude from the plant splits. Several vegetable fruits are susceptible including pepper fruits. Infection may occur prior to harvest following insect punctures or other mechanical wounds. Alternatively, the rot may progress from infected branches.

Dickeya spp. and *P. carotovorum* spp. *carotovorum* soft rot cause severe damage to the flower bulb industry (Yedidia et al. 2011). Bulbous ornamentals such as *Hyacinthus, Dahlia, Iris, Muscari, Freesia* and *Zantedeschia* can be infected. The bacterial species *P. aroidearum* sp. nov., accommodates the distinctive pectobacteria which mainly, but not exclusively, cause soft rot diseases in monocotyledonous plants including *Zantedeschia* spp. (Nabhan et al. 2013). *Dickeya* spp. (mainly *D. chrysanthemi*, *D. dianthicola*, *D. dadantii*, *D. diaffenbachiae*) are also vascular

Fig. 2.2 Bacterial stem rot caused by *Pectobacterium* sp. on grafted eggplant (**a**, **b**) and tomato (**c**). Symptoms of Tomato pith necrosis, adventitious roots along affected stem (**d**) hollowing and necrosis of the stem pith (**e**). Small spots with yellow halo on tomato leaves induced by *Pseudomonas syringae* pv. *tomato*. (Reproduced with permission from Bella and Catara (1998))

wilt pathogens, they could also necrotize the xylem causing both stem rots and wilting. The ornamentals hosts include *Chrysanthemum* spp., *Dianthus* spp., *anthurium, dieffenbachia, philodendron*, *syngonium* and more (Samson et al. 2005; Toth et al. 2011).

2.1.2.2 Tomato Pith Necrosis

Pith necrosis is a disease characterized by the necrosis of parenchymal tissues of the plant stem. The most common disease is tomato pith necrosis (TPN) which is caused by two closely-related bacterial species *Pseudomonas corrugata* and *P. mediterranea* (reviewed in Catara 2007). However, a number of fluorescent pseudomonads, namely *P. cichorii*, *P. viridiflava*, *P. fluorescens* and *P. marginalis*, have also been identified as being associated with similar syndromes in several countries (Catara 2007; Bella and Catara 2010; Trantas et al. 2013). *Pectobacterium* spp. and *Xanthomonas perforans* have also been associated with pith necrosis in tomato (Aiello et al. 2013; Caruso et al. 2016).

P. corrugata and *P. mediterranea* are considered opportunistic pathogens, although in some cases TPN may reach 100% incidence (Catara 2007). This disease is more frequent in unheated greenhouses where marked differences between the day and night temperature range cause water condensation and free water on the plant surface.

Symptoms usually appear when the plants have formed the first fruit trusses, although the disease has also been reported in nursery plantlets. A slight wilting in the hottest hours of the day can be seen, which is a common symptom followed by chlorosis of the apical leaves. Dark green to brown water-soaked area may be present on the epidermis and extend along the entire stem associated with long conspicuous adventitious roots very far from the soil (Fig. 2.2d). Internally the pith of the stem (peduncles, petioles) appears as necrotic dry or water soaked, disaggregated with ladder-like cavities (Fig. 2.2e). *P. corrugata* and *P. mediterranea* have been reported as causal agents of pith necrosis also in pepper and chrysanthemum with similar symptoms to those observed in tomato.

P. corrugata is able to survive in soil (longer in sandy-loam than sandy soils) and in the rhizosphere of the host plant species. It can also colonize the tomato rhizosphere and start endophytic colonization from the inoculum present in the soil as well as from infected seeds (Bella et al. 2003; Cirvilleri et al. 2000). *P. corrugata* enters the host through wounds on the stem, collar and roots. From infected plants, the bacterium can be dispersed by rain splash, sprinkler splash and dew, or during handling. It can efflux from the roots into the water of the circulating solution of the soil-less system and hence infect healthy plants. Irrigation water may play a role in the dissemination of the pathogen.

2.1.3 Bacterial Leaf Spots and Fruit Blotches

2.1.3.1 Bacterial Spot of Tomato and Pepper

Bacterial spot is one of the most devastating diseases in pepper and tomato grown in warm, moist environments. Once present in the crop and when environmental conditions remain favorable, it is almost impossible to control the disease and prevent major fruit losses.

Although *Xanthomonas campestris* pv. *vesicatoria* is often described as the causal agent of tomato and pepper bacterial spot, it is not a single taxonomic entity. Strains known with that name have now been allocated to *X. euvesicatoria*; *X. gardneri* and *X. vesicatoria. X. euvesicatoria* includes two pathovars: pv. *euvesicatoria* and pv. *perforans* (previously *X. perforans*) (Constantin et al. 2016).

Many of the disease features are similar for both crops. In tomato, leaves initially show pinpoint water-soaked lesions that increase in size and became necrotic. The spots can coalesce and be surrounded by chlorotic haloes. The entire leaf may necrotize and blight. Necrotic spots may enlarge and coalesce and can appear also on petioles and stems. Strains of *X. perforans* have also been associated with stem pith necrosis (Aiello et al. 2013). Small, frequently raised, necrotic spots can be seen on fruits. The lesions become enlarged and later crack and evolve into canker-like lesions. These lesions may act as an entry point for secondary rotting organisms.

On pepper, the spots on the fruits are raised and the necrotic tissue is blackish (scab like) which results in poor quality and non-marketable products. However, the biggest crop losses result from the shedding of blossoms and young, developing fruits.

The primary source of inoculum relies on bacteria that survive in contaminated seeds (on and/or under the tegument) and transplants (Gitaitis et al. 1992; Dutta et al. 2014; Potnis et al. 2015). Moreover, infected plant residues from previously infected crops and volunteer tomato plants may contribute as minor inoculum sources (Jones et al. 1986). Pepper seeds can be more frequently contaminated than tomato seed lots (Black et al. 2001). Bacteria can penetrate the plant through wounds caused during field operations such as grafting, topping, clipping, tying, harvesting and from natural openings, namely stomata, hydathodes and lenticels (Potnis et al. 2015). Bacterial spot is a particular threat in transplant production since plants are irrigated frequently, are very close to each other, and humidity is typically high. Bacterial cells can exudate from the lesions in leaves and stems (secondary inoculum), contributing to the formation of epiphytic populations (Zhang et al. 2009; Potnis et al. 2015). Bacterial cells are spread by the splashing of irrigation water or rain in the open field. Cultural operations play an important role in dispersal and inoculation through contaminated tools such as pruning scissors, knives and clips used for agronomic practices (Mclnnes et al. 1988; Potnis et al. 2015). The long-distance spread of tomato and pepper *Xanthomonas* spp. is commonly related to the trade in infected seeds and transplants (EFSA 2014).

2.1.3.2 Bacterial Speck of Tomato

Bacterial speck of tomato affects many tomato-growing regions. The disease is bolstered by cool temperatures and high moisture conditions. Serious disease outbreaks are relatively infrequent, and are favored by high leaf wetness, cool temperatures and cultural practices which enable the bacteria to be disseminated between host plants.

Bacterial speck of tomato is caused by *Pseudomonas syringae* pv. *tomato*. There are two known races of *P. syringae* pv.*syringae* – race 0 and race1.

Plant resistance to race 0 is due to the tomato gene *Pto* introgressed from *Solanum pimpinellifolium*, a wild tomato species, into tomato cultivars and which has provided effective disease control for several decades (Pitblado and Kerr 1979, 1980). Race 1 strains can defeat Pto-mediated resistance. The *P. syringae* pv. *tomato* population has evolved to overcome genetic resistance by altering the expression and sequence of avrPto and avrPtoB effectors (Kunkeaw et al. 2010). The races can be identified by inoculating the tomato Cultivar Ontario 7710 (Jones et al. 2014).

The first symptoms of bacteria speck appear on cotyledons and true leaves as small round green dark water-soaked spots which are sometimes surrounded by a narrow yellow water-soaked halo (Fig. 2.2f). The lesions quickly necrotize and are surrounded by a yellow halo, and when they coalesce, the entire leaf, or most of it, may necrotize. Circular to elongated lesions which initially are water-soaked and later become necrotic may form on petioles, peduncles and pedicels. On fruits, the bacterium causes raised necrotic spot lesions which are 1–3 mm in diameter. Fruit lesions are limited to the external cellular layer thus if the epidermis is removed, the tissues have a normal coloring. The disease thus interferes with the fresh market commercialization, but not with the processing industry. Symptoms can be confused with those of bacterial spot (*Xanthomonas* spp.), thus laboratory analyses are necessary to differentiate between them.

P. syringae pv. *tomato* is seed transmitted. Seedlings obtained from contaminated seeds may be asymptomatic but may also bear high epiphytic bacterial populations.

In conditions of high humidity and temperatures of between 13 and 25 °C, which often occur in a cold greenhouse, the bacteria rapidly multiply on the plant surfaces and penetrate through the stomata and wounds of leaves and fruits (Goode and Sasser 1980). The bacterial toxin coronatine help to overcome the plant response to *P. syringae* pv. *tomato* infection by promoting the opening of stomata for bacterial entry (Panchal et al. 2016).

Once infection takes place, the secondary inoculum that exudes from the lesions is quickly dissipated by water splashing or by contact between the leaves (in the presence of a film of water on the surface) or by cultural operations (Gitaitis et al. 1992).

The bacterium survives in infected plant residues (very little in the bare soil) and in the rhizosphere of crops and wild plants and on contaminated tomato seeds. From primary sources of inoculum, the bacterium may colonize the leaves where a resident population develops. The probability of infection increases with temperatures of between 13 and 25 ° C and a relative humidity above 80% (Gitaitis et al. 1992; Gullino et al. 2009).

2.1.3.3 Cucurbit Leaf Spot and Blight

‘Angular leaf spot’, the most commonly reported bacterial disease of cucurbits worldwide, is mainly ascribed to *P. syringae* pv. *lachrymans* but also to the pvs. *syringae*, and *aptata*, which are causal agents of epidemics affecting various cucurbit species (Fatmi et al. 2008; Harighi 2007; Langston et al. 2003; Morris et al. 2000; Sedighian et al. 2014). Phylogeny studies have revealed that pathovar *lachrymans* is constituted of strains, which converge as a result of pathogenicity toward cucurbits but belong to different genomospecies of the so-called *P. syringae* complex (Marcelletti and Scortichini 2014; Słomnicka et al. 2015, 2018).

The disease is worldwide and affects most of the commercially important Cucurbitaceae including watermelon, cucumber cantaloupe and muskmelon, and squash. It is characterized by initial pin-point water soaked lesions that turn necrotic. As they enlarge, they remain delineated by the leaf veins thus forming the typical angular leaf spots. The lesions can coalesce thus leading to a foliar blight.

When dry, the spots are commonly torn away from the healthy portions of the leaf, leaving large irregular holes which lead to major destruction of the leaf canopy (Zitter et al. 1996). On fruits they are tiny and water-soaked but dry to form whitish, chalky spots. Under humid conditions, a white exudate may ooze from the lesions, which dries to form a white crust on or near the lesions.

The disease emerges sporadically under humid to wet conditions, and epidemics of similar bacterial spot disease on cucurbit have led to up to a 100% disease incidence. Variable disease incidence and severity can be ascribed to the different virulence of different genotypes (Marcelletti and Scortichini 2014). The disease is seedborne, therefore many epidemics have occurred in new areas, associated with crops grown in greenhouses or under plastic tunnels (Fatmi et al. 2008; Harighi 2007; Morris et al. 2000; Sedighian et al. 2014). The disease may take place one year and disappear the next season, due to the bacteria overwintering in infested crop residues (Fatmi et al. 2008; Morris et al. 2000)

High relative humidity to free moisture on the foliage and fruit is essential for infection. As with the other bacterial diseases, rain splash or irrigation, insects, and pickers and farm machines play an important role in the spread of the disease.

2.1.3.4 Bacterial Fruit Blotch of Cucurbits

Bacterial fruit blotch (BFB) is an economically important disease of cucurbits affecting leaves at all growth stages and fruits (Burdman and Walcott 2012). The disease is caused by the Gram-negative bacterium *Acidovorax citrulli*. The disease has spread to many parts of the world, mainly via contaminated seeds. *A. citrulli* populations are categorized into two phenotypical and genetically distinct groups (I and II) (Burdman and Walcott 2012; Eckshtain-Levi et al. 2014; Zivanovic and Walcott 2017). Group I *A. citrulli* strains have been reported to be moderately to highly virulent in several cucurbit hosts, whereas group II strains have exhibited high virulence in watermelon but low virulence in other cucurbits. Additionally, group I strains are recovered from a range of cucurbit hosts, while group II strains are predominantly found in watermelon (Burdman and Walcott 2012; Eckshtain-Levi et al. 2014)

Symptoms can be initially observed on cucurbit seedlings, mostly characterized by water-soaking areas on the undersides of cotyledons, with a greasy appearance and persistent under dry conditions. Lesions can extend along the stems to tissues of true leaves and, in severe cases, seedlings collapse or the lesions dry.

Economic losses result from the fruit rot phase of the disease. Lesions on fruit appear as small irregularly-shaped, green spots located on the upper surfaces of the fruit which can spread and cover the entire exposed surface. Lesions are initially firm, but brown cracks may develop in the rind lesions from which an amber-colored ooze is released. On melon and pumpkin, the lesions do not expand on the rind surfaces but penetrate the pericarp causing brown cavities which may rot.

On mature leaves, symptoms can be confused with those of other biotic or abiotic stresses. They consist in tan to reddish-brown lesions along the leaf veins and/or v-shaped lesions which extend from a margin to the base of the leaf. On pumpkin leaves, extensive chlorosis may be present.

A. citrulli is seed borne and transmitted by seeds which represent the most important source of primary inoculum (Dutta 2011). Blossom invasion by *A. citrulli* can lead to seed infection, also in the absence of BFB fruit symptoms (Dutta et al. 2012). Other inoculum sources are volunteer cucurbit seedlings, non cucurbit and cucurbit weeds and infected plant debris (Burdman and Walcott 2012).

The primary inoculums increase during seedling transplant production or grafting since transplant house conditions, including high temperatures and RH, dense plant populations and overhead irrigation, are highly conducive to the development and spread of BFB. Infections of up to 100% of transplants can result. Asymptomatic plantlets can support epiphytic inoculum, and the disease can develop after planting in favorable conditions. In the greenhouse, high RH and high temperatures promote the development of BFB. Secondary infections are caused by the penetration of *A. citrulli* through stomata and wounds to establish infections which result in foliar lesions and blight or fruit blotch. The fruit is susceptible via penetration of fruit stomata 2–3 weeks after anthesis before waxy deposits on the surface of the fruit block the stomata and prevent invasion.

Seed disinfestation treatments, seed health testing and chemical control in the field are limited in their ability to reduce the yield losses associated with BFB. In addition, there are currently no reliable sources of BFB resistance (Burdman and Walcott 2012).

2.2 Conclusions and Future Perspectives

Strategies for controlling bacterial diseases to a manageable level rely on eradication, exclusion, therapy, protection and regulation (Kado 2010). Disease control is best achieved using an integrated management approach by combining appropriate cultural practices, chemicals such as bactericides or plant activators where applicable, introgression of plant resistance genes, and biological control strategies (Jones et al. 2007).

The use of pathogen-free plant materials is an important method to control bacteria diseases by preventing their introduction in the nurseries and in the cultivation area, and the production requires strict certification (Janse and Wenneker 2002; Janse 2006).

Given that greenhouse conditions are favourable for all bacterial epidemics, healthy seeds and transplants are still the main goal to control some diseases (e.g. tomato bacterial canker and cucurbit fruit blotch) (De Leon et al. 2011; Gitaitis and Walcott 2007). Increasingly optimised detection methods as well as grower-friendly monitoring methods could be of great help. To be easily used by growers, extension agents, regulators or laboratory services, methods need to be accessible, robust, readily available, cost-effective, and possibly multiplexed to different pathogens (De Boer and Lopez 2012).

Very few chemicals targeting plant bacterial diseases have been marketed and the most traditionally used chemicals are copper compounds and, in some countries, antibiotics (Sundin et al. 2016). Their use is integrated with biocontrol agents and resistance inducers. Populations of bacteria, in different genera, that are resistant to copper and streptomycin have evolved above all by the acquisition of genes encoding resistance determinants, thus also implicating non-target microbiota in the horizontal transmission of resistance determinants within agricultural ecosystems (see review in Sundin and Wang 2018).

Using bacteriophages as a means of controlling bacterial diseases continue to be of great interest and commercial products are now available (Jones et al. 2007, 2012; Buttimer et al. 2017). One of the most studied targets is tomato bacterial spot by *Xanthomonas* spp. (Obradovic et al. 2004; Gašic et al. 2011, 2018; Balogh et al. 2018).

The current challenge in phytopathogenic bacteria management relates to compounds (above all natural compounds obtained from agricultural waste or by-products) that interfere with pathogen virulence. These compounds show little effect on bacterial growth and do not have as high a selective pressure for resistance development as traditional bactericides (Sundin et al. 2016). Bacterial targets include the type III secretion system (T3SS), which translocates effector proteins directly from the bacterial cytoplasm into the host cell cytoplasm and Quorum sensing (QS) cell-to.cell bacterial communication system (Sundin et al. 2016).

Cultivated plant hosts are not resistant to most bacterial pathogens. New genome editing technologies based on TALE nucleases (TALENs) and the CRISPR/Cas9 system are encouraging methods for the development of durable resistance to bacterial pathogens (Boch et al. 2014; Ortigosa et al. 2018).

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Chapter 3
Fungal Diseases

Marc Bardin and Maria Lodovica Gullino

Abstract Greenhouses are intensive cropping systems where microclimatic conditions are particularly favourable for the development of different fungal diseases (fungal-like organisms and true fungi) and if no proper control measures are taken in time, losses may be high. The principal fungal diseases are presented, as well as examples of emerging or re-emerging diseases, which may represent, in the future, a major threat to greenhouse production in some areas. Examples of fungal diseases are given based on their specificity towards target plant organs (aerial organs, vascular system, roots/collar).

This chapter provides information relevant to the diagnosis, biology of the main fungal plant pathogens and the epidemiology of the diseases encountered in such greenhouse cropping systems. Basic information on plant protection methods is also provided: control strategies of fungal diseases still rely on the use of chemicals but transition to integrated pest management (IPM) is in progress in many countries worldwide.

Keywords Fungal diseases · Diagnosis · Biology · Epidemiology · Control

3.1 Introduction

Greenhouses are intensive cropping systems where climate is generally warm, humid and wind free, making it a particularly ideal system for the development of many pests and diseases and above all those caused by fungi (Jarvis 1992). Among the so-called fungal diseases, one can encounter fungal-like organisms (or lower fungi) and true fungi (i.e. chytridiomycetes, zygomycetes, ascomycetes and basidiomycetes).

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The structure and equipment of greenhouses can vary considerably (glasshouses, plastic tunnels, soil or soilless cultivation, heated or non-heated…, see Chap. 2 in this book) which can accordingly lead to the development of different fungal diseases. The development of soilless substrates has for instance led to the reduction of some soil-incited fungal diseases (Jarvis 1992). Regulation of climate (and particularly control of humidity) within the greenhouse, and particularly in high-technology structures wherein growers can exercise a precise control of their environment, is considered as a key lever to avoid epidemics of fungal-incited diseases (Jarvis 1992). However, energy-saving procedures may question this strategy of disease management.

This chapter provides information relevant to the diagnosis, biology of the main fungal plant pathogens and the epidemiology of the diseases encountered in such greenhouse cropping systems. Pathogenic fungi are grouped based on their specificity towards target plant organs (aerial organs, vascular system, roots/collar). Basic information on plant protection methods is also provided. But more data is available in the book in chapters corresponding to protection methods (Part III) and to specific crop case studies (Part IV). Additional information can also be found in books dealing with greenhouse crop diseases (Jarvis 1992) or in books relative to specific crops (Blancard et al. 1991, 2003, 2009) or on the web.

3.2 Aerial Fungal Pathogens

3.2.1 Powdery Mildews

The powdery mildew plant diseases are caused by ascomycete fungi of the order Erysiphales. Various species can cause powdery mildew on the main crops grown in greenhouse structures, i.e. *Oidium neolycopersici* and *Leveillula taurica* on tomato (Blancard et al. 2009; Kiss et al. 2001), *Podosphaera xanthii*, *Golovinomyces cichoracearum* and *L. taurica* on cucurbits (Bardin et al. 1997, 1999; Vakalounakis et al. 1994), *L. taurica* on pepper (Palti 1971; Cerkauskas et al. 2011), *G. cichoracearum* on lettuce (Lebeda and Mieslerovà 2011), *Podosphaera aphanis* and *Golovinomyces orontii* on strawberry (Pei et al. 2017; Sombardier et al. 2010) or *Podosphaera pannosa* on rose (Linde and Debener 2003; Felix-Gastelum et al. 2014). They are all obligate biotrophs and they have long been considered to have a rather narrow host range generally restricted to a single botanical family or even a single plant species (Yarwood 1978). But this is not always the case, i.e. *G. cichoracearum* can attack various plant species from different botanical families (Lebeda and Mieslerovà 2011) and *L. taurica* can attack an even greater number of host plants (Correll et al. 1987; Cerkauskas et al. 2011; Glawe et al. 2009), estimated to reach 1000 plant species belonging to 74 botanical families (Blancard et al. 2009).

Powdery mildews are easily recognizable by their obvious symptoms: white powdery spots that can enlarge and coalesce to cover large area on leaves, stems and other green plant organs (Fig. 3.1). Symptoms caused by *L. taurica* are slightly different with light green or yellow spots on the upper leaf surface and white spots on

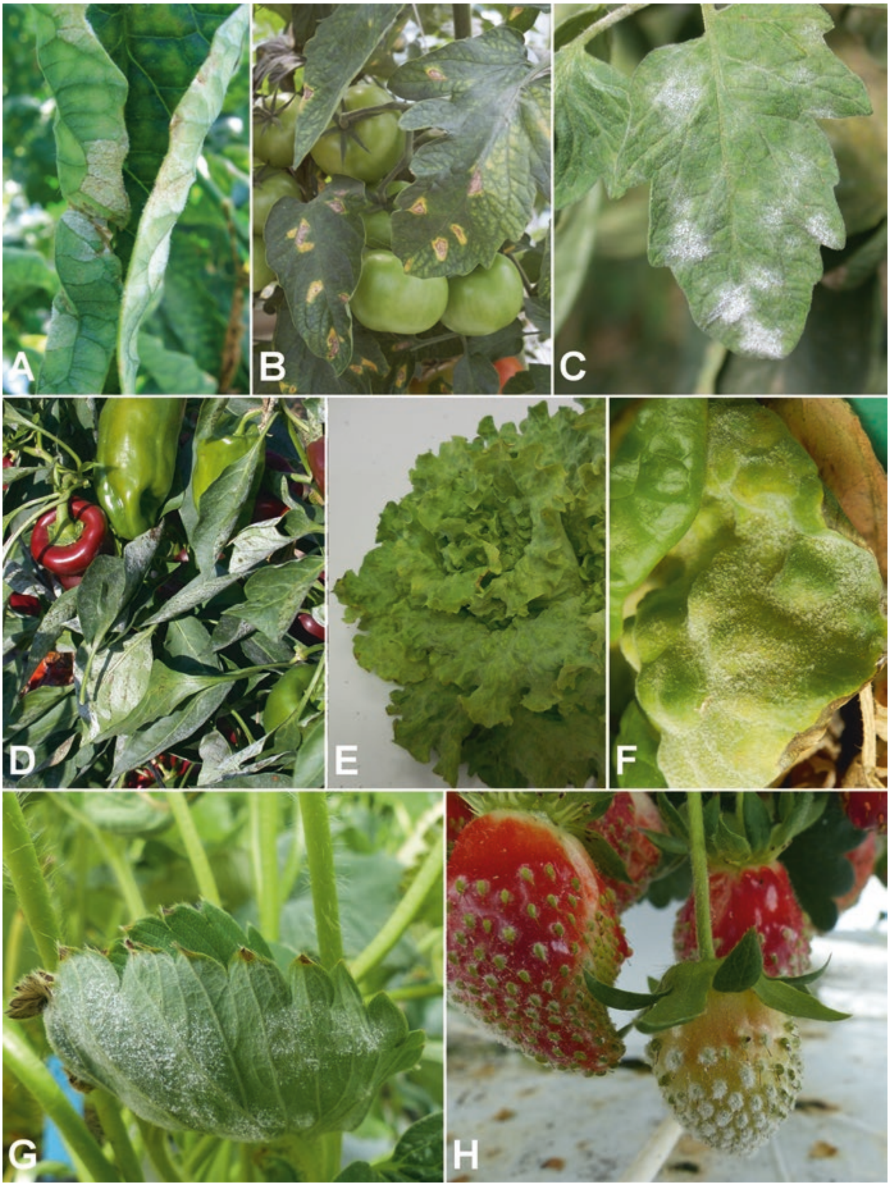

Fig. 3.1 Symptoms of powdery mildew on tomato caused by *Leveillula taurica* (**a**, **b**) and by *oidium neolycopersici* (**c**), on pepper (*L. taurica,* **d**), on lettuce (*Golovinomyces cichoracearum*, **e**, **f**) and on strawberry (*Podosphaera aphanis,* **g**, **h**)

the lower surface (Blancard et al. 2009). Leaf necrosis and premature defoliation of heavily contaminated plants can also occur, sometime in a cultivar-related manner (Jones and Thomson 1987; Reuveni et al. 1974; Jarvis et al. 2002). Relationship between disease severity and crop yield has been established for greenhouse cucumber attacked by *P. xanthii,* pepper and tomato attacked by *L. taurica* and strawberry attacked by *P. aphanis* (Jarvis et al. 2002; Carisse et al. 2013; Jones and Thomson 1987).

Infection process during the growing seasons occurs by conidia. In optimal laboratory conditions, conidia can germinate rapidly in few hours, and the fungus can penetrate the plant cell walls in less than 24 h through the formation of an appressorium, and then take nutrients from the plant cells by the development of a haustorium with branched finger-like projections (Kunoh 2002). In conducive conditions, a rapid progression of the disease can be observed in greenhouse crops. Data concerning microclimate conditions required for the development of the disease reveal that these fungi are able to grow in a wide range of temperature, with an optimum between 21 and 29 °C and a wide range of relative humidity, including dry environments (Jarvis 1992). They also show that temperature and humidity requirements depend on the species or even on the strain of the pathogen (Jarvis et al. 2002; Butt 1978). However, one common trait of all powdery mildew species is that excessive water is generally detrimental to the development of disease (Jarvis et al. 2002).

For most powdery mildew species, production of chasmothecia (= cleistothecia) normally occurs at the end of the crop's growing season, possibly due to environmental stress (Jarvis et al. 2002). However, chasmothecia have never been observed in the field or produced in the laboratory for several powdery mildew species, such as *O. neolycopersici* (Kiss et al. 2001). Therefore, the exact role of ascospores in the epidemiology of the disease in greenhouse crops is still uncertain (Gadoury et al. 2010; Bardin et al. 1997, 1999). In the case of annual crops, inoculum is perpetuated between growing seasons through alternative hosts (wild or cultivated). Moreover, inoculum probably remains readily present in the case of rapid crop sequences, which is potentially the case for greenhouse crops. In areas with dense concentrations of greenhouses, powdery mildew epidemics probably never stop (Jarvis 1992; Jarvis et al. 2002).

Various protection tools are available to control powdery mildews in greenhouse crops. Chemicals, including sulphur-based products and various systemic fungicides, remain the main means to control the disease in greenhouses. However, resistance of powdery mildew fungi to fungicides has become an increasing concern, rendering numerous systemic fungicides ineffective (Hollomon and Wheeler 2002; Sombardier et al. 2010; Bellon-Gomez et al. 2015). Alternative control methods such as varietal resistance and biocontrol agents are also available. Sources of resistance have been identified for many greenhouse crops (Pitrat et al. 1998; Lefebvre et al. 2003; Kennedy et al. 2013; Seifi et al. 2014; Jahn et al. 2002; Debener and Byrne 2014) and selection has led to the development of commercial cultivars with partial or complete resistance for some of these crops such as melon, cucumber, tomato or strawberry for example. However the diversity and variability of powdery mildew species can lead to the breakdown of resistance for instance on melon or lettuce (Lebeda et al. 2012, 2016). Partial resistance to the disease can also be achieved through grafting on resistant genotypes: it has for instance been shown on pepper towards *L. taurica* (Albert et al. 2017), on cucumber and melon towards

P. xanthii (Lemaire et al. 1998; Guan et al. 2012). Biological control of powdery mildew has been widely studied in the past years (Bélanger and Labbé 2002; Nicot et al. 2011), leading to the development of commercial biopesticides against this plant disease, such as microbial preparations with *Ampelomyces quisqualis*, *Bacillus subtilis* or *B. amyloliquefaciens* or with plant extract from *Reynoutria sacchalinensis* (Paulitz and Belanger 2001; Gwynn 2014). Finally, various salts (i.e. silicon, sodium or potassium bicarbonate, calcium chloride, calcium nitrate, potassium phosphate) have shown a high level of efficacy against powdery mildews (Fauteux et al. 2005; Ehret et al. 2002; Fallik et al. 1997; Reuveni et al. 1996), (see Chap. 15 in this book). Under shelter, cucumber powdery mildew can also be reduced by polyethylene films altered in their transmission of the light spectrum (Elad 1997).

3.2.2 **Botrytis-*Incited Diseases***

The *Botrytis*-incited diseases are caused by ascomycete fungi classified within the *Sclerotiniaceae* family. The genus *Botrytis* comprises approximately 30 species (Walker 2016) that can infect more than 1400 plant species (Elad et al. 2016). Most species have a narrow host range except *B. cinerea* (teleomorph *Botryotinia fuckeliana*), the causal agent of grey mould, which can infect a wide range of plants estimated at 586 plant genera, including most greenhouse crops (Elad et al. 2016). The new species *B. pseudocinerea* living in sympatry on several hosts with *B. cinerea* was described based on phylogenetic, biological, morphological, and ecological criteria (Walker et al. 2011) and was found in greenhouses of tomato and lettuce (Leyronas et al. 2015b; Adjebli et al. 2015). Recently a host-specific new species named *B. fragariae* was described on strawberry in Germany and in the Southeastern United States (Rupp et al. 2017).

Botrytis cinerea is among the most damaging fungal plant pathogens worldwide (Dean et al. 2012), with significant economic impact for numerous crops including those grown under greenhouses (Elad 2016). All aerial parts of the plant (leaves, stems, flowers, fruits) can be affected by the fungus (Fig. 3.2). Whatever the plant organs, the diseased tissues are covered with a characteristic grey mould, consisting of conidiophores and conidia of the fungus. The structure and equipment of greenhouses (glasshouses, plastic tunnels, heated or non-heated) can lead to the development of different types of symptoms on the plants. For instance, in heated tomato greenhouses where leaf pruning is a routine practice, tomato infections mainly occur on the pruning wounds, resulting in stem cankers that can kill the plants (Decognet et al. 2010). In non-heated greenhouses (such as plastic tunnels), where leaf pruning is generally not performed, tomato infections occur on leaves, flowers and fruits but the fungus can also develop through the petiole into the stem (Aissat et al. 2008; Shtienberg et al. 1998). In strawberry the main problem consists in flower and fruit attacks with infection occurring also after harvest causing fruit rot (Boff et al. 2001; Xiao et al. 2001). On other greenhouse crops such as cucumber, pepper, eggplant, *B. cinerea* cause stem canker killing the upper part of the plant; in

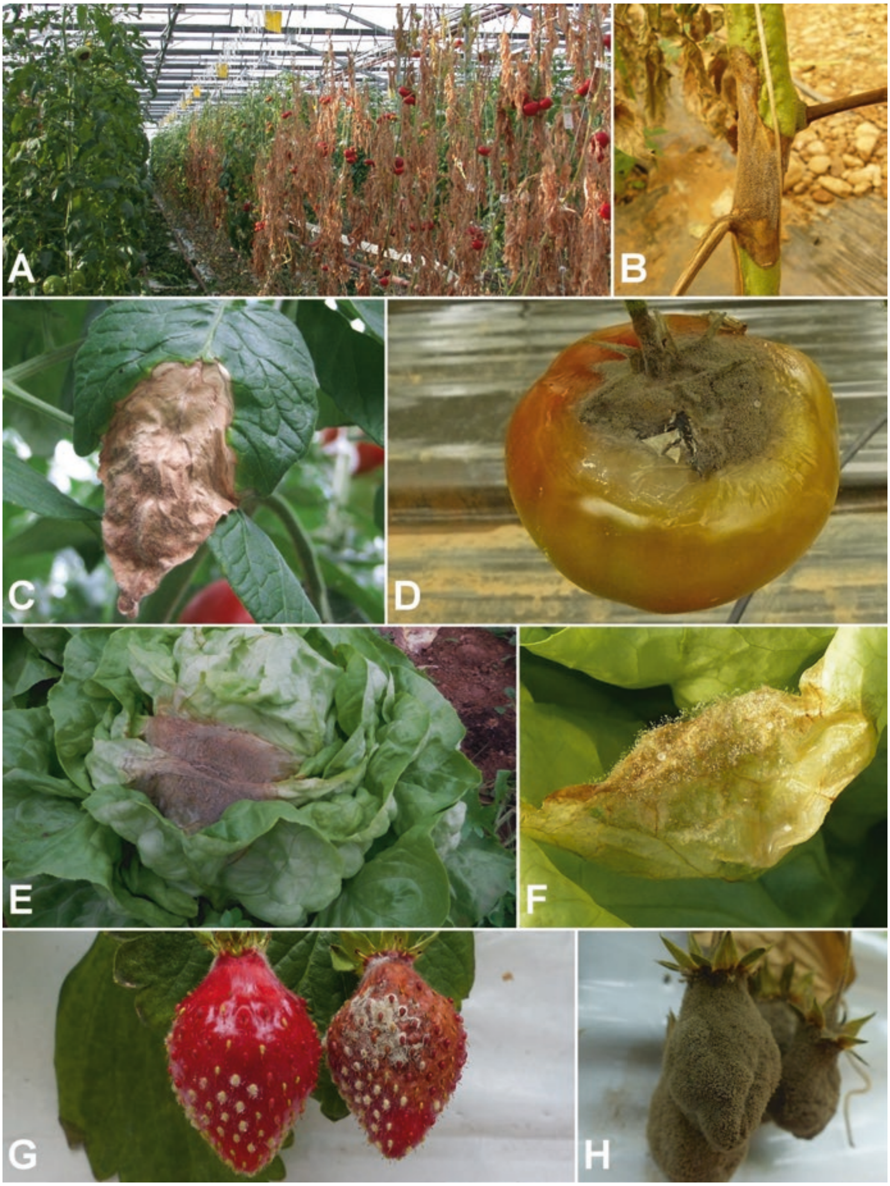

Fig. 3.2 Symptoms of grey mold caused by *Botrytis cinerea* on tomato (**a**–**d**), on lettuce (**e**, **f**) and on strawberry (**g**, **h**)

rose and gerbera, petals are infected, thereby strongly reducing their market value (Dik and Wubben 2004; Malathrakis and Goumas 1999). In lettuce *B. cinerea* essentially infects old leaves and causes collar rot, as part of a complex of collar rot fungi which may also involve *Sclerotinia* sp., but it can also affect the heart of lettuce and moreover it can cause post-harvest damages (Blancard et al. 2003).

However, several plant-pathogenic *Botrytis* species, including *B. cinerea*, can be isolated within symptomless plant tissues, including lettuce, suggesting that these fungi can complete their life-cycles as endophytes in several healthy plant-hosts (Shaw et al. 2016).

The molecular and biochemical mechanisms related to the infection process of plants by *Botrytis* has been a very prolific research topic for several decades and have reached a high level of understanding with the advent of -omics techniques. Thanks to these tools, the involvement of secreted proteins (proteases, plant-cell wall degrading enzymes…), phytotoxic secondary metabolites (oxalic acid, botrydial…), and small RNAs (sRNAs) in the infection process of plants by *B. cinerea* is now established (Gonzalez et al. 2016). Moreover, the fungus is able to manipulate the hypersensitive response of the plant and the associated plant cell death machinery for its benefit (Govrin and Levine 2000) and to suppress plant immunity using its fungal sRNAs that are delivered into host cells (Weiberg et al. 2013, 2014).

Perennation of the fungus between cropping seasons is ensured by the maintenance of mycelium in leaves, crop debris, mummified fruits, straw mulches, weeds or by the production of sclerotia that can survive for months in the soil (Carisse 2016). Sclerotia can undergo myceliogenic or carpogenic germination producing either conidia or ascospores. However, the role of ascospores in the epidemiology of the disease is quite contradictory (De Miccolis Angelini et al. 2016). Inoculum could also originate from non-agricultural habitats (Bardin et al. 2018), from alternative hosts (wild or cultivated), from neighbouring or overlapping cultures (Jarvis 1992; Bardin et al. 2014; Leyronas et al. 2015a), from the soil (Leyronas et al. 2015b), and it can potentially be transported over long distances (Leyronas et al. 2015c; Monteil et al. 2014). In greenhouses, secondary inoculum produced within the crop greatly contributes to the epidemics of grey mould (Bardin et al. 2014; Decognet et al. 2009; Walker et al. 2015).

In greenhouses, microclimatic conditions are globally favourable for grey mould development. *Botrytis cinerea* can develop over a wide range of temperature with an optimum comprised between 11 and 30 °C depending on its growth phase (Jarvis 1992). This fungus is a water-dependent pathogen and extraction of humid air to the outside of the greenhouse is essential to control the disease (Jarvis 1992). Fertilization can affect the level of infection of plants within greenhouses. On tomato, disease severity was lower on plants with higher nitrogen input (Lecompte et al. 2010) whereas on lettuce, damage on leaves increased with the level of nitrogen fertilization applied (Lecompte et al. 2013). The type of irrigation can also have an impact on disease development, and drip irrigation is for instance preferable to furrow irrigation in tomato plastic tunnels (Aissat et al. 2008). In tomato greenhouses, improvement of pruning practices by carefully removing leaves systematically close to the stem without leaving any petiole stubs can decrease the incidence of stem cankers (Decognet et al. 2010). Plastic films altered in their transmission of the light spectrum (near-ultraviolet or far-red absorbing films) have an effect on sporulation of *B. cinerea* (Nicot et al. 1996; Elad 1997) and are able to reduce the disease in greenhouses (Elad 1997).

Classical plant protection tools such as chemicals remain an essential mean to control the disease. However the amazing variability in phenotypic traits of this fungus makes it a risk candidate for fungicide resistance development. Strains of *Botrytis* having specific resistance to single molecules or multidrug resistance to various chemicals are regularly detected in the field (Fillinger and Walker 2016; Liu et al. 2016; Kanetis et al. 2017). Biocontrol has been widely studied since this disease represents an important economical market, and a wide range of microbial and botanical preparations have been reported to exhibit inhibitory activity against the fungus (Nicot et al. 2011). Numerous commercial biopesticides, having different modes of action, are now available. At least 14 microbial-based products and 2 botanical-based products are registered in various countries to control *Botrytis*-incited diseases (Nicot et al. 2016). However vigilance is required to ensure the durability of biocontrol against this fungus as it can develop resistance to biocontrol agents (Bardin et al. 2015; Ajouz et al. 2010; Fillinger et al. 2012). Field data reveal differences in sensitivity of cultivars of several plant species to this disease. In tomato, different wild accessions proved to present a high level of partial resistance to stem or to leave colonization (Nicot et al. 2002; Guimaraes et al. 2004; Urbasch 1986), indicating a potential for the selection of resistant cultivars in the future.

3.2.3 Downy Mildews and Late Blight

The causal agents of downy mildews and late blight are oomycetes, which are fungal-like organisms members of the kingdom chromista. Different oomycete species are responsible for important diseases on greenhouse crops, such as downy mildew, caused for instance by *Bremia lactucae* on lettuce (Blancard et al. 2003), *Pseudoperonospora cubensis* on cucurbits (Blancard et al. 1991) or *Peronospora sparsa* on rose (O'Neill et al. 2002), or late blight on tomato, caused by *Phytophthora infestans* (Blancard et al. 2009). Some of these oomycetes have a rather narrow host range, generally restricted to a single botanical family (i.e. *Phytophthora infestans* on solanaceous crops, *Pseudoperonospora cubensis* on cucurbits), or a more extended host range (i.e. *B. lactucae*).

Bremia lactucae is one of the most important diseases of lettuce worldwide. It causes white to light-green and to yellow spots on the upper part of the leaves (Fig. 3.3); these spots eventually become necrotic and leaves ultimately die (Blancard et al. 2003). It can attack the plant throughout its crop cycle.

Within the cucurbits, melon and cucumber are more susceptible to downy mildew than watermelon and *Cucurbita*. It provokes yellow to light brown spots on the upper surface of the leaves that eventually die (Blancard et al. 1991). On rose, *P. sparsa* damages all green parts of the plant (Malathrakis and Goumas 1999). On tomato *P. infestans* can attack all aerial plant organs and symptoms may progress fast, possibly resulting in the rapid death of the plant (Blancard et al. 2009). Fruits

Fig. 3.3 Symptoms of downy mildew caused by *Bremia lactucae* on lettuce

can also rot rapidly in the field or during storage. On basil, downy mildew is caused by *Peronospora belbahrii* (Belbahri et al. 2005; Thines et al. 2010). It is one of the most economically important basil diseases, and has caused significant yield losses in several countries in Europe (including Switzerland, Italy, France and Belgium), in the United States (where it has been reported in several states since 2009), in Argentina, Israel (Cohen et al. 2013) and China (Farr and Rossman 2017). The transmission of *P. belbarhii* via infected seeds is generally recognised as the main means of survival from season to season, because the pathogen rarely produces oospores (Cohen et al. 2013; Djalali Farahani-Kofoet et al. 2012; Gullino et al. 2014; Wyenandt et al. 2015).

These fungal-like pathogens are able to survive as oospores or as mycelium in the soil on plant debris (Agrios 2005). In perennial plants (such as rose) it can survive as dormant mycelium on the twigs or on the stems (Malathrakis and Goumas 1999). Inoculum usually consists of airborne sporangia from diseased plants located close to or within the crop (Blancard et al. 2003, 2009). The mycelium from germinating sporangia, oospores or more rarely zoospores penetrates the plant directly through the cell wall or through stomata on the leaves. Mycelium develops inside host tissues, generates haustoria to take nutrients from the cell and produces branched sporangiophores on leaf or other organs through natural openings (stomata or lenticels). Sporulation (production of sporangia) and development of the disease can occur for a wide range of temperatures (from 2 to 26 °C, depending on the fungal species) and are generally optimal at high relative humidity (above 90%) (Barriere et al. 2014; Blancard et al. 2003, 2009; Nordskog et al. 2007).

Fungicides are widely used to control downy mildew and late blight and numerous products having different active ingredients are registered worldwide (Blancard et al. 1991, 2003, 2009). But resistance to fungicides has been frequently detected, for instance in natural populations of *B. lactucae* (Schettini et al. 1991; Brown et al. 2004; Cobelli et al. 1998). In the case of basil, because no cultivars of marketable interest are known to be resistant or tolerant to downy mildew (Ben-Naim et al. 2015), the control of this disease is mainly based on the application of fungicides, such as for examples mefenoxam, potassium phosphite, mandipropamid, fluopicolid, mancozeb and azoxystrobin (Gilardi et al. 2013, 2015; Wyenandt et al. 2015). This plant pathogen has shown a high risk of development of strains resistant to fungicides through specific modes of action. Field resistance of *P. belbahrii* to phenylamides was for instance observed, first in Israel (Cohen et al. 2013), and later in Italy (Garibaldi et al. 2016d). Furthermore, it has been shown that basil seeds are a potential source of mefenoxam-resistant inoculum for this oomycete (Pintore et al. 2016). Moreover, the use of chemicals in the field is complicated by the continuous nature of the harvest. An integrated approach to basil downy mildew control is suggested, in which the microclimate environmental conditions are managed (Gilardi et al. 2018).

Breeding programs for cultivar-resistance to downy mildew and late blight have been widely developed for different greenhouse crops (Barriere et al. 2014; Perchepied et al. 2005; Pitrat et al. 1998; Schulz et al. 2009; Foolad et al. 2008). For most lettuce breeding programs, selection for resistance to *B. lactucae* remains for instance a major priority and many resistance genes have been reported over the past 50 years (Parra et al. 2016) leading to the development of numerous commercially lettuce cultivars resistant to the disease. However, resistance breakdown caused by new virulent strains of *B. lactucae* is an important and constant concern that leads to a rapid turnover of cultivated lettuce cultivars (Lebeda and Zinkernagel 2003; Sharaf et al. 2007; Nordskog et al. 2014; Van Hese et al. 2016). Currently, breeding efforts on lettuce focus on the selection of durable resistance to downy mildew, with the pyramiding of different major resistance genes involved (Barriere et al. 2014). Few botanical or microbial species have been reported as having successful control effect against downy mildew and late blight on field vegetable or tomato (Nicot et al. 2011). Only a small number of biocontrol products (*Bacillus pumilus*, *B. subtilis* and *B. amyloliquefaciens*-based products) are commercialized so far worldwide (Gwynn 2014). However, elicitors, including acibenzolar-S-methyl, have shown a significant effect to reduce the disease on lettuce, but with a strong plant genotype effect (Maisonneuve et al. 2013). Acibenzolar-S-methyl also reduces significantly the disease on basil (Gilardi et al. 2013; Mersha et al. 2013).

3.2.4 Rusts

Rusts are caused by basidiomycetes fungi and can be particularly damaging on ornamental greenhouse crops such as carnation, rose or *Chrysanthemum* (Malathrakis and Goumas 1999). The fungal species are *Uromyces dianthi* on carnation (Spencer 1979), *Phragmidium mucronatum* and *P. tuberculatum* on rose (Wilson and Aime 2014) and *Puccinia horiana* on *Chrysanthemum* (Bonde et al. 2015; Dheepa et al. 2015; Alaei et al. 2009). Fungi attack the aerial part of the plants leaving noticeable spots on the leaves. Symptoms can differ according to the plant host and the fungal species.

Free water is necessary for spore germination and the disease is favoured by high relative humidity (Horst 1989; Malathrakis and Goumas 1999). *Puccinia horiana* can overwinter in volunteer plants (O'Keefe and Davis 2012). Uredospores can be spread from infected neighbouring crops to healthy plants (Malathrakis and Goumas 1999).

Fungicide can be used to control the disease on Carnation (Spencer 1979), rose (Paulus et al. 1986) or *Chrysantemum* (Lam and Lim 1993). Resistance to fungicides have been detected for instance with *P. horiana* (Cook 2001). Variation for resistance to rusts has been observed in various species or cultivars of *Chrysanthemum* (Zeng et al. 2013; De Backer et al. 2011). In parallel with this resistance, a complex race structure has been pointed out in *P. horiana* (De Backer et al. 2011). In rose, resistance has been observed in the rose-related species *R. rubiginosa*, thus indicating a potential to select resistant cultivars (Ritz et al. 2005). Potential biocontrol agents have been identified against *U. dianthi* (Spencer 1980) or *P horiana* (Torres et al. 2017; Dheepa et al. 2016), for example.

3.2.5 **Alternaria** *Diseases*

Alternaria is an ubiquitous ascomycete fungal genus that includes plant pathogenic species associated with a wide variety of plants and for which the taxonomy of species is still controversial (Woudenberg et al. 2013, 2015). Historically, the causal agents of the *Alternaria*-incited diseases have been declared through various species of the genus *Alternaria* (Simmons 2000; Woudenberg et al. 2013). On tomato, the causal agents can be *A. solani*, *A. tomatophila*, *A. subcylindrica*, *A. subtropica*, *A. alternata* f. sp. *lycopersici* or *A. tomato* (Blancard et al. 2009).

Alternaria spp. causes early blight disease on tomato. It is able to attack all aerial organs at all stages of growth of the plant. On young plants, it can cause collar rot and damping off. On adult plants it usually induces small irregular brown spots, dark lesions on stem that may kill the plant. Fruit rot lesions can also be observed on tomato at all stages of ripening (Blancard et al. 2009). Other species of *Alternaria* has been reported on other greenhouse crops such as cucurbits, lettuce, carnation, basil, rocket (Blancard et al. 1991, 2003, 2009; Malathrakis and Goumas 1999; Gilardi et al. 2018).

Conidia or mycelium are able to overwinter in infected plant debris, on seeds or on tubers in the case of potato (Agrios 2005). It can grow and invade the plant tissues over a wide range of temperatures. Sporulation occurs preferably with free water (dews, rains) and spores are disseminated through wind or splashing (Agrios 2005).

Prophylactic measures (debris removal, soil disinfection, use of healthy seeds, seed dressing, plant quality, crop rotations ...) are essential to prevent the disease (Blancard et al. 2009). Seed dressing with physical, biological and or chemical treatments have been developed for a number of *Alternaria* species on different crops (Amein et al. 2011; Lopez-Reyes et al. 2016). Various fungicides can be applied to protect plants against *Alternaria*-incited diseases. Fungicide should be used as soon as the first symptoms of the disease appear. However, resistance to various fungicides have been observed (Chapin et al. 2006; Malandrakis et al. 2015; Shi et al. 2015). Genetic resources for resistance to early blight (*A. solani* and *A. tomatophila*) have been identified within the tomato wild species (Foolad et al. 2008). However, a varietal screening of tomato varieties revealed no resistant varieties but different level of sensitivity to the disease (Chohan et al. 2015). Alternative methods of control have also been explored, with for example the use of chitosan, *Bacillus* spp., *Trichoderma* spp. or essential oils against *A. solani* on tomato (Ramkissoon et al. 2016; Shanmugam et al. 2011; Tomazoni et al. 2017; Chohan et al. 2015). Postharvest tomato biocontrol has also received particular attention (Zhao et al. 2008).

3.2.6 Didymella *Diseases*

Didymella-incited diseases are caused by various ascomycete species that can affect cucurbitaceous and solanaceous crops in the greenhouse. On tomato, *Dydimella lycopersici* is the causal agent of stem canker and fruit rot in numerous countries in the word (Blancard et al. 2009). Gummy stem blight of cucurbits is caused by three genetically distinct species: *D. bryoniae* (syn. *Stagonosporopsis cucurbitacearum*), *S. citrulli*, and *S. caricae* (Li and Brewer 2016; Stewart et al. 2015; Brewer et al. 2015). *Dydimella bryoniae* has a worldwide distribution and is found on at least 12 genera and 23 species of cucurbits (Keinath 2011). It represents a threat to cucurbits cultivated in humid environments around the world (Keinath 2011). Recently, sensitive and rapid diagnosis methods using Visual Loop-Mediated Isothermal Amplification Assay have been developed to detect *D. bryoniae* during early stages of disease development in cucurbit crop production (Yao et al. 2016).

These fungi cause lesions on aerial parts of the plants, mainly on the stems (canker especially at the base of the stem that can kill the plants) and more occasionally on the fruits. Both diseases are favoured by cool temperature (around 20 °C) and high relative humidity. *Dydimella* species can survive on plant debris in the soil for weeks (Blancard et al. 1991, 2009; Keinath 2008). Incorporation of crop debris into soil promptly after harvest can reduce the survival time of *D. bryoniae* (Keinath 2008). These fungi can penetrate the plant tissues through natural openings (stomata) or wounds. Cell wall degrading enzymes (particularly polygalacturonases and β-galactosidases) appear to be virulence factors of *D. bryoniae* in melon fruit decay (Zhang et al. 2014).

Prophylactic methods (debris removal, disinfection of structures and equipment, crop rotations, greenhouse climate management…) are recommended to avoid the appearance of disease in greenhouses (Blancard et al. 1991, 2009). Disinfectant treatments of cutting tools (with heat, ethanol or sodium hypochlorite) are required to prevent or reduce transmission during grafting in cucurbits (Keinath and DuBose 2017). Seed treatment can also be used to limit the occurrence of the disease (Kasselaki et al. 2008; Sudisha et al. 2006). Fungicides treatments can control the disease during the cropping period but resistant strains have been detected towards various fungicides (Keinath 2009, 2012; Keinath and Zitter 1998; Li et al. 2016; Malathrakis and Vakalounakis 1983). However a study has shown that isolates of *D. bryoniae* remain sensitive to DMI fungicides despite multiyear exposure (Keinath and Hansen 2013). Screening tomato and cucurbit species germplasms for their resistance to *Dydimella* spp. have been carried out for a long time, revealing diversity in resistance level to the fungi (Martinson and Hogenboom 1968; Knight and Keyworth 1960; Wehner and Shetty 2000; Keinath 2014). Resistance genes were identified in *Cucumis sativus* (Lou et al. 2013) and in *Cucumis melo* (Wolukau et al. 2007; Zuniga et al. 1999). Strategy of gene pyramiding has been carried out in melon to enhance the level of resistance to the disease and to increase its durability (Zhang et al. 2017). Rootstock of tomato are usually resistant to the disease (Blancard et al. 2009) and the grafting has been reported to improve crop resistance to the disease on melon (Guan et al. 2012; Gasparotto et al. 2016). Various microbials with potential biocontrol effect have been identified (Utkhede and Bogdanoff 2003; Nga et al. 2010; Utkhede and Koch 2002, 2004; Zhao et al. 2012) and biocontrol agents (i.e. *Gliocladium catenulatum* or *Trichoderma* spp. based-product) are registered worldwide against *D. bryoniae* (Gwynn 2014).

3.2.7 Cladosporium-*Incited Diseases*

The genus *Cladosporium* form a monophyletic group which falls within the order Ascomycotina (Curtis et al. 1994). On tomato, the species responsible for leaf mold has been renamed *Mycovellosiella fulva* (syn = *Cladosporium fulvum*; syn = *Fulvia fulva*) (Blancard et al. 2009). This fungus has a narrow host range restricted to tomato and a worldwide distribution. It has for instance been reported in greenhouses in southeastern Spain (de Cara et al. 2008). On cucurbit, *C. cucumerinum* is responsible for scab mainly on cucumber but also on zucchini and melon (Blancard et al. 1991). Other species of *Cladosporium* has been recovered on other important greenhouse crops such as *C. subuliforme* on pepper in cuba (Ramos-Garcia et al.

2016). *Cladosporium*-incited diseases cause leaf spot but it can occasionally attack fruits, particularly on cucumber (Blancard et al. 1991, 2009; Malathrakis and Goumas 1999). *Cladosporium tenuissimum* has for instance been found to cause fruit rot of immature cucumbers under greenhouse conditions in Oman (Al-Sadi et al. 2011a).

Interaction between *M. fulva* and tomato and plant infection process have been widely studied for years revealing that the fungus secretes various proteins that are recognized by resistant plants that respond with a hypersensitive response (Cai et al. 2007; de Wit and Joosten 1999; Lozano-Torres et al. 2012). Strains of the fungus that escape recognition by tomato are virulent. Conditions conducive to the disease are temperatures comprised between 15 and 25 °C and high relative humidity (Blancard et al. 1991, 2009). Spores are easily disseminated by the wind or splashed by water drops (Malathrakis and Goumas 1999). The pathogen can survive in plant debris and on the greenhouse structure.

In greenhouses, prophylactic measures (debris removal, disinfection of greenhouse structures, seed treatment with hot water at 50 °C, greenhouse climate management…) are essential to limit the occurrence of the disease. During the cropping period, reduction of relative humidity can limit the development of the disease. Reduction of the disease incidence has also been obtained by the use of polyethylene films with light blockers in the far-red region of the spectrum (Elad 1997). Management of leaf mould on tomato can be achieved with various fungicides (Damirdagh 1981; Veloukas et al. 2007). However, benzimidazole-resistant isolates of *M. fulva* has been characterized (Yan et al. 2008). Numerous tomato cultivars are resistant to *M. fulva* thanks to intensive breeding programs. However, several races of the pathogen have been described on tomato all over the word (Lindhout et al. 1989; Laterrot 1986; Laterrot et al. 1985; Laterrot and Clerjeau 1979; Blancard et al. 2009; Enya et al. 2009; Lee et al. 2013). Various biocontrol agents have been identified to control the disease on tomato, such as *Trichoderma harzianum* (Elad 2000), *Burkholderia pyrrocinia* (Lee et al. 2011), *Streptomyces albidoflavus* (Chen et al. 2015), or *S. lavendulae* (Gao et al. 2016). Chitosan has also shown an effect against leaf mould on tomato (Li et al. 2009).

3.2.8 Minor Foliar Pathogens

New leaf spots incited by different pathogens have recently received increase attention because they cause extensive losses (Gilardi et al. 2018). Among others, *Phoma valerianellae* and *Pleospora betae*, repeatedly observed on lamb's lettuce and on swiss chard grown under plastic tunnels as well as *Allophoma tropica* on lettuce (Gilardi et al. 2018). Controlling the environmental conditions does not always provide adequate disease suppression and chemical control is sometime needed.

The number of first reports regarding *Myrothecium verrucaria* and *M. roridum* on new hosts has increased in recent years. *Myrothecium roridum* has also been found on lamb's lettuce (Garibaldi et al. 2016a), while *M. verrucaria* has been

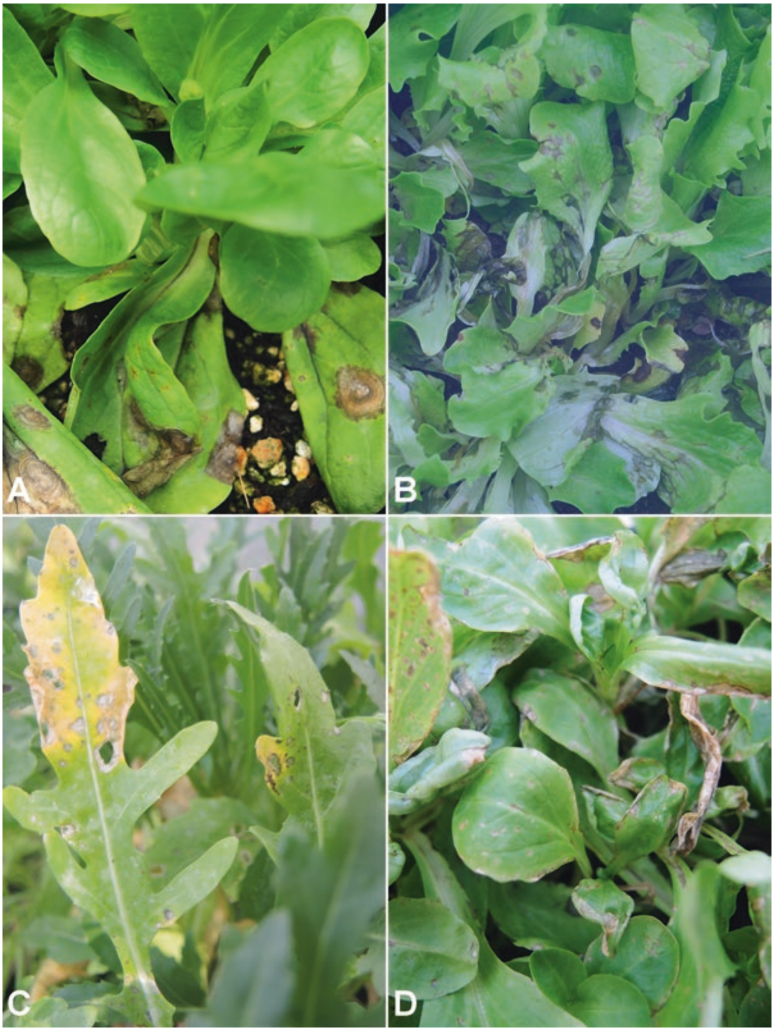

Fig. 3.4 Symptoms of leaf spots caused by *Phoma valerianellae* on lamb lettuce (**a**), *Allophoma tropica* on lettuce (**b**), *Myrothecium verrucaria* on wild rocket (**c**), and *M. roridum* on lamb lettuce (**d**)

isolated from spinach (Garibaldi et al. 2016b) and wild rocket (Garibaldi et al. 2016c). These *Myrothecium* species were first observed in Italy in 2015 under plastic tunnels. The symptoms caused by both species are similar: circular, sunken, grey-brown spots, with a well-defined border, that develop on affected leaves (Fig. 3.4). Creamy to black sporodochia appear on the leaf surface, in concentric rings, under high relative humidity. The management of *Myrothecium* leaf spot is complicated, because this pathogen is seed-transmitted in many cases (Belisario et al. 1999; Bharath et al. 2006; Nguyen et al. 1973). Moreover, no information is available for the control of *Myrothecium* leaf spot on leafy vegetables by chemical or biological means, and further investigations are needed.

Myrotechium leaf spot may become important in the future considering the forecasted climate change scenario. Another characteristic that makes this genus a serious threat is linked to its capability to produce macrocyclic trichothecenes, which are cytotoxic compounds (Gilardi et al. 2018).

3.3 Vascular Wilts

3.3.1 Verticillium-*Incited Diseases*

The genus *Verticillium* includes several phytopathogenic species causing vascular wilts of plants. The two most common species are *V. dahliae* and *V. albo-atrum*, causing severe losses on many important vegetable and ornamental crops grown under greenhouse. The genus *Verticillium* was established in 1816 (Isaac 1967; Pegg and Brady 2002), based on its unique branched conidiophores. *Verticillium dahliae* and *V. albo-atrum* are solely anamorphic with no evidence of sexual recombination or a meiosporic stage. *Verticillium* spp. are identified based on the types of resting structures produced: pigmented resting mycelium, pigmented microsclerotia, and chlamydospores. The two most distinctive features used or separating *V. dahliae* and *V. albo-atrum* are: (1) the production of melanised microsclerotia as survival structures by *V. dahliae*, while *V. albo-atrum* produces melanised hyphae but not microsclerotia and (2) the ability of *V. dahliae* to grow and infect plants at 30 °C, while *V. albo-atrum* does not grow in culture neither infects plants at 30 °C. Phylogenetic studies clearly identify *V. dahliae* and *V. albo-atrum* as distinct taxa (Atallah et al. 2007; Klosterman et al. 2009). The production of longer conidia permitted to elevate some strains of *V. dahliae* to a new species, *V. longisporum*. *V. dahliae* lacks host specificity, although some strains are more aggressive on certain hosts than others. This characteristic permits *V. dahliae* to infect a wide range of hosts (more than 200 plant species), including annual and perennial crops, landscape, fruit, ornamental trees and shrubs (Klosterman et al. 2009). The list of the hosts infected by *V. dahliae* continuously increases and new hosts are frequently identified (Farr and Rossman 2017). Strains of *V. albo-atrum* are divided into two groups based on their virulence and aggressiveness to lucerne, while *V. dahliae* strains are divided into six groups based on vegetative compatibility (Bhat and Subbarao 1999). Although vegetative compatibility groups (VCGs) do not describe the genetic diversity among strains, gene flow or the potential for recombination, they help in the deployment of resistant cultivars.

Symptoms of *Verticillium* wilt are very similar to those of *Fusarium* wilt, with vascular discoloration (Fig. 3.5). *Verticillium* infection may result in defoliation, gradual wilting and death of successive branches or abrupt collapse and death of the entire plant (Agrios 2005). In comparison with *Fusarium* wilt, *Verticillium* wilt

Fig. 3.5 Symptoms of vascular wilt caused by *Verticillium dahliae* on tomato (**a**, **b**) and eggplant (**c**)

develops at lower temperatures and symptoms develop more slowly, often interesting only the lower or outer part of the plant or few branches. Older affected plants are stunted (Agrios 2005).

For *V. dahliae,* disease cycle starts with dormant microsclerotia, that permit the pathogen to overwinter in soil. Microsclerotia can survive up to 15 years. Both *V. da*hliae and *V. albo-atrum* can overwinter also as mycelium within perennial host, in propagative organs and in plant debris. *Verticillium albo-at*rum produces dark, thick walled mycelium, but not microsclerotia. It grows better at 20–25 °C, while *V. dahliae* prefers higher (25–30 °C) temperatures. *Verticillium* penetrates young roots directly or throughout wounds. The fungus spreads by infected seeds, vegetative cuttings, tubers, wind, water, soil. The pathogen is often introduced in a soil for the first time with infected propagative material. Solanaceous crops help increasing its inoculum potential in soil (Agrios 2005). *Verticillium* can also be found at low levels in virgin soil: when a susceptible host is planted the disease cycle will start.

Although losses due to *Verticillium* wilt can be very high, reaching 100% on some crops and being very severe on solanaceous crops such as tomato, eggplant and pepper, the availability of resistant cultivars for most vegetable and ornamental crops, can strongly reduce the importance of this disease. The control of *Verticillium* wilt relies on planting disease-free material in disinfested soil or substrate, as well as avoiding planting susceptible hosts in soils repeatedly planted with solanaceous crops. Soil disinfestation, largely applied in the past, is now complicated by the high cost of steaming and by the very limited availability of fumigants. Fortunately, for most of the vegetable and ornamental crops grown in greenhouse there is a good availability of resistant cultivars.

3.3.2 **Fusarium-*Incited Diseases***

Fusarium oxysporum causes wilt diseases in a wide range of economically important crops (Booth 1984). *Fusarium* wilts of greenhouse vegetable and ornamental crops caused by *formae speciales* of *Fusarium oxysporum* (Nelson 1981) are numerous, economically important, and their management represents a challenge to growers (Gullino et al. 2012). Genetic diversity, as well as mechanisms of pathogenicity, have been addressed in *F. oxysporum* in the past 20 years with the use of molecular tools (Di Pietro et al. 2003; Kistler 1997), clarifying many aspects of disease specificity. Improved diagnostic tools have also permitted a better discrimination of *formae speciales* (Lievens et al. 2008, 2012). *Fusarium* taxonomy is a difficult, sometimes even controversial issue. Wollenweber and Reinking (1935) outlined the first comprehensive taxonomy for the genus, describing many species and subspecies, not considering pathogenic capacity as a major criterion. Overall, their treatment of the genus was complicated. Soon after, Snyder and Hansen (1940) greatly simplified Wollenweber and Reinking's complex view of the genus by lumping all of their taxa into nine species, and all of the taxa in Section *Elegans* into a single species, *F. oxysporum.* Notably, pathogenic strains of *F. oxysporum* were considered *formae speciales*, based on host range. Although these subspecific taxa are now known to be artificial groups of often distantly related strains, this classification remains a convenient means of categorizing plant-pathogenic members of the species. The classical approach for identifying *formae speciales* and race is the pathogenicity test. Since such tests can be time-consuming and their results equivocal, attempts have been made in the last 25 years to make these determinations with laboratory assays based on vegetative compatibility grouping, molecular tools and other criteria.

Fusarium wilts can cause serious losses in vegetable and ornamental plants at all stages of crop development, and their control has become even more challenging since the phase-out of methyl bromide (Katan 2005). Major changes in culture techniques to reduce the problems caused by soilborne pathogens include the use of hydroponics and artificial substrates controlled by computerized systems. However, soilless systems do not completely resolve these problems, since they are easily colonized by plant-pathogenic oomycetes, bacteria and *F. oxysporum*.

Wilts are easily recognized in most plants and are characterized by a loss of turgor on plant parts or in the whole plant. Common symptoms of *Fusarium* wilt include drooping or wilting of a portion of a leaf or the entire leaf, a portion of the plant or the entire plant, often accompanied by vein clearing, chlorosis, vascular discoloration, and stunting (Fig. 3.6). Wilt symptoms develop due to a lack of water flow to the affected plant part through the water-conducting or vascular system, and they may occur suddenly or develop gradually. In some cases, plants are only debilitated or stunted; in other cases, they die. Certain *Fusarium* pathogens produce conidia (mainly macroconidia) on the stems of the plants, e.g. the *formae speciales radicis-lycopersici, basilici* and *radicis-cucumerinum.* These propagules are easily disseminated through the air and contaminate new areas, which makes it more difficult to manage the associated diseases. Nonpathogenic forms of *F. oxysporum* frequently colonize roots and are easily isolated. Thus, they have been erroneously reported as causes of some diseases (Snyder and Smith 1981). The development of tools to distinguish pathogenic from nonpathogenic members of the species is therefore an important objective for virtually all of these diseases.

Generally, *formae speciales* of *F. oxysporum* are highly host-specific, affecting only one or a few species of plants, and in many cases, only certain cultivars of that plant. In rare cases, the same pathogen may be pathogenic on plants from different families. A pathogen's specificity for a particular host and for cultivars of that host is designated, respectively, *forma specialis* and race. Plant-pathogenic members of *F. oxysporum* are morphologically indistinguishable from each other as well as from nonpathogenic members of the species. Although the pathogens are host-specific, they are often nonpathogenic colonizers of roots of other unrelated plants (Armstrong and Armstrong 1948; Katan 1971): they colonize without inducing symptoms, as symptomless carriers, and may cause growth retardation in certain cases. This colonization capacity contributes greatly to the pathogen's ability to survive long periods in the absence of a susceptible host. More than 120 *formae speciales* have been described based on specificity to host species in diverse plant families, including field crops such as cotton and tobacco, plantation crops such as banana, coffee and sugar cane, and a few shade and palm trees. *Fusarium* wilts are particularly serious on fruit and vegetable crops, including tomato, melon, watermelon, cucumber, lettuce and other salad crops; and ornamentals, including carnation, gladiolus, lily,

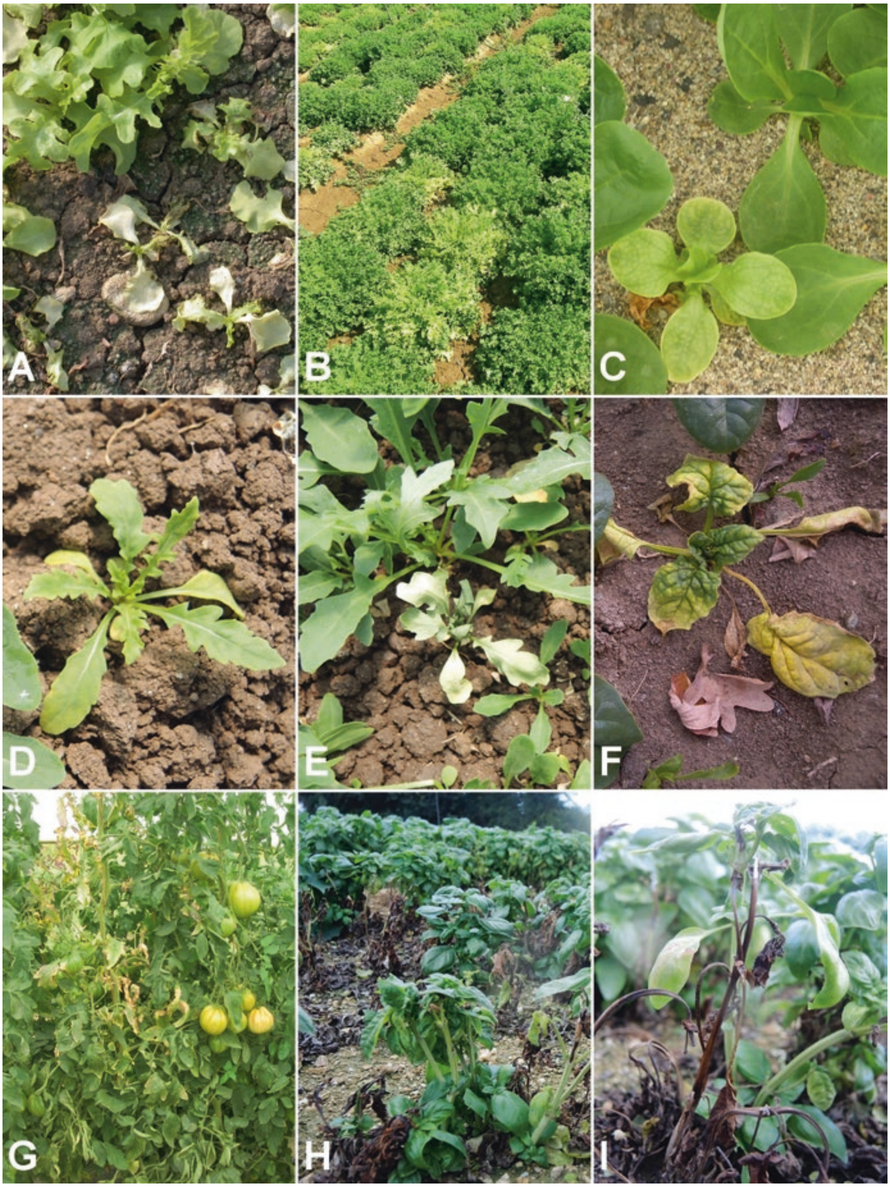

Fig. 3.6 Symptoms of wilt caused by *Fusarium* spp. on lettuce (**a**), on chicory (**b**), on lamb lettuce (**c**) on wild rocket (**d**, **e**), on spinach (**f**), on tomato (**g**) and on basil (**h**, **i**)

tulip, ranunculus, cyclamen, chrysanthemum, gerbera, Paris daisy and lisianthus. New *formae speciales* are frequently reported.

Losses due to wilt diseases vary greatly. The amount of actual loss depends on when disease development occurs and its extent. Slight wilting of one or several leaves late in the production cycle may not result in extensive losses, as would severe wilting or death of young plants, or if a similar disease developed on mature plants. Losses in cutting beds or nurseries may be slight to severe if proper precautions are not taken. The actual amount of loss varies with the specific host and with different cultivars of a host, and will be greatly influenced by environmental conditions during the particular phase of production (Campbell 1985). If a pathogenic *Fusarium* is detected in a nursery, then nothing in the nursery can be used, resulting in a total loss.

Although *F. oxysporum* is unusual among vascular wilt pathogens due to the extent of pathogenic specialization in this species, the *formae speciales* possess unexceptional mechanisms for survival and dissemination. Seed transmission occurs when propagules are carried as surface or internal contaminants of seeds or in associated plant debris. Many *Fusarium*, including those of tomato, basil, lettuce and rocket, possess these traits. *Fusarium oxysporum* may also be carried in vegetative propagation materials, as for instance for carnation, gerbera, chrysanthemum and bulb crops. Another interesting feature of *F. oxysporum* is its ability to produce chlamydospores in decaying host tissue and soil. Chlamydospores are resting structures which are more resistant to biotic or abiotic stresses than conidia (Nash et al. 1961; Schippers and van Eck 1981). They do not germinate, due to soil fungistasis, until stimulated to germinate by root exudates or appropriate nutrients. Thus, *Fusarium* wilt pathogens can survive in the soil for many years in the absence of susceptible host plants. *Fusarium* wilts are usually more severe under warm soil conditions and in greenhouses, but *formae speciales radicis-lycopersici* and *radicis-cucumerinum* develop better at lower temperatures.

Some *F. oxysporum formae speciales*, such as *radicis-lycopersici* and *cucumerinum*, cause root and crown rot. Lesions develop on the stem at or below the soil line, and affected plants wilt and die from rot of the roots and of the stem at the base of the plant. In some plants, a brown discoloration extends into the stem for a considerable distance above the ground. In older plants, roots are often rotted. This may also result in wilt. In the case of bulbs, corms and tubers, *F. oxysporum* can cause rots, often starting at wounds or through cuts formed during harvest. Invaded bulbs and corms may show external symptoms, and the basal plate, scales and roots are usually brown to black. The rot is generally dry and firm, and foliage turns yellow or brown and dies prematurely.

The dynamic and wide range of products, continual innovations in products and cultivation, and intensive international trade in the vegetable and ornamental sectors have exposed them to considerable risk from new diseases. In addition, the rapid substitution of varieties to adapt to market demand, the use of mono- and oligogenic resistance to these diseases, the production of propagation materials in just a few big nurseries, and the use of organic-based propagation media in which these pathogens can be disseminated, have all enhanced the threat posed by these diseases (Gullino and Garibaldi 2006). Therefore, new and reemerging *Fusarium* wilts are potential threats to vegetable and ornamental production in many areas (Gullino et al. 2012). Garibaldi and Gullino (2010) recently reviewed new *formae speciales* of *F. oxysporum* on vegetables and ornamentals. *Fusarium* wilts have for instance been recently observed on lettuce (*Lactuca sativa*), wild (*Diplotaxis* spp.) and cultivated (*Eruca sativa*) rocket, lamb's lettuce (*Valerianella olitoria*) and endive. These diseases emerged as major production problems where these crops were grown continuously in the same soil. However, since they are seed-transmitted, they have begun to spread to other areas. Although seed dressing may provide some disease control, the production and use of pathogen-free seed is expected to be most effective in reducing the spread of these pathogens. In the affected areas, use of resistant cultivars is one of the best strategies (Garibaldi et al. 2004; McCreight et al. 2005). *Fusarium* wilt of basil, caused by *F. oxysporum* f. sp. *basilici*, was first described in the former USSR and later detected in many basil-growing areas, causing severe damage due to its soil- and airborne behavior (Gamliel et al. 1996). *Fusarium* crown and root rot of tomato, incited by *F. oxysporum* f. sp. *radicis-lycopersici*, was first reported in Japan in 1969 and later spread to many tomato-growing areas in North America, Europe and the Mediterranean region (Katan and Katan 1999). Similarly, *F. oxysporum* f. sp. *radicis-cucumerinum* is a new disease of cucumber. On ornamental crops, a significant number of new *Fusarium* wilts have also been detected (Garibaldi and Gullino 2010). For example, starting in 1997, new outbreaks occurred in northern Italy on Paris daisy (*Argyranthemum frutescens*), *Osteospermum* sp., chrysanthemum, gerbera and lisianthus (*Eustoma grandiflorum*).

The control of Fusarium wilts relies on the use of resistant varieties, largely available for many important crops (tomato, lettuce,…), healthy seeds and transplants, disinfested soil or substrates, fungicides for localized applications. Soil/substrate disinfestation is complicated by the high cost of steaming and by the limited availability of fumigants. Very few chemicals are active against *Fusarium* wilts, whereas interesting results are provided by the use of organic amendments (Pugliese et al. 2015), resistance inducers such as phosphite-based products, often applied at the nursery level (Gilardi et al. 2016), as well by the application of biological control agents. Among biocontrol agents, the most effective are saprophytic *Fusarium oxysporum*, originally isolated from suppressive soils (Hoitink and Locke 2012; Termorshuizen 2012).

3.4 Root Rots and Damping-Off

3.4.1 Sclerotinia-*Incited Diseases*

Sclerotinia-incited diseases are caused by ascomycete fungi classified within the *Sclerotiniaceae* family. They have a word-wide distribution and can attack at least 408 plant species from 278 genera encompassing 75 plant families (Boland and Hall 1994). This host range includes important greenhouse crops, such as lettuce, tomato, cucurbits, eggplant or pepper (Tok et al. 2016; Blancard et al. 1991, 2003, 2009; Cuadrado et al. 2000). *Sclerotinia sclerotiorum* is the major plant pathogens in this group but *S. minor* is also of economic importance on lettuce. *Sclerotinia minor* produces smaller sclerotia than *S. sclerotiorum* but their symptoms are similar on this plant: infection of the leaves begins near the soil and spreads to the collar and inside the plant until it collapses and dies (Blancard et al. 2003). On other plants, *S. sclerotiorum* attacks stems and even fruits like in melon, cucumber, tomato or pepper. Whatever the location of the attack, a white cottony mycelium (white mold) develops on the infected tissues and then numerous black and hard sclerotia are produced (Fig. 3.7). Sclerotia play a major role in the disease cycle and they can survive for years in the soil (Blancard et al. 2003; Bolton et al. 2006). They can undergo myceliogenic or carpogenic germination producing either mycelium or apothecia, depending on environmental conditions (Bolton et al. 2006). Apothecia produce ascospores which are the primary inoculum in most host plants. In this case, ascospores require a nutrient source (generally senescent or necrotic tissues) to germinate before the invasion of plant tissues. However, in some crops and depending on the environment conditions encountered, the role of ascospores in the epidemiology of the disease is not clearly stated. For instance in dry areas of lettuce production, the disease is predominantly initiated by the mycelial germination of sclerotia (Chitrampalam and Pryor 2013). This type of germination is conditioned by environmental factors such as humidity and temperature (Huang et al. 1998). In such cases, mycelia can directly infect roots and collar of the susceptible plants. Development of epidemics are generally favoured by humid and fresh periods. Some greenhouse characteristics (dimension, surface area, mean height, colour of the plastic cover, ventilation capacity and use of lateral netting) can affect the incidence of *S. sclerotiorum* on pepper (Cuadrado et al. 2000). In cucumber greenhouses, disease caused by *S. sclerotiorum* can be reduced by plastic films altered in their transmission of the light spectrum (Elad 1997). On lettuce, damages on leaves inoculated with *S. sclerotiorum* increase with the level of nitrogen fertilization applied to the plant (Lecompte et al. 2013).

Control methods include fungicides treatments with the risk of frequent appearance of resistant strains (Li et al. 2017; Zhu et al. 2016; Di et al. 2016). Various microbial-based biopesticides are commercially available against *Sclerotinia* spp. (Paulitz and Belanger 2001; Gwynn 2014). For example, the fungus *Conyothirium minitans* that parasites the sclerotia of *Sclerotinia* spp. is registered in numerous countries. Recent results reveal however that differences in susceptibility to *C. minitans* among strains of *S. sclerotiorum* can be observed, suggesting that the efficacy of this biocontrol method might vary depending on the frequency of susceptible vs less susceptible strains of the fungus (Nicot et al. 2019). To our knowledge, there are no vegetable varieties selected for their complete resistance to *Sclerotinia* spp. However, some varieties of *Lactuca sativa* exhibit different level of sensitivity to the disease, suggesting the presence of partial resistance genes that can be selected in lettuce (Barriere et al. 2014; Grube and Ryder 2004; Hayes et al. 2010).

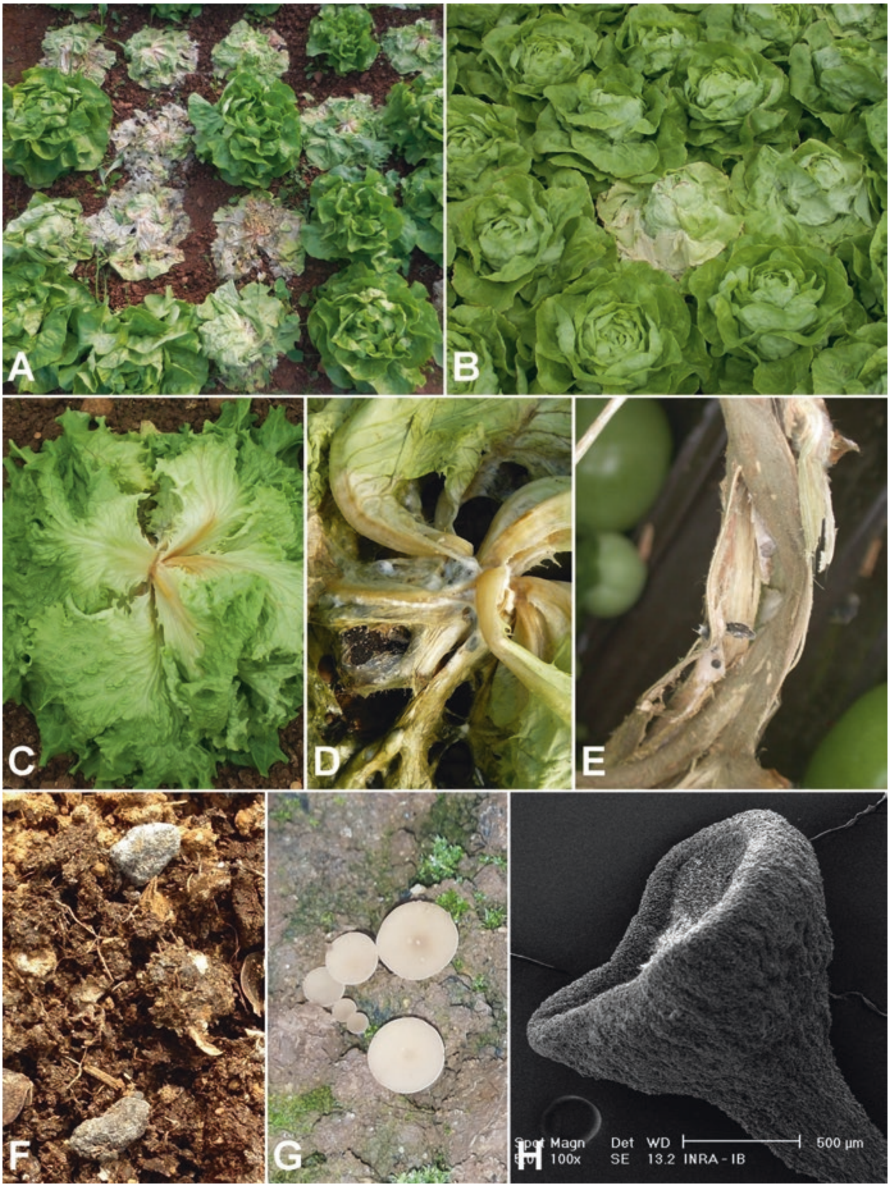

Fig. 3.7 Symptoms of white mold caused by *Sclerotinia sclerotiorum* on lettuce (**a**–**d**) and on tomato (**e**). Sclerotia (**f**) and apothecia (**g**) of *S. sclerotiorum* on the soil in a greenhouse. Detail of the tip of an apothecium by electron scanning microscopy (**h**)

3.4.2 Pythium *and* Phytophthora

Numerous species of *Pythium* and *Phytophthora*, belonging to the phylum *Oomycota*, are responsible for soil-borne diseases worldwide and on various greenhouse crops, including tomato, lettuce, cucumber, pepper, eggplant, carnation… (Blancard et al. 1991, 2003, 2009; Malathrakis and Goumas 1999; Li et al. 2014; Al-Sadi et al. 2011b; Van Beneden et al. 2009; Bolton 1984). *Pythium aphanidermatum* has retained particular attention and analysis of population structure reveals phenotypic and genotypic diversity within this species (Al-Sadi et al. 2012; Lee et al. 2010). These fungal-like organisms cause damping-off and root rots on plantlets in nurseries or on adult plant in soil or soilless conditions. These zoospore-producing microorganisms are particularly well adapted to aquatic environments so that to hydroponic conditions and their growth can be favored by the recirculation of the nutrient solution (Vallance et al. 2011; Menzies et al. 1996). In these conditions, zoospores can spread quickly from plant to plant (Li et al. 2014). It can be particularly damaging in soilless crops such as tomato (Blancard et al. 2009) or cucumber (Menzies et al. 1996).

These microorganisms can survive as saprophytes in the soil. Primary inoculum of *Pythium* species generally come from contaminated soils introduced into greenhouses via soil mixture, cultivation equipment, growers' shoes and reused irrigation pipes (Al-Sa'di et al. 2008). Larval stages and in a lesser extent adult stages of the fungus gnats insects can transmit *Pythium* sp. between plants (Jarvis et al. 1993). Pythium species are generally tolerant to high-temperatures, even though low temperatures can enhance the disease (Pivonia et al. 2012).

These pathogenic microorganisms are usually controlled by disinfection methods but such methods are only effective as preventive measures (Blancard et al. 2003, 2009). In recirculating hydroponic systems, root diseases caused by *Pythium* can be suppressed by filtrations through membranes or biofilters (Schuerger and Hammer 2009; Deniel et al. 2006; Goldberg et al. 1992). In soil greenhouses, solarization and biofumigation can reduce the incidence of damping-off (Deadman et al. 2006; Blancard et al. 2003, 2009). Plant nutrition with mineral or organic fertilizers, compost, silicon can induced resistance of plant to *Pythium* and *Phytophthora* (Mohaghegh et al. 2011; De Corato et al. 2016; Gilardi et al. 2014; Vestberg et al. 2014). Some fungicides exhibits inhibitory activity against plant-pathogenic oomycetes (Miao et al. 2016; Utkhede et al. 2000). Biocontrol methods using microorganisms or plant extracts have been widely studied resulting in the development of registered biopesticides (Paulitz and Belanger 2001; Gwynn 2014; Utkhede et al. 2000; Sabaratnam and Traquair 2015; Gilardi et al. 2014; Postma et al. 2013; Liu et al. 2009; Postma et al. 2009; Ghasemi et al. 2012). Coating of seeds with biocontrol agents or phosphonate can also be useful in the management of *Pythium* damping-off on cucumber or tomato (Kipngeno et al. 2015; Abbasi and Lazarovits 2006). To our knowledge, there is no resistance in vegetable and ornamental cultivars but rootstocks was shown to induce resistance to the disease, for instance against *Pythium aphanidermatum* on cucumber (Al-Mawaali et al. 2012).

3.4.3 **Rhizoctonia** ***Stem Rot***

The necrotrophic fungus *Rhizoctonia solani* (teleomorph *Thanatephorus cucumeris*) is a basidiomycota fungus that causes stem rot and root rot worldwide on numerous greenhouse crops including tomato, cucumber, bean, eggplant, pepper, carnation… (Yildirim and Erper 2017; Al-Sadi et al. 2011b; Blancard et al. 2009; Misawa and Kuninaga 2010; Malathrakis and Goumas 1999). It generally causes damping-off and can also occasionally cause foliar blight on tomato (Ivors et al. 2009). At least ten anastomosis groups (AG) and numerous sub-groups have been determined and differences in aggressiveness depending on the anastomosis groups or sub-groups have been identified on specific plant species (Pourmahdi and Taheri 2015; Yildirim and Erper 2017; Trujillo et al. 1988; Blancard et al. 2009; Yildiz and Doken 2002). Hypovirulent strains of the fungus have also been isolated (Cardinale et al. 2006). The fungus can survive as sclerotia and mycelia on plant debris in the soil. It can develop on various soils in a wide range of temperature from 5 to 36 °C (Blancard et al. 2009).

In infested soils, disinfection with fumigants or by solarisation can be envisaged (Blancard et al. 2009). In plant nurseries, diseased plants should be remove and fungicides can be applied (Blancard et al. 2009). Seed treatment (Kataria et al. 2002) or drench application of chemicals (Vatchev and Maneva 2012) has been successfully used to control the disease in greenhouse cucumbers. Diversity in cultivar sensitivity has been observed on tomato (Yildiz and Doken 2002) and partially resistant transgenic tomato plants have been created (Elad et al. 2012). Biocontrol of *R. solani* has been widely studied (Lewis et al. 1990), and different *Trichoderma* strains have shown protective efficacy on various greenhouse-grown crops (Lewis and Lumsden 2001) including tomato (Strashnov et al. 1985; Malolepsza et al. 2017; Youssef et al. 2016; Montealegre et al. 2014), cucumber (Caron et al. 2002), melon (Abdel-Kader et al. 2017), or carnation (Elad et al. 1981). Antagonistic bacteria have also been identified (Zohora et al. 2016; Youssef et al. 2016; Solanki et al. 2014, 2015; Goudjal et al. 2014; Sabaratnam and Traquair 2002; Lee et al. 2011). Biocontrol agents can be delivered through a drip irrigation system (De Curtis et al. 2010) and they can be applied in combination (Roberts et al. 2005; Berta et al. 2005). Other products such as formulated peppermint and oregano oils (Helal 2017), composts (De Corato et al. 2016), biochar (Jaiswal et al. 2014), methanolic garlic extract (Mostafa et al. 2013), seaweeds (Sultana et al. 2011) significantly minimized the pathological symptoms caused by *R. solani* on various plants. Several biopesticides, including species of *Trichoderma*, *Pseudomonas* or *Streptomyces* have been registered worldwide to control *Rhizoctonia* (Paulitz and Belanger 2001; Gwynn 2014).

3.4.4 Corky Root Rot of Tomato

The *Ascomycota* fungus *Pyrenochaeta lycopersici,* causal agent of corky root, is an important soilborne disease of tomato and other solanaceous crops including eggplant. Isolates from this fungus are classified into two types on the basis of physiological and molecular features (Bayraktar and Oksal 2011; Hieno et al. 2016). Recent population structure analysis using molecular markers revealed that three molecular groups can be identified (Infantino et al. 2015). PCR-based assay has been settled to detect *P. lycopersici* (Infantino and Pucci 2005) and a loop-mediated isothermal amplification method (LAMP) was developed to identify Type 1 and Type 2 isolates (Hieno et al. 2016). *Pyrenochaeta lycopersici* attacks the root system of the tomato, revealing browning and corky lesions on the cortex (Blancard et al. 2009). The consequence of root infection is a limitation of the development of the plant, a possible drying and falling of leaves.

During penetration of the fungus inside root cells, several molecules that might favour infection of host species are secreted by the fungus, such as toxic compounds (Fiume and Fiume 2003), endoglucanase (Valente et al. 2011) and proteinaceous inducer of cell death (Clergeot et al. 2012). Complete genome sequence of the fungus will provide molecular and genetic basis to better understand fungal lifestyle, pathogenic behaviors and increased genetic diversity of this fungus (Aragona et al. 2014).

Pyrenochaeta lycopersici can survive in the soil several years on plant debris thanks to mycelium and chlamydospores (Blancard et al. 2009). The fungus has been recovered in tomato root debris for up to 33 month after they were buried in the soil (Shishkoff and Campbell 1990). The optimal in vitro growth temperature of isolates of *P. lycopersici* is 23 °C (Infantino et al. 2003). Cool temperatures between 16 and 21 °C improve root infection, lesion expansion and symptom development (Augustin et al. 2002; Shishkoff and Campbell 1990). Severity of the disease increases with increasing nitrate and ammonium concentrations in soil and with total nitrogen in tomato tissue when ammonium nitrate fertilizer was added (Workneh and Vanbruggen 1994).

In sunny countries, reduction of corky root infection on tomato can be achieved by soil solarisation in greenhouse (Diaz-Hernandez et al. 2017; Vitale et al. 2011; Ioannou 2000). Resistance to *P. lycopersici* have been observed in wild tomato genotypes and genes for resistance have been identified (Doganlar et al. 1998; Blancard et al. 2009). Grafting on corky root-resistant rootstocks provides also a high level of protection against *P. lycopersici* (Ioannou 2001; Giotis et al. 2012). Other alternative methods have been tested with some success for the control of corky root of tomato, such as acibenzolar-S-methyl (Bubici et al. 2006), *Trichoderma harzianum* (Sanchez-Tellez et al. 2013; Perez et al. 2002), *Streptomyces* spp. (Bubici et al. 2013; Minuto et al. 2006), chitin soil amendments (Giotis et al. 2012), compost with low NH(4)-N concentration and high Ca concentration (Hasna et al. 2007, 2009), fermented extracts of composted plant materials (Pane et al. 2012).

3.5 Future Prospects

Fungal diseases remain a serious phytosanitory concern in most greenhouse vegetable and ornamental crops. Control strategies of these plant diseases still rely on the use of chemicals but transition to integrated pest management (IPM) is in progress in many countries worldwide, which should ensure the reduction of pesticides and encourage natural mechanisms for pest management. This will constitute a challenge for the future of crop protection against fungal diseases.

Moreover, new and re-emerging fungal diseases are potential threats to these productions in many areas. Appropriate means of avoidance should be prepared in advance of these outbreaks, and innovative methods of protection should be rapidly developed and implemented. Continuous and thorough monitoring of fields and greenhouses, using sensitive and reliable diagnostic tools, is essential for achieving these goals.

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Chapter 4
Insect and Mite Pests

Markus Knapp, Eric Palevsky, and Carmelo Rapisarda

Abstract Insect and mite pests are a major constraint to greenhouse production of vegetables, fruits and ornamentals. As the abiotic conditions in greenhouses are relatively stable and uniform in most parts of the world, the insect and mite pest fauna is dominated by a relative small number of usually polyphagous species. Many of these pests have a worldwide distribution. This chapter provides an overview of the most important insect and mite pests in protected cultivation and a brief summary on control options. The following groups are covered: gall mites (Eriophyidae), spider mites (Tetranychidae), flat mites (Tenuipalpidae), tarsonemid mites (Tarsonemidae), thrips (Thripidae), whiteflies (Aleyrodidae), aphids (Aphididae), scale insects (Coccoidea), caterpillars (Lepidoptera), dipteran leafminers (Agromyzidae), sciarid flies (Sciaridae) and beetles (Coleoptera).

Keywords Gall mites · Spider mites · Flat mites · Tarsonemid mites · Thrips · Whiteflies · Aphids · Scale insects · Caterpillars · Dipteran leaf miners · Sciarid flies · Beetles

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4.1 Introduction

Greenhouses are designed to optimize plant growth. However, it is not only plants that benefit from the stable conditions in greenhouses but also their pests. In addition, greenhouses often provide herbivores with a nearly unlimited amount of host plants in monoculture and natural regulating factors such as predators, parasitoids and pathogens are lacking. Herbivores that are accidentally introduced into greenhouses or migrate into greenhouses through open vents will most likely find almost all biotic and abiotic conditions in favor of rapid population increase during most of the months of the year. Hence, herbivores from several insect and mite orders have obtained pest status in greenhouse crops. Although belonging to various taxonomic groups, the major greenhouse arthropod pests share several traits in their biology that allow them to quickly exploit ephemeral but extremely favorable habitats. They are usually polyphagous, are able to develop continuously with no diapause, and have high rates of population increase (Brødsgaard and Albajes 1999; Pilkington et al. 2010). On the other hand, greenhouse structures can also be used to minimize the risk of invasion of pests from the surrounding environment for instance by covering the vents and entrances with insect netting (Weintraub et al. 2017a).

Many of the major greenhouse pests are characterized by high pesticide resistance levels (Bass et al. 2015; Bielza 2008; van Leeuwen et al. 2010) and have a global distribution. Through the intensive international trade in plant material, pests can spread from their area of origin and reach a nearly cosmopolitan distribution in relatively short time. This has happened for instance with the western flower thrips, *Frankliniella occidentalis* (Pergande), which started to spread from the western US in the 1970s and 80s (Mouden et al. 2017), or more recently with the South American tomato pinworm, *Tuta absoluta* (Meyrick), which was found for the first time outside South America in 2006 in Spain. From there it spread rapidly and it is now present throughout Europe, Africa, the Middle East as well as parts of Asia (Campos et al. 2017). In this chapter a brief review of the major insect and mite pests in protected culativation wordwide and the current status of their control is provided follewd by some ideas on future development. The pests are discussed in order of their systematic postion.

4.2 Major Mite and Insect Pests

4.2.1 Gall Mites – Tomato Russet Mite

Mite species within the super family Eriophyoidea, belonging to the order Trombidiformes, live exclusively on plants. Many species of Eriophyidae, the largest of the three eriophyoid families, form galls, and thus are known as gall mites (Lindquist and Amrine 1996). There are, however, many other species which live freely on the plant surface. These species are called vagrants, as opposed to the gall-formers. The damage caused by eriophyid mites varies enormously depending on the species and can include curling of leaf edges, blistering of leaves, swollen buds, galls, and silvering or browning of leaves and stems. Some eriophyid species transmit viruses (Oldfield and Proeseler 1996). While several species cause substantial economic damage to orchards and vineyards, the only important eriophyid pest in greenhouses is the tomato russet mite *Aculops lycopersici* (Tryon) (Duso et al. 2010; Messelink 2014). It does not produce galls but lives freely (vagrant) on tomato plants. *Aculops lycopersici* was detected for the first time in Australia and is a pest in tomatoes in all areas where they are grown (Massee 1937; Brust and Gotoh 2018). Other members of the plant family Solanaceae may be affected to a lesser extent (Brust and Gotoh 2018). The severity of damage caused by *A. lycopersici* in European greenhouse tomato production has increased dramatically during the last few years and control is becoming increasingly difficult as the mites are developing resistance to the few acaricides available (van Houten et al. 2017).

4.2.1.1 Life Cycle and Appearance

Nymphs and adults of the tomato russet mite are extremely small and have only two pairs of legs, whereas other mite groups have four pairs. Eggs, roughly 0.05 mm in diameter, are laid on the underside of leaves, on leaf petioles, and on stems on the lower portion of plants. The mites have two nymphal stages, and adult males and females. All stages are cream to orange-yellow in color. The females are wedge-shaped and very small (roughly 0.17 mm in length), with males being slightly smaller than the females (Van der Ent et al. 2017; Brust and Gotoh 2018).

4.2.1.2 Population Development

Optimal temperature for population growth was observed to be approximately 27 °C, as at higher temperatures fecundity and juvenile survival decreased. At 30 °C females laid up to 3.5 eggs per day and at 25 °C fecundity was 51.7 eggs in total (Haque and Kawai 2003). Fertilized eggs give rise to both males and females, whereas unfertilized eggs produce only males (Sabelis and Bruin 1996).

4.2.1.3 Damage

The damage is first seen on the lower part of the plant and moves upwards as the mites ascend (Gerson and Weintraub 2012). Damage is caused by mites feeding on epidermal cells (Royalty and Perring 1996). Affected leaves are slightly curled and damaged surfaces acquire a silvery sheen on the underside. Later they become brown and brittle. Badly affected tomato leaves and stems lose their trichomes (Van Houten et al. 2013). Affected stems turn a rusty brown color, and in serious cases they may snap. The fruit can also be affected, and when this happens in tomatoes, the skin becomes coarse and turns reddish brown and the fruit itself is sometimes deformed. Recent research has shown that the interaction between drought stress and the manipulation of plant defenses by the pest results in higher tomato russet mite populations and subsequent damage (Ximénez-Embún et al. 2017b).

4.2.1.4 Monitoring and Control

The tomato russet mite spreads through a crop mainly on air currents. When plants begin to die, the mites often congregate on the highest parts of the plant where they are picked up by the wind more easily. However, they can also walk from one plant to the next, especially where leaves touch each other, or be dispersed on clothing and other materials (van der Ent et al. 2017).

Although several commercially available predatory mites, such as *Amblyseius swirskii* Athias-Henriot (Park et al. 2010) and *Amblydromalus limonicus* (Garman & McGregor) (Van Houten et al. 2013), feed and develop on tomato russet mite on leaves in laboratory trials, biological control in greenhouses has not been successful so far. This is mainly due to the glandular hairs of tomato plants, which impair movement of predatory mites, releasing sticky and toxic substances when they are touched by predatory mites, and providing a sort of 'forest' for the russet mites to hide in.

4.2.2 Spider Mites

Spider mites is the common name of mites belonging to the family Tetranychidae and order Trombidiformes. Spider mites are pests that present a threat to many vegetable and ornamental crops throughout the world. Cucurbits, beans, and a variety of foliage and flowering ornamental plants are among the most affected crops in greenhouses. Under intensive chemical control, many other crops, such as tomatoes, maybe severely infested by spider mites. Despite their small size, they are capable of causing severe damage very rapidly due to their high reproductive capacity (Shih et al. 1976). There are more than 1300 species worldwide (Migeon and Dorkeld 2006), many of them are common crop pests. The two-spotted spider mite, *Tetranychus urticae* Koch, is by far the most important species in greenhouses (Gerson and Weintraub 2012; Gerson and Applebaum 2018) and many outdoor crops and is found worldwide (Migeon and Dorkeld 2006). Its genome was published in 2011, and it was the first chelicerate to be fully sequenced (Grbic et al. 2011). *Tetranychus cinnabarinus* Boisduval, considered a synonym of *T. urticae*, is a red morph of this polymorphic species (Auger et al. 2013). *Tetranychus evansi* Baker & Pritchard, the tomato spider mite, has received considerable attention over the last decade with respect to global distribution as an invasive species (Boubou et al. 2011; Brust and Gotoh 2018), reproductive performance (Gotoh et al. 2010), manipulation of plant defense (Ataide et al. 2016), and biocontrol (Furtado et al.

2007; Maniania et al. 2016). Originating in the Americas it has spread to Africa, Europe and Asia (Migeon et al. 2015), causing considerable damage to solanaceous crops primarily in Africa (Knapp et al. 2003; Azandémè-Hounmalon et al. 2015).

4.2.2.1 Life Cycle and Appearance

Adult female spider mites are about 0.5 mm long. They have an oval body that is rounded at the rear end. Males are smaller and more active than the females, with a body that is narrower and more pointed at the rear. Color is very variable: from light yellow or orange to dark yellow or brown. The red eyes can be seen in all stages. For *T. urticae* the color of the adults often depends on the crop in which they occur (e.g. on cucumbers they are often yellow-brown, on tomatoes they are mainly red-brown). Both males and females of *T. urticae* usually have two large black spots, giving rise to the common name, "two-spotted spider mite". By contrast, in *T. evansi*, usually pests of only solanaceous plants, adults are orange-red with less pronounced spots. Spider mites go through five developmental stages: egg, larva, protonymph, deutonymph and adult. In the larval and nymphal stages, an active period and a resting period of roughly equal duration can be distinguished. In the resting period the mites do not move or feed and the next stage develops within the cuticle of the current stage. Eggs are round and usually found on the underside of leaves. Larvae have only three pairs of legs, protonymphs, deutonymphs and adults have four pairs (van der Ent et al. 2017).

4.2.2.2 Population Development

Spider mites reproduce via arrhenotokous parthenogenesis (Helle and Sabelis 1985). Unfertilized eggs develop into haploid males while diploid females are produced biparentally from fertilized eggs, with a female biased sex-ratio for *T. urticae* (Carey and Bradley 1982) and *T. evansi* (Bonato 1999). Population growth of spider mites is driven by temperature (Bounfour and Tanigoshi 2001) and can be affected by plant host (Krips et al. 1998; Kasap 2004). *Tetranychus urticae* population development is also substantially higher at low humidity and drought stressed plants are more susceptible to both *T. evansi* and *T. urticae* (Ximénez-Embún et al. 2016, 2017a). Shortest reported developmental time for *T. urticae* was at 30 °C whereas for *T. evansi* it was at 36 °C while optimal conditions for population development were 25 °C and 40% relative humidity for *T. urticae* and 31 °C for *T. evansi* (Hazan et al. 1974; Bonato 1999; Bounfour and Tanigoshi 2001).

When plants are heavily infested, mites fall to the ground and walk to other plants, or migrate to new plants along crop wires (Nachman and Zemek 2002) or from one leaf to another if plants are touching each other. They also produce silk threads on which they can "rope-down" to the ground, or to other leaves or plants. Long-range dispersal is by wind. To achieve this, adult female mites migrate to the top of the plants and sit in a position exposed to the wind (Kennedy and Smitley 1985).

Mites can also be inadvertently dispersed mechanically, either by the movement of infected plant material, or on clothing and other objects. Despite the ease of dispersal, spider mites often appear locally in greenhouses in particular spots. Such spots may have more favorable (drier, warmer) conditions for spider mites.

When environmental conditions deteriorate in temperate regions, female *T. urticae* enter diapause. The major factor inducing diapause is decreasing day length (Veerman 1977; Takafuji et al. 1991). Falling temperatures and deterioration in food supply also play a role (Hussey 1972). Females entering diapause become orange-red. They overwinter hidden within the structure of the greenhouse, or in other concealed spaces. During diapause, they do not eat, lay no eggs, and are less susceptible to pesticides. When conditions become more favorable again in spring, the females become active and resume egg-laying. Where days do not become short enough to initiate diapause, i.e. at lower latitudes or in greenhouses with artificial lighting, *T. urticae* reproduces throughout the whole year.

4.2.2.3 Damage

Spider mites are phytophagous and feed on several parts of the plant, mainly on the underside of leaves, by piercing the tissue with stylets and sucking epidermal and mesophyll cell contents, which can cause significant reductions in photosynthetic rate, total chlorophyll content, and greenness of the leaf (Park and Lee 2002). *Tetranychus urticae* damage is accompanied by physiological alterations in the plant, resulting in biomass reductions and significant decreases in economic yield (Park and Lee 2005).

4.2.2.4 Monitoring and Control

Various sampling methods have been developed for monitoring spider mites in different cropping systems, all requiring trained scouts and the respective time to scout, count and process the data (e.g. Nachman 1984; Gacheri et al. 2015). Remote sensing of spider damage has been studied in outdoor crops (Nansen et al. 2013) with the aim of quickly identifying hot spots, thereby reducing costs of labor for monitoring and limiting the application of pesticides or biocontrol to the infested hot spots. Recently these precision agriculture methodologies have been studied in greenhouses (Martin et al. 2015; Herrmann et al. 2017) and we expect that they will soon be used in greenhouses for pest and disease monitoring as well for the application of both chemical and biological control measures.

The availability of the whole genome of *T. urticae* has transformed this mite to a model organism for studies on mode of actions and resistance mechanisms (Demaeght 2015; van Leeuwen et al. 2015; Snoeck et al. 2017). As more mechanisms of resistance are being revealed (Bajda et al. 2017; Pavlidi et al. 2017) it is becoming apparent that biological control is the only permanent and durable method with which to control spider mites in greenhouses. The most effective biocontrol agents are the predatory mites, *Phytoseiulus persimilis* Athias-Henriot and *Neoseiulus californicus* (McGregor) (Gerson and Weintraub 2007), and the predatory gall midge, *Feltiella acarisuga* (Vallot) (Mo and Liu 2006).

4.2.3 Flat Mites

Mites of the family Tenuipalpidae are known as false spider mites because they closely resemble spider mites (family Tetranychidae) or as flat mites because their body is rather flat compared to other mites. Tenuipalpidae, belonging to the order Trombidiformes, have a worldwide distribution (Mesa et al. 2009) with over 1100 species belonging to 38 genera (Beard et al. 2012) and can be found on many cultivated plants. Compared to spider mites (Tetranychidae) the flat mites have been understudied (Gerson 2008). On many host plants, flat mites are overlooked as they remain at low densities and do not cause economic damage. However high populations of several species can be responsible for extensive economic damage. For example, the red palm mite *Raoiella indica* Hirst is a serious pest of coconut, areca palm, banana and ornamentals (Flechtmann and Etienne 2004; Kane et al. 2012). *Brevipalpus* species attack fruit trees and ornamentals (Childers et al. 2003b) and are responsible for vectoring viruses (Kitajima et al. 2010, Childers and Rodriguez 2011). Several viruses composing the Leprosis complex cause significant reduction to yield and decline of citrus trees (Roy et al. 2015). Care must be taken to avoid misidentification of *Brevipalpus* species as more than one species can co-occur on the same leaf and species are difficult to distinguish even for experts. As an example of the taxonomic complexity of this group, the *Brevipalpus phoenicis* (Geijskes) complex was separated into eight species recently (Beard et al. 2015). The same authors have developed web based digital keys to flat mite genera of the world and species of *Brevipalpus*, *Raoiella* and *Cenopalpus* (Beard et al. 2012). Species of *Tenuipalpus* also have a wide host range (Hatzinikolis 1986; Pontier et al. 2000), and are important pests of orchids and ferns (De Moraes and Freire 2001; Cating et al. 2010; Denmark 2012).

4.2.3.1 Life Cycle and Appearance

Most false spider mites are brick-red to yellow in color. They have the same body shape as spider mites but are usually smaller (around 0.25–0.3 mm in length). The different species all look very similar. False spider mites pass through the same developmental stages as spider mites: egg, larva, protonymph, deutonymph and adult (Childers et al. 2003a). They move slowly and are mostly found along the veins on the underside of leaves. The mites are flattened and egg-shaped when seen from above, with their dorsal surface showing a net-like pattern. The legs appear crumpled. The eggs are a clear red color and elliptical. They are usually laid in a fold in the leaf or along the mid-vein, often in dense clusters laid by different females (van der Ent et al. 2017).

4.2.3.2 Population Development

The development time of false spider mites is longer than that of spider mites and depends on temperature, relative humidity, and host plant. For example, egg to adult development at 25 °C and 70%RH of *B. phoenicis* was faster on citrus than on coffee leaves (17 vs. 25 days, respectively). Similarly, longevity and fecundity were also higher on citrus than on coffee leaves (Teodoro and Reis 2006). Reproduction is for the most part parthenogenetic, with females producing almost only female progeny, and males occurring only in very small numbers (Childers et al. 2003a).

4.2.3.3 Damage

False spider mites are usually found on the underside of leaves where they cause a brown, scabby discoloration spreading from both sides of the main vein into the leaf blade. The damage often leads to premature ageing of the plant and leaf drop. In some crops, plants can become misshapen, presumably because the mites secrete toxic saliva into the plant while feeding. In places where mites have been feeding, sunken patches can often be found (Childers and Rodrigues 2011). *Brevipalpus phoenicis* also feeds on fruits of, for instance, citrus (Vacante and Gerson 2011). Unlike most true spider mites, false spider mites do not produce webs.

4.2.3.4 Monitoring and Control

As flat mites are small and slow moving, dispersal by walking is expected to be very limited. Deteriorating conditions of the host plant and overcrowding can stimulate wind dispersal of mature females. Additionally, the mites can be dispersed by people working in the crop and by distribution of infested fruits and plants (Childers and Rodrigues 2011). In this regard, it is interesting to note the speed and area of dispersal of the invasive species *R. indica*. Since its arrival in the Caribbean it has spread in less than a decade through the Caribbean, Florida, Mexico, Columbia and Brazil (Kane et al. 2012). On greenhouse grown ornamentals *Brevipalpus* spp. can be controlled with *A. swirskii* Athias-Henriot. Good results have been achieved for instance in *Phalaenopsis*, palms and *Schefflera* sp. (van der Ent et al. 2017).

4.2.4 Tarsonemid Mites

Mites of the family Tarsonemidae (tarsonemids), belonging to the order Trombidiformes, display a greater diversity of feeding habits than the families discussed above. There are species that feed on fungi, algae, plants, as well as mite predators and parasites of insects. Tarsonemids are only 0.1–0.3 mm long and difficult to observe. Those living on plants can cause considerable damage to their host. Unlike spider mites and gall mites, phytophagous tarsonemids need a high relative humidity (at least 70%) in order to survive (Jones and Brown 1983). Tarsonemids can occur both on vegetable and ornamental crops. The most prevalent species in greenhouse crops are the broad mite *Polyphagotarsonemus latus* (Banks) and the cyclamen mite *Phytonemus pallidus* (Banks) (Zhang 2003). *Polyphagotarsonemus latus* occurs in the tropics and in greenhouses in temperate regions. The broad mite has a very wide range of host plants, including peppers, eggplants, tomato, cucumber and many ornamental crops such as azalea, begonia, gerbera and cyclamen (Gerson 1992). Generally, in temperate climates, broad mite is not considered a problem in outdoor crops since it is unable to overwinter. Interestingly, since 2007 broad mite has been recorded as a pest on primocane-fruiting blackberry in Arkansas and several other US states, thereby demonstrating its ability to overwinter in a moderate temperate climate (Johnson et al. 2016; Rebek 2017). *Phytonemus pallidus* is a harmful strawberry pest as well as a common pest found in cyclamen, gerbera and other ornamentals. Evidently it has been moved across the globe on unopened leaflets and on the tubers of cyclamen (Denmark 2000).

4.2.4.1 Life Cycle and Appearance

The life cycle of *P. latus* and *P. pallidus* consists of egg, larva and adult. The larvae remain in their larval cuticle as a quiescent nymph for 1 or 2 days. The male uses its modified fourth pair of legs to carry the young pharate females (quiescent nymphs). The hind legs of females are reduced to slender threadlike structures. Mating occurs as soon as the adult female emerges from the larval cuticle. Female broad mites lay their eggs mainly on the underside of the leaf or on the fruit surface. The oval eggs are strongly attached to the surface and are rather large (about 0.07 mm) compared with the subsequent, active stages. They are transparent and speckled with white dots. The larva of the broad mite resembles the adult, but is slightly smaller and has only three pairs of legs. The adult female mite is roughly 0.2 mm long, oval, yellow-green, with a white stripe on its back. Males are smaller than the female, with a body that tapers towards the rear end. They have longer legs, and lack the white stripe (Fasulo 2000; Peña and Campbell 2005). Adult females of *P. pallidus* are yellowish brown and about 0.25 mm long. The males are smaller than the females. Eggs of the cyclamen mite are about half the size of the adult mite, oval in form, smooth and transparent. The larvae are opaque white and have only three pairs of legs (Zhang 2003).

4.2.4.2 Population Development

The development of *P. latus* is short compared to other mite pests. On azalea, female development was completed in approximately 14 days at 15 °C and 4 days at 25 °C (Luypaert et al. 2014). Fertilized eggs produce females, whilst unfertilized eggs produce males (Gerson 1992). Cyclamen mites avoid light. They require high humidity and are usually found in young unfolded leaves of their host plants. Under favorable conditions (20–25 °C and high relative humidity), the egg to adult development takes 9–12 days. Females can live up to 45 days and lay 25–30 eggs (Easterbrook et al. 2003). Under greenhouse conditions, all stages of the mite can be found throughout the year. Adult female mites are capable of overwintering outdoors in temperate areas, usually in the crown of strawberry plants, between folded leaves, or in buds. Sex determination is known to be complicated in *P. pallidus*. In addition to normal haplodiploidy, unfertilized females of some populations can produce male and female progeny, whereas other populations are known to be thelythokous (Zhang 2003).

4.2.4.3 Damage

The damage caused by *P. latus* can look similar to that caused by viruses or herbicides and was in the past confused with disease symptoms. The mechanism causing this deformation is not yet fully understood (Gerson 1992). *Polyphagotarsonemus latus* feeds on the epidermis, but structural and ultrastructural studies revealed aberrations in the whole leaf tissue. Severe infestation leads to a complete loss of epidermis and an increase in mesophyll cell size and number. The mites show a preference for young, developing plant tissue, like the growing tips, young leaves and flower buds. When plants are severely attacked, the growing tip can be killed, plant growth stops and, in time, the whole plant dies off (Grinberg et al. 2005). *Phytonemus pallidus* is also mostly found within flower buds, growing tips and young folded leaves where the humidity is highest and they are protected from direct sunlight. Infested leaves are twisted or curled, distorted, brittle and smaller than normal. In cyclamen and gerbera, the flowers are deformed and discolored and leaf growth is inhibited. Gerbera leaves turn bronze, mainly along the midrib. With heavier infestations plant growth is arrested and the flower buds eventually shrivel and die. Damaged strawberry leaves are wrinkled and irregularly folded. Affected plants have an unnaturally dense appearance because the petioles remain short. Severely attacked leaves become brittle, turn brown or silvery and die. Flowers and young fruits become brown near the base (Jeppson et al. 1975; Gratwick 1992).

4.2.4.4 Monitoring and Control

Male broad mites and cyclamen mites carry the pharate females within the plant. Mites can be moved from plant to plant by workers tending the crop and between crops on wind currents. Additionally, the wax of whiteflies serves as a cue for female broad mites to board their insect vectors, allowing them to abandon spent hosts and seek out new ones (Palevsky et al. 2001; Soroker et al. 2004). Cyclamen mites can migrate towards the base of the host plant, when the conditions in the plants become less favorable (drier, for example), returning when conditions improve again. Several commercially available predatory mite species can control *P. latus* in greenhouses; the best results have been achieved with *A. swirskii* (Weintraub et al. 2003; Jovicich et al. 2008; van Maanen et al. 2010; Onzo et al. 2011; Rodríguez-Cruz et al. 2017) and contribute to the control of cyclamen mite (Croft et al. 1998; Easterbrook et al. 2001; Tuovinen and Lindqvist 2010). Removal of affected plants or plant parts and lowering the relative humidity can contribute to the control of *P. latus* (van der Ent et al. 2017).

4.2.5 Thrips

Thrips are insects belonging to the order Thysanoptera, a name that literally means 'fringed wings', and refers to the eyelash-like fringe of hairs along both edges of the thin wings. There are more than 6000 species among which half are phytophagous, most harmless, and fewer than 20 species can cause serious economic damage in greenhouses. Despite the limited number of pest species, thrips are among the most important pests in greenhouse crops all over the world. This is mainly due to the spread of insecticide resistant tropical or subtropical polyphagous species into greenhouse crops in temperate regions, often through the trade in ornamentals and other plant material (Morse and Hoddle 2006; Reitz 2009). Due to their small size and their tendency to seek out narrow spaces to live in, they are often overlooked by quarantine services and growers. The most damaging species are *Frankliniella occidentalis* (Pergande), *Thrips tabaci* Lindeman, *Thrips palmi* Karny and *Echinothrips americanus* (Morgan) (Jenser and Szenasi 2004; Cannon et al. 2007; Reitz 2009; Zhu et al. 2017; Weintraub et al. 2017a). Another species that originates from southern Asia and has recently spread to the northern hemisphere is the chili thrips *Scirtothrips dorsalis* Hood, which is now present in Florida, Israel, Spain and Great Britain (Dickey et al. 2015; EPPO 2017). Other species are pests of ornamentals and vegetables of local importance but are rarely widely distributed. For more information see Lewis (1997) and Moritz et al. (2004).

Frankliniella occidentalis, the western flower thrips, is the most important thrips pest world-wide. Its original distribution area was in the western USA, but it spread during the 1970s and 80s and has obtained an almost cosmopolitan distribution in greenhouse crops (Mouden et al. 2017). This spread occurred predominantly by the movement of horticultural material, such as potted plants, cuttings and seedlings

(Morse and Hoddle 2006, Reitz 2009). *Thrips tabaci* probably originates from the Middle East but is now a cosmopolitan pest both in greenhouse and outdoor crops (Jenser and Szenasi 2004). *Thrips palmi* originates from Sumatra, and it is widespread in Asia and the Pacific and also found in Florida, the Caribbean as well as parts of South America, Africa and Australia (Akella et al. 2014). *Echinothrips americanus* is native to eastern North America. In recent decades, it has spread rapidly into several European and Asian countries (Zhu et al. 2017).

4.2.5.1 Lifecycle and Appearance

All major plant-damaging thrips are small insects with an adult size of 1–1.5 mm. They develop through six stages: the egg, two larval instars, a prepupa and a pupa, and the adult insect. The eggs are laid into the plant tissue of leaves, flower petals and in the soft parts of stalks. The larvae are smaller than the adults and lack wings. In the pre-pupae and pupae, the developing wing buds can be seen and the adults have two pairs of fully developed wings (van der Ent et al. 2017). A detailed description of the anatomy of thrips can be found in Moritz (1997). Depending on the species, thrips pupate in the ground, on plant debris or on the plant. *Frankliniella occidentalis, T. palmi* and *T. tabaci* usually pupate in the ground, although pupae of *F. occidentalis* can also sometimes be found on leaves or flowers and in other sheltered places. *Echinothrips americanus* spends its entire lifecycle on the plant (Cannon et al. 2007; van der Ent et al. 2017).

4.2.5.2 Population Development

Frankliniella occidentalis, *T. palmi* and *E. americanus* have a haplo-diploid reproduction mode and reproduce via arrhenotoky. Diploid females arise from fertilized eggs, whereas unfertilized eggs produce haploid males. The sex-ratio is usually female biased. *Thrips tabaci* produces females parthenogenetically in greenhouses. All four species have a high population growth rate due to their short development time and high fecundity. In *F. occidentalis*, for instance, immature development lasts about 10–15 days at 25–30 °C (van der Ent et al. 2017) and the development times for *T. palmi, T. tabaci* and *E. americanus* are in a similar range (Yadav and Chang 2014; van der Ent et al. 2017; Zhu et al. 2017). Females can live for up to 30 days. Fecundity values reported in the literature differ widely depending on host plant and experimental conditions. Around 60–50 eggs per female are common in all four species; the highest values reported are 200–300 (Li et al. 2014, 2015a, b, Yadav and Chang 2014; Ullah and Lim 2015). All four species remain active throughout the winter under mild conditions outdoors and can reproduce year-round in greenhouses.

4.2.5.3 Feeding and Damage

Thrips have piercing-sucking mouthparts. The phytophagous species feed on all aerial plant parts by puncturing epidermal and parenchymal cells, and sucking out the cell contents leaving typical grey or silvery chlorotic spots on infested plant parts. The most serious thrips pests of greenhouse crops are characterized by being highly polyphagous on both flower and leaf tissues. Their host plants include most vegetables, cereals, fruit trees and ornamentals. In greenhouses, for instance, cucumbers, peppers and eggplants, strawberries, roses, chrysanthemums and gerberas can be heavily damaged. *Frankliniella occidentalis* prefers to feed on developing plant tissues such as growing tips and flower buds. When these tissues develop further, the leaves and flowers can appear severely deformed. Heavily infested flower buds may not open at all. It is also often found in flowers where it feeds on pollen. Pollen has a strong positive effect on population development of this species (Hulshof et al. 2003; Riley et al. 2007). Fruits can also be damaged, even at low densities, giving rise to deformities such as the 'pig-tail' fruit sometimes found in cucumber crops. In many ornamental crops, even very low numbers of thrips can cause economic losses by damaging flowers (van der Ent et al. 2017). *Thrips tabaci*, *T. palmi* and *E. americanus* are found mainly on the leaves where *T. tabaci* tends to aggregate along the main leaf veins; fruit damage only occurs when crops are heavily infested. In contrast to *T. palmi* and *T. tabaci*, *E. americanus* is often found more in the lower part of plants and does not move very much. Therefore, it is found much less frequently on sticky traps and monitoring needs to be done by inspecting plants carefully (Rosenheim et al. 1990; Seal 2001; van der Ent et al. 2017).

Besides the direct feeding damage, *F. occidentalis*, *T. palmi*, *T. tabaci* and several other species are vectors of tospoviruses which infect more than 1000 plant species including many vegetables and ornamentals. Tospoviruses are considered emerging diseases and tomato spotted wilt virus (TSWV), the most damaging species, is considered one of the ten most damaging plant viruses due to its wide host range and the ubiquitous nature of the thrips vector (Rotenberg et al. 2015).

4.2.5.4 Monitoring and Control

Frankliniella occidentalis, *T. palmi* and *T. tabaci* can be monitored by colored sticky traps. Blue traps generally provide the best results. These traps can also be combined with semiochemicals to increase the number of thrips caught and at high trap densities they can also be used for mass-trapping (Gillespie and Vernon 1990; Broughton and Harrison 2012; Sampson and Kirk 2013). As *E. americanus* flies very little, sticky traps are not suitable for monitoring this species.

Because of rapid insecticide resistance build-up in several thrips species, reduced numbers of insecticides registered for use in greenhouse crops and restrictive rules imposed by governments and supermarkets on maximum residue levels of pesticides, biological control is often the only option to manage thrips in greenhouses. Biological control of thrips is generally based on the use of *Orius* spp. and predatory mites. The growing number of beneficial species makes biological control possible in many different crops and cultivation systems (van der Ent et al. 2017, see Chap. 16).

4.2.6 Whiteflies

Whiteflies belong to the family Aleyrodidae in the order Hemiptera, which includes more than 1500 species in almost 160 genera (Mound and Halsey 1978; Martin and Mound 2007). Most species have an inter-tropical distribution but several of them are also present in temperate regions, where they attack many agricultural and horticultural crops as well as forest plants, causing severe damage especially in greenhouses. Losses due to whiteflies are difficult to estimate because of the vast number of crops they attack, their extremely wide geographical distribution, the variety of cropping systems in which they can occur, and especially due their ability to transmit virus diseases, which can cause much more damage than the insects themselves (Piper 2011; Legg et al. 2014). On US vegetable crops, the United States Department for Agriculture (USDA) estimates losses between US$ 100–500 million every year, despite employing the best available technologies to control whiteflies and viruses. In temperate areas, the major whitefly species attacking greenhouse crops are the tobacco whitefly, *Bemisia* spp. gr. *tabaci* (Gennadius), and the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood). Both species are able to transmit viruses (Brown and Czosnek 2002; Jones 2003). On outdoor vegetables, damage by *Aleyrodes proletella* (Linnaeus (for consistency, see 4.2.8)) or *A. lonicerae* Walker has also been reported (Eördegh et al. 2003; Collins 2016); but these species are of secondary importance in protected cultivation.

Whitefly species belonging to the *B. tabaci* species complex are among the world's worst top 100 invasive organisms (Lowe et al. 2000; ISSG 2017) and are among the most harmful plant pests in the world, causing serious economic losses especially in tropical and subtropical regions (Legg et al. 2014). Until a few years ago, *B. tabaci* was considered a single though heterogeneous species, but recent studies show that it is a highly diverse species complex comprising more than 35 morphologically indistinguishable cryptic species which may be characterized through molecular methods only and are distributed throughout the world (De Barro et al. 2011; Boykin 2014). *Bemisia* spp. gr. *tabaci* are frequently a limiting factor to greenhouse vegetable production. Most of the infestations in temperate areas are by the Mediterranean (MED) and the Middle East-Asia Minor 1 (MEAM 1) genetic groups, known in older literature as the Q and B biotypes, respectively.

4.2.6.1 Life Cycle and Appearance

Adult whiteflies are small insects, usually 1–3 mm long, with body and wings covered by fine, usually white powdery wax, where their common name derives from. At the caudal part of their abdomen, they show a typical dorsal structure connected to the anal pore and called “vasiform orifice”, made by an “operculum” and a “lingula” that, with their movement, help to remove the honeydew drops from the anal pore (Gill 1990). Young stages (nymphs) are flattened, usually sub-elliptical and frequently covered with variously arranged waxy protrusions. They also have a dorsal vasiform orifice, which is of great importance for species identification based on morphological characters. Adults of *B.* spp. gr. *tabaci* are usually smaller than *T. vaporariorum* and, when at rest, have their wings closed at a roof-shape, compared to the broadly flattened shape shown by the resting wings of the greenhouse whitefly. Striking differences exist in the nymphs, with regard to their general shape and dimensions, the presence of dorsal papillae and setae-like waxy dorsal protrusions, and especially the more elongated vasiform orifice of *B.* spp. gr. *tabaci* compared to *T. vaporariorum*. Adult females fix their eggs with a stalk to tender plant tissue, mainly on the underside of leaves. After hatching, the mobile first instar nymphs (crawlers) move for a short while on the leaf, looking for a place to settle. Once their stylets are inserted and they start to feed, they become sedentary for the rest of their nymphal life. The fourth instar nymph hosts the adult development and therefore it is called “puparium”.

4.2.6.2 Population Development

Whitefly reproduction is usually sexual, though some species or even geographic populations of a species, as for instance in *T. vaporariorum* may reproduce parthenogenetically. Both *B.* spp. gr. *tabaci* and *T. vaporariorum* are highly polyphagous, living on a broad variety of host plants belonging to dozens of families (Mound and Halsey 1978). The development from egg to adult takes about 40 days at 20 °C and 20–22 days at 25 °C in *B. tabaci* and 33 days at 20 °C and 21 days at 25 °C in *T. vaporariorum* (Dorsman and van de Vrie 1987; Tsueda and Tsuchida 2011). In greenhouses, they have no diapause even in cold regions (Naranjo et al. 2010), where their development slows down their during the coldest months.

4.2.6.3 Feeding and Damage

Damage caused by whiteflies is both direct, due to removal of phloem sap and production of honeydew, on which sooty mold develops, and indirect by transmission of viruses. Direct damage is important especially in case of high populations. More than 300 virus species are known to be transmitted by whiteflies; they belong to various virus genera from different virus families. *Begomovirus*, as those belonging to the Tomato Yellow Leaf Curl Virus group and *Crinivirus* as for instance Tomato Chlorosis Virus or Tomato Infectious Chlorosis Virus are the most important ones injuring greenhouse crops (Cavalieri et al. 2014, see also Chap. 3).

4.2.6.4 Monitoring and Control

Control of whiteflies is difficult due to the speed of their development, their overlapping generations, as well as their capacity to acquire resistance to insecticides. Preventive methods based on exclusion from the greenhouse should to be used, such as the application of whitefly-proof (50 mesh) screens, at the greenhouse openings (Berlinger et al. 2002), or UV-absorbing covers, which interfere with flight activity and their capacity to land on the plants and transmit viruses (Antignus and Ben-Yakir 2004; Rapisarda et al. 2006). Higher efficiency can be reached by impregnating screens and nets with insecticides (Martin et al. 2014). Within greenhouses sticky traps can be used for mass-trapping of adult whiteflies. However, biological control is the most successful approach to reduce whitefly populations. In many greenhouse crops, releases of predatory mites like *A. swirskii* and *A. limonicus* are the base of whitefly control. In addition, inoculative releases of the parasitoid *Encarsia formosa* Gahan are widely used in temperate greenhouses and to a lesser extent also in warmer regions against *T. vaporariorum* (van Lenteren 2000; Albajes et al. 2003); however they do not control *B.* spp. gr. *tabaci* sufficiently in winter greenhouse crops. The parasitoids *Eretmocerus eremicus* (Rose and Zolnerowich) and *E. mundus* Mercet are used to control *T. vaporariorum* and *B.* spp. gr. *tabaci* in greenhouse crops in warm regions (Hanafi and Rapisarda 2017). In crops where predatory mites do not establish, like for instance in tomato, inoculative releases of the predatory mirids *Macrolophus pygmaeus* Rambur and *Nesidiocoris tenuis* (Reuter) can also be used. Monitoring can be carried out through the application of yellow sticky traps.

4.2.7 Aphids

Aphids, also known as “plant lice”, belong to the phloem-feeding hemipteran insect superfamily Aphidoidea, comprising approximately 5000 species of soft-bodied small insects having piercing-sucking mouth parts (Foottit et al. 2008). All species that are important pests in greenhouses belong to the family Aphididae. They have complicated heterogonic life cycles, with an alternation of sexual reproduction and parthenogenesis, which ensure respectively genetic variability and a rapid colonization of the host plants. Many polyphagous species may infest both vegetables and ornamental plants worldwide, depending on ecological conditions and cropping systems. Often they are secondary pests, but can play an important role when occurring in large populations or when associated with pathogens, especially viruses, which they can transmit. The most important species in protected cultivation are the green peach aphid, also known as peach-potato aphid, *Myzus persicae* (Sulzer), the cotton or melon aphid, *Aphis gossypii* Glover, the potato aphid, *Macrosiphum euphorbiae* (Thomas), the rose aphid, *M. rosae* (Linnaeus), and the foxglove aphid, also known as glasshouse-potato aphid, *Aulacorthum solani* (Kaltenbach) (Blümel 2004; Blackman and Eastop 2006; Sanchez et al. 2010). Despite their polyphagy, these species have certain host-plant preferences, so that some of them are prevailing on Cucurbitaceae, like e.g. *A. gossypii*, which also frequently infests ornamentals, while others live mainly on Solanaceae, for instance *Macrosiphum* spp. or *A. solani*. In extremely polyphagous species, such as *A. gossypii*, host-plant selection has been demonstrated to be related with differences in genotypes, and genetically unambiguous host races have been identified (Carletto et al. 2009; Wang et al. 2016). The currant and lettuce aphid, *Nasonovia ribisnigri* (Mosley), is a minor pest of blackcurrant and gooseberry, but the most important aphid infesting lettuce (ten Broeke et al. 2013). Various minor, but occasionally important aphid species, such as the Buckthorn-potato aphid, *Aphis nasturtii* Kaltenbach, or the mottled arum aphid, *Aulacorthum circumflexum* (Buckton) can also attack greenhouse crops (Yovkova et al. 2013; Musa et al. 2017).

4.2.7.1 Life Cycle and Appearance

Aphids are usually 2–3 mm long, with 6-segmented antennae, comparatively long and thin legs, and typical structures called siphunculi and cauda at the abdominal end. Aphid adults may be winged or apterous, with notable morphological diversity between the two forms, which have different ecological roles. The winged adults are responsible for dispersion, while the wingless forms ensure rapid colonization of the host plant. The life cycle of aphids can be very complicated, showing a sequence of sexual reproduction, with egg-laying females, and several parthenogenetic generations of viviparous females. Very often, this cycle may involve a host plant alternation, with a primary host, on which the eggs are laid for overwintering and several secondary host plants, on which parthenogenic generations occur during spring to autumn (Hardie 2017). The cycle is usually simpler in greenhouses, where only parthenogenesis occurs throughout the year by females "laying" larvae on the secondary host plants and both eggs and males are absent.

Proper identification of aphid species is important for successful biological control, but may be complicated by morphological and color variability shown by many species. *Myzus persicae* and *A. gossypii* are the most common aphids occurring in greenhouses. *Myzus persicae* varies in color from pale yellow to green or pinkish-red, but may be easily distinguished from *A. gossypii* due to its larger body size (1.7–2.3 mm vs. 0.9–1.8 mm) and by the length and color of the siphunculi, which are approximately as long as the body with blackish tips in the green peach aphid but only about on third of the body length and totally black in the cotton aphid. The latter shows a remarkable color variation, with specimens in the same colony varying from yellow to green, purplish-gray and even black, with distinctive white patches on the abdomen. *Aulacorthum solani* has a more stable shiny green color, with large dark green spots at the base of the siphunculi and black markings on the leg joints and the antennae. Adult females of this species are larger in size than those of the green peach aphid (1.8–3.0 mm) and, when disturbed, they tend to fall off the plants. *Macrosiphum* spp. are long and slender, usually green, but sometimes pink or red, with a dark longitudinal stripe, with the antennae longer than their body. They have typical long siphunculi, curved outward and light brown in color with a dark tip.

4.2.7.2 Population Development

An anholocyclic life cycle, i.e. viviparous, unfertilized females continuously producing new generations of females, is the norm in aphid populations developing in greenhouses. Females reach sexual maturity in about one week from their birth and each produces up to 100 living youngs during a reproductive period of about 3 weeks. Therefore, large populations can build up very rapidly, starting from just a few specimens landed on the crop. In greenhouses, this rapid development can make aphids producing several dozens of generations per year. The number of migratory winged aphids increases when the colony becomes overcrowded or when the food supply is depleted. Temperature has a major role in influencing development, longevity and fecundity of aphids. In *A. gossypii*, the lower threshold for preimaginal development ranges from 6 to 7 °C, depending to the stage considered, and the sum of effective temperature required from birth to the start of reproduction is 114 °C (Kocourek et al. 1994; Parajulee 2007). The time required for the development of immature stages, up to the birth of the first progeny, progressively decreases with temperature: 26 days at 10 °C, 15 at 15 °C, 8 at 20 °C and only 5 days at 25, 30 and 35 °C (Parajulee 2007). A temperature of 25 °C is optimal for the population growth of both *A. solani* and *M. persicae*, with longevity decreasing with temperature in the latter species from 45 days at 15 °C to 24 days at 30 °C (Jandricic et al. 2010; Barbosa et al. 2011).

4.2.7.3 Feeding and Damage

Damage caused by aphids to plants may be direct (loss of sap, leaf curling or deformation, production of honeydew and following development of sooty mold fungi) and/or indirect (virus transmission) (Katis et al. 2007; Quisenberry and Ni 2007). Aphids feed on plants by inserting their stylet-like mouthparts directly into the phloem and removing plant sap. While feeding, aphids excrete large amounts of sugary excrements, known as honeydew, that promotes the growth of black sooty mold fungi. These fungi cover the plant, reduce photosynthesis and downgrade the aesthetic value of fruits and ornamentals. When high aphid populations develop, plants may become stunted with curling and twisting of the young leaves, up to premature leaf fall. Some species also feed on flowers and flower buds, causing flower discoloration or abortion of the buds. Moreover, as aphids molt, their whitish cast skins may often remain on the plants, reducing the aesthetic quality of many crops. Last but not least, ants may be associated with aphid-infested plants.

Aphids are responsible for the transmission of several plant viruses (Ng and Perry 2004, see also Chap. 3). However, in greenhouse crops direct feeding damage is generally of more concern than virus transmission.

4.2.7.4 Monitoring and Control

To control aphids in greenhouses, regular scouting at a weekly base is necessary to detect their presence before populations become too high. Inspection should be directed preferably to leaf undersides and buds of the crop, but also to wild aphid-susceptible plants that might be growing in the greenhouse. Monitoring can also be done with yellow sticky traps. However, these only attract winged aphids that either have entered the greenhouse from outdoors or were produced by an already established aphid infestation in the greenhouse. Therefore, they are not a reliable indicator of aphid population levels in the greenhouse.

IPM of greenhouse aphids is mainly based on physical and biological control. Mechanical barriers such as fine mesh screens at the greenhouse openings are very important against aphids (Rapisarda et al. 2003). Biological control may be achieved by many natural enemies available to control all aphid species attacking greenhouse crops (Perdikis et al. 2008). Parasitoids of the genus *Aphidius*, especially *A. colemani* Viereck, are important biocontrol agents as well as predators like *Aphidoletes aphidimyza* (Rondani) which can be used preventively in combination with aphid parasitoids and *Chrysoperla carnea* Stephens (van der Ent et al. 2017). Repeated inundative releases of these natural enemies are usually made in temperate regions to control aphids in greenhouses. However, despite the large number of natural enemy species available, biological control of aphids remains a serious problem in several important greenhouse crops.

4.2.8 Scale Insects

Greenhouse environments are very suitable for scale insect (superfamily Coccoidea) population development. Scale insect pests in greenhouses belong to three main families: soft scales (Coccidae), mealybugs (Pseudococcidae) and armored scales (Diaspididae). For reviews of these groups see Rosen (1990), Ben-Dov and Hodgson (1997), Camacho and Chong (2015) and Mani and Shivaraju (2016). Many scale insect pests are invasive. Their cryptic lifestyle favors spread with international trade (Mazzeo et al. 2014). Detailed information on their distribution and host plants can be found on ScaleNet (García Morales et al. 2016). Coccoidea are at first sight barely recognizable as insects. The females are wingless and usually immobile, and covered with a hard scale (armored scales and soft scales) or with waxy threads (mealybugs). They suck the sap of plants and are mostly host-plant specific, though all species important in greenhouse crops are polyphagous. Most soft scales and armored scales lay their eggs under the scale, and mealybugs in an egg sac. The nymphs are mobile and responsible for the dispersal of the insects.

In greenhouses, mealybugs appear most frequently in ornamental crops, but can also generate problems in tomato and other vegetables. The citrus mealybug, *Planococcus citri* (Risso), is the most common and most damaging species in greenhouses. Other important greenhouse pests are *Planococcus ficus* (Signoret), *Pseudococcus viburni* (Signoret) and *Pseudococcus longispinus* (Targioni-Tozzetti). Soft scale insects are a less significant pest than mealybugs in greenhouses, but still cause problems more frequently than armored scales. They often damage perennial, woody crops. The most commonly occurring species are *Coccus hesperidum* Linnaeus and *Saissetia coffeae* (Walker) (van der Ent et al. 2017). The most important armored scales in greenhouses are the oleander scale, *Aspidiotus nerii* Bouché, and the rose scale, *Aulacaspis rosae* Bouché.

4.2.8.1 Life Cycle and Appearance

Mealybugs got their name because the females from the third nymphal instar onwards are covered with white waxy material. Unlike most other members of the superfamily Coccoidea, they retain their legs throughout their life. The females are wingless and may be up to 9 mm long, however the most important species in greenhouses are not longer than 5 mm. Their body consists of a single unit of fused head, thorax and abdomen with a white, powdery wax layer. They are often pink to yellow in color. Adult male mealybugs are totally different. They are usually no longer than 1 mm and have wings but lack mouthparts. They have a short lifespan during which they are wholly engaged in seeking females to fertilize them. Eggs are laid in a sticky, foamy mass of wax threads, called an egg sac. First instar nymphs are yellow-brown and not yet covered with wax. Second instar nymphs are darker and less active. After the second instar, the males form a pre-pupa followed by a pupa. The female second instar nymphs, settle on the plant and begin to secrete wax, molting to a third instar nymph and then the adult female (van der Ent et al. 2017).

Different species of mealybugs are very difficult to distinguish from one another; furthermore, the taxonomy of these species is not entirely clear. Adult *P. citri* are oval when seen from above, 2–4.5 mm long and 2–3 mm wide. They are soft and covered with fine waxy material. *Planococcus ficus* is slightly larger and darker. Generally, the number of wax rods around the end of the body and the length of the tail filaments can be used for diagnostics. A detailed description of their morphology and characters for field identification can be found in Mani and Shivaraju (2016).

Infestations with soft scales can be easily overlooked because the immobile insects are often situated in concealed places, grey or brown in color, and are dispersed over the whole plant. They can settle on any part of the plant, including the roots, but most species are to be found close to the veins of the leaf on upper and lower surfaces, or on leaf stalks, branches and (woody) stems. The life cycle of males differs from that of females. Adult females emerge after two or three nymphal instars. The small, winged males emerge from a pupa formed within the scale of the second instar. The size of adult female soft scales varies considerably per species, from about 1.5 mm to 18 mm long (Matille-Ferrero 1997). *Coccus hesperidum* is about 3–4 mm long and the size, shape and markings of the scale vary depending on the host plant. It is the most common soft scale species in interior plantings. The size of *S. coffeae* can be between 2–4.5 mm depending on the host plant (van der Ent et al. 2017). In contrast to the armored scales, the scale of a soft scale cannot be removed from the insect, even after death. All instars except the adult female possess legs and are capable of movement. The female generally lays a vast number of eggs under the scale (up to 3000). From these eggs the first instars (crawlers) emerge and disperse over the plant to find a feeding place and settle down. In some species, the females bear living youngs (van der Ent et al. 2017).

Also in armored scales the two sexes show different life cycle traits. Females only have two nymphal instars, the second of which resembles a small adult and develops directly into an adult female. Males have three nymphal instars, a prepupal stage and a pupa, from which the winged male develops. Nymphs and adult females are small, with a scale whose shape and color is distinct for different species. There are round, oval, elongated or oyster-shaped scales. The scale is not connected to the body and can be easily removed. Without its shield, however, the insect soon dehydrates. The color of the scales is usually white to greyish brown. Only the first instar crawlers and the adult males have legs and are able to move. The crawlers disperse over the plant before settling down in the feeding position. The adult females lack antennae, legs and wings. The head, thorax and abdomen are fused into a single unit which is always flattened and measures usually 1–2 mm (Takagi 1990). Adult *A. nerii* are a greyish, dirty white or yellowish, round, with a scale that resembles a miniature fried egg with a diameter of about 2 mm. Adult female rose scales are protected by a 1.5–2 mm large whitish, flat and almost circular scale. Eggs are laid in a single batch under the body. Hundreds of small orange crawlers will emerge and spread out. Males have long wings and are orange-red in color (van der Ent et al. 2017).

4.2.8.2 Population Development

The development time of mealybugs differs widely according to species. Development of *P. citri* females from egg to oviposition takes 94 days at 15 °C and goes down to 30 days at 25 °C (Goldasteh et al. 2009). Mudavanhu (2009) reported a development time from egg to oviposition of 132 days at 18 °C, and 48 days at 25 °C for *P. viburni*. *Planococcus ficus* takes 90 days from egg to oviposition at 18 °C and 28 at 25 °C. (Walton and Pringle 2005). The fecundity of these species is typically between 200 and 300 eggs per female at 25 °C (Copland et al. 1985; Walton and Pringle 2005; Mudavanhu 2009). The female of *P. longispinus* is viviparous and produces around 200 live young, which she deposits under her body. The life cycle takes 6–12 weeks depending on the temperature (Mani and Shivaraju 2016). A female *C. hesperidum* produces 80–250 offspring and the life cycle at

20 °C is approximately 60 days (Annecke 1966). The life cycle of *S. coffeae* takes approximately 58 days at 25 °C. Each female may produce 200–500 eggs (Abd-Rabou et al. 2009). At 25 °C, females of *A. nerii* produce 30–175 offspring during their lifespan. The generation time from egg to egg is 44–48 days (Rocha et al. 2006; González-Zamora et al. 2012). Female *A. rosae* produce between 50–150 eggs. Outdoors, normally one generation per year is observed. Under optimal conditions in greenhouses, four generations can be found (Pijnakker et al. 2010).

4.2.8.3 Damage

Mealybug and scale insect populations can reach high densities. Apart from the damage they cause by sucking plant sap, mealybugs and soft scales also produce honeydew, on which sooty molds grow, resulting in considerable damage in ornamental and fruit crops and loss of value. Armored scales do not produce honeydew. In ornamentals, the mere presence of mealybugs or scale insects can be sufficient to render the plants unfit for sale. The feeding of nymphs and adult females of mealybugs and soft scales on plant sap causes stunting of growth, deformations and/or yellowing of leaves, sometimes followed by defoliation. The overall effect reduces photosynthesis and therefore the yield. Where flowers and fruit are concerned, these often drop off. Armored scales feed by sucking the contents of epidermal cells, into which they inject toxic substances that cause yellow, red or brown patches to appear on leaves and fruit. This can eventually kill the leaf.

4.2.8.4 Monitoring and Control

Due to their concealed life-style, mealybugs and scales are often initially overlooked. In fact, they are sometimes only observed after their honeydew has been seen. Together with their protective covering this life-style also protects them against many natural enemies and synthetic insecticides. Especially in ornamentals where the threshold is practically zero, intensive scouting is necessary and control is difficult. The sex pheromones of mealybugs can be used for monitoring the pests in greenhouses (Waterworth et al. 2011) and for mating disruption (Walton et al. 2006). Armored scales also produce sex pheromones but the males are very weak fliers and only mate with females in close vicinity. About pheromones in soft scales very little is known (Camacho and Chong 2015).

Because Coccoidea can be such a serious problem, it was one of the first groups of insects against which classical biological control was implemented. In 1888, an Australian ladybird, *Rodolia cardinalis* (Mulsant), was introduced into California and successfully released against the cottony cushion scale, *Icerya purchasi* Maskell, which had become a huge problem in citrus cultivation (Grafton-Cardwell and Gu 2003). Another example is the release of *Cryptolaemus montrouzieri* Mulsant to control mealybugs in citrus crops in California, by the beginning of the twentieth century (Kairo et al. 2013). *Cryptolaemus montrouzieri* is also a species commonly used for biocontrol of mealybugs in greenhouses (van der Ent et al. 2017). Furthermore, there are many parasitoids that can be used for the control of particular scale insect species (see Chap. 16).

4.2.9 Lepidoptera

Many important insect pests of both vegetable and ornamental greenhouse crops are known in the order Lepidoptera, with numerous species especially in the family Noctuidae, showing the highest diversity in geographical distribution, type of attack and severity of damage they cause to different crops (Brødsgaard and Albajes 1999; Rapisarda et al. 2003). Here, cosmopolitan species like the cotton bollworm *Helicoverpa* (= *Heliothis*) *armigera* (Hübner), the beet armyworm *Spodoptera exigua* (Hübner), the cabbage looper *Trichoplusia ni* (Hübner) or various species in the genus *Agrotis* Ochsenheimer; the holarctic silver-Y *Autographa gamma* (Linnaeus); the cabbage moth *Mamestra brassicae* (Linnaeus) and the bright-line bright-eye *Lacanobia oleracea* (Linnaeus), both widespread in the Palearctic region should be mentioned. *Chrysodeixis* species, such as the green looper *C. eriosoma* (Doubleday), native to the Indo-Australian region but now also present in Europe and the Americas, and the golden twin-spot moth *C. chalcites* (Esper), diffused from southern Europe and the Middle East to Africa; with an almost similar distribution, and the cotton leafworm *Spodoptera littoralis* (Boisduval) are also important pests. During recent years, also the family Gelechiidae has become more important, due to the rapid diffusion of the South American tomato pinworm, *Tuta absoluta* (Meyrick), which is one of the most devastating tomato pests worldwide and has become a major threat for the global tomato industry, following its introduction into Europe almost a decade ago and the follwing invasion of the Afro-Eurasian continent (Desneux et al. 2011; Biondi et al. 2018). Occasionally, damage can also be caused by polyphagous species belonging to other families, such as *Cacoecimorpha pronubana* (Hübner) (family Tortricidae).

4.2.9.1 Life Cycle and Appearance

Commonly known as cutworms or armyworms, noctuid moths infesting greenhouse crops are medium size insects whose adults, with a wingspan ranging from 3.5 to 4.0 cm, approximately, usually have greenish-grey to orange-reddish-brown color (though with paler hindwings) and show bronze to brownish areas, spots and drawings on the forewings, characteristically arranged in each species. The name given to the family derives from the fact that, in most species, adults are nocturnal. At larval stages, noctuids can show bright (pale yellow to green, with green to grey head) or dark (blackish-grey to dark green, becoming reddish-brown) colors, depending on the species, showing also typical bands, spots or drawings. They can be hairless (e.g. *S. littoralis* or *T. ni*) or show tufts of short bristles over the entire body (e.g. *C. chalcites*). Last instar caterpillars are usually 3.0–4.5 cm long.

After emergence, females mate and start oviposition soon, usually during the night, on both upper and lower leaf surfaces and at different plant heights, depending on the species. First instar caterpillars move on the underside of leaves and feed on epidermis and parenchyma. Older larval instars produce larger holes on leaves, roll their edges together and wrap their flaps with siliceous threads. Depending on the species, mature larvae may also feed on buds and flowers, as well as on fruits. At the end of its development, the mature larva stops feeding, enters a prepupal stage and spins a cocoon. Pupation takes place on foliage or in the soil.

The South American tomato pinworm is a much smaller moth, whose adults are about 1 cm long, silvery-grey in color and with small black spots on the forewings. They lay small, cylindrical, creamy white to yellow eggs, about 0.35 mm long, on the aerial part of the plants. The eggs hatch in 4–5 days and young larvae, a bit less than 1 mm long, soon penetrate into leaves, stems or even green fruits, in which they create mines and galleries. Larvae are initially creamy, with dark head, but they become greenish to light pink starting from the second instar. Mature larvae leave their mines and move to new locations for feeding. The last instar larva is about 7.5 mm long and usually exits the gallery to pupate hidden on the plant or in the soil, but pupation may also occur inside the mines. The pupa is brown to dark-brown and normally protected by a thin, silky cocoon (Uchôa-Fernandes et al. 1995).

4.2.9.2 Population Development

Most of the Noctuids damaging greenhouse crops are extremely polyphagous; some species have also migratory habits, broadly influencing their biology and ecology (Cardé 2008; Feng et al. 2009; Alerstam et al. 2011). They are polyvoltine, with most species having no diapause and having up to 8–10 overlapping generations per year in warm areas, especially in greenhouses. The number of generations varies between species but also with latitude and availability of suitable hosts. At the optimal temperature of 25 °C, *C. chalcites* develops through six larval instars, each one lasting approximately 2.5–3.5 days (Rashid et al. 1971; Harakly and Farag 1975); at lower temperatures the entire larval period lasts 44–50 days (Gaumont and Moreau 1961). The number of eggs laid shows considerable variation in most of the noctuid species.

In addition to tomato, *T. absoluta* lives on many species of Solanaceae, both cultivated (especially potato, eggplant or pepino) and non-cultivated (Urbaneja et al. 2007; Viggiani et al. 2009). Alternative host plants are an important factor allowing *T. absoluta* to survive in the absence of tomato crops; this must be considered when applying integrated control strategies. *Tuta absoluta* is multivoltine and in greenhouses it may produce up to 12–13 overlapping generations per year (Vercher et al. 2010). Its life cycle is short and is completed in 29–38 days, depending on ecological factors, especially temperature. According to Barrientos et al. (1998), in Chile *T. absoluta* requires about 76 days at 14 °C to develop, 40 at 20 °C and 24 at 27 °C. The temperature threshold for development is 8.1 °C, and the pest requires 453 degree days to complete its development cycle. Overwintering may occur as eggs, pupae (especially in colder areas) or, if food is available and ecological conditions favorable, active adults (Sannino and Espinosa 2010). Adults avoid direct sunlight and usually hide between vegetation during the day, performing short flights if disturbed. Being more active at night, as other moths, they are attracted by light sources and particularly by light frequencies close to blue. The adult lifespan is 10–15 days for females and 6–7 days for males (Tropea Garzia et al. 2012); during her lifetime, a female may produce up to 260 eggs, laid singly or in small groups on young leaves but also on stems, sepals and green fruits (Uchôa-Fernandes et al. 1995).

4.2.9.3 Feeding and Damage

Adults of Lepidoptera have sucking mouthparts and feed on nectar, which makes them virtually harmless; therefore, damage is due to the feeding activity by the caterpillars only. Noctuid larvae may feed on different plant organs, such as leaves, flowers, fruits, stems (at ground level) or roots; however, each species shows a preference towards one or the other plant part: *Autographa gamma* or *Chrysodeixis* spp. mainly feed on leaves, whereas *H. armigera* and *Spodoptera* spp. often infest fruits. Fruit-feeding species have a high damaging potential because one larva may consume several fruits. *Agrotis* spp. mainly attack the basal stems of young seedlings, causing their death.

Tuta absoluta attacks to tomato plants may occur at any developmental stage, from seedlings to mature plants. When attacking leaves, mining larvae live on mesophyll and leave the epidermis intact, creating irregular galleries which widen with the larval development and later may become necrotic. This leaf damage reduces photosynthesis and consequently has a negative impact on plant growth and yield (Borgorni et al. 2003). Similar mines are produced on stems, depressing the general plant vigor (Pereyra and Sánchez 2006). On fruits, where larvae penetrate under the sepals through small entrance holes, attacks usually occur as soon as they are formed and when they are still green. Fruit damage is extremely serious economically, due to its impact on post-harvest processes and restrictions it imposes to the international trade of tomato produce (Desneux et al. 2011). Wounds caused on plant tissues by the larvae of Lepidoptera make the plants more vulnerable to secondary infections by pathogens, especially bacteria.

4.2.9.4 Monitoring and Control

Monitoring is very important in decision-making processes aimed at applying integrated control methods of Lepidoptera attacking greenhouse crops. Particularly for Noctuids, pheromone traps may give valuable indications on initial infestation and phenology (Rapisarda et al. 2003), especially if combined with direct sampling on plants. When a direct control is required, sprays of *Bacillus thuringiensis* Berliner may give adequate results, especially if treatments are applied on young larvae (Hanafi and Rapisarda 2017). An effective impact on Noctuid populations is shown by many entomophagous insects, both predators, as *Podisus* spp., especially *P. maculiventris* (Say), and egg parasitoids, as *Trichogramma* spp. (Smith 1996; De Clercq et al. 1998; Mohaghegh et al. 2001; Zuim et al. 2017). Effectiveness of larval parasitoids is variable. Chemical control may be considered only when taking into account selectivity standards required by IPM. Several insect growth regulators that effectively control caterpillars have negative side effects to many beneficial insects. However, their use for preparing poisoned baits can be considered although insecticide sublimation at high greenhouse temperatures may also impact natural enemies.

On tomato, *T. absoluta* can be effectively contained by applying integrated control strategies, based on both pre- (e.g. removal of crop residues, soil sanitation, use of insect-proof nets) and post-transplanting techniques (e.g. sex pheromones, natural enemies, rational insecticide applications) (Siscaro et al. 2013). Exclusion of the insect from the greenhouse can be achieved by applying insect-proof screens at the greenhouse openings (Hanafi and Rapisarda 2017). Insecticide-impregnated nets significantly reduce longevity and reproduction of *T. absoluta* adults, and have a repellent effect (Biondi et al. 2015). Mating disruption based on sex pheromones has shown contradictory results, and was only effective in greenhouses where introduction of adults from the outside was prevented by insect screens (Martí et al. 2010; Navarro Lopis et al. 2010; Cocco et al. 2013). They are more effectively applied in mass trapping techniques, where sex pheromones can be used to bait water traps (Abbes et al. 2012; Cocco et al. 2012) or in combination with light and/or color traps (Siscaro et al. 2013; Cherif et al. 2018). Generalist predators are the most promising antagonists for biological control of the moth, such as the mirid bug *Nesidiocoris tenuis* (Reuter), which is largely employed in biocontrol programs in tomato crops. By using this predator, problems could derive from its zoo-phytophagy, which is remarkable under low prey density or high temperature conditions; this may be reduced by intercropping adequate companion plants, such as *Sesamum indicum* L., which are attractive to the predator (Naselli et al. 2017) though do not interfere with its predatory activity on *T. absoluta*.

4.2.10 Dipteran Leafminers

The dipteran leafminers belong to the family Agromyzidae, which includes approximately 2500 species. The species causing most damage belong to the genus *Liriomyza*. In contrast to the vast majority of species in the Agromyzidae, they are truly polyphagous (van der Ent et al. 2017). The most damaging species in greenhouses are *Liriomyza trifolii* (Burgess), *L. bryoniae* (Kaltenbach), *L. huidobrensis* (Blanchard) and *L. sativae* (Blanchard). *Liriomyza trifolii*, *L. huidobrensis* and *L. sativae* have a nearly cosmopolitan distribution but *L. sativae* does not occur in Europe. All three are native to South and North America (Kang et al. 2009; Weintraub et al. 2017b). The tomato leafminer fly *L. bryoniae* is a European species and also occurs in Asia and North Africa (van der Ent et al. 2017). All these species have a history of rapid dispersal and colonization of new environments, often in association with global trade (Kang et al. 2009). *Liriomyza trifolii*, for instance, was introduced to Europe around 1976, probably on infected chrysanthemum cuttings (Minkenberg and van Lenteren 1986).

All four species are very polyphagous; *L. huidobrensis*, for instance, has been reported from 365 plant species in 49 plant families (Weintraub et al. 2017b). In greenhouses, *L. bryoniae* is a pest of, among others, tomato and sweet pepper, *L. trifolii* is often found on gerbera and chrysanthemum, *L. huidobrensis* on tomato and chrysanthemum and *L. sativae* on tomato and other vegetables (van der Ent et al. 2017). For a detailed review of their biology see Parrella (1987).

4.2.10.1 Lifecycle and Appearance

Adult leaf miner flies are small yellow and black colored flies, at most only a few millimeters long. Because the color of the adults of different *Liriomyza* spp. can vary, it is often difficult to distinguish one species from the other. The life cycle of a dipteran leaf miner consists of the egg, three larval instars, a pupal instar and the adult fly (for a detailed description of all stages see Parrella 1987). Eggs are inserted into the leaf just under the epidermis. The larvae begin feeding immediately after eclosion, tunneling in the leaf tissue but leaving the outer layers of the leaf intact and thereby creating mines that are initially very narrow and gradually enlarge, and are often, but not always, serpentine (Parrella 1987). The larvae are transparent whitish or yellow, about 1 mm long in the second stage and 3–4 mm when fully grown. *Liriomyza* spp. usually pupate in the ground, or in folds of the plastic foil if plants are grown on artificial substrate. Occasionally, pupae can also be found on the leaves. Fully-grown larva cut a sickle-shaped exit hole in the leaf, crawl out and fall to the ground where they search for a suitable pupation place (Parrella 1987). Pupae can vary enormously in color also within species and can be yellow, orange, brown or black. They are about 3 mm long and 2 mm wide. Adults emerge from the pupae generally during early morning; females are larger than males and emerge from larger pupae.

4.2.10.2 Population Development

The population development of dipteran leaf miners is mainly influenced by temperature, light, the species and quality of the host plant and population density. Generally, at 20 °C, development from egg to adult of the 4 species mentioned above takes 22–28 days in total: 3–5 days for the eggs, 6–9 days for the larvae and 12–15 days for the pupae. At 25 °C, the development time is 15–17 days (Minkenberg 1988; Wang et al. 2014; Mujica et al. 2017). A leaf miner population usually consists of 50% females. Adult females live for about 15–20 days and males about

10–15 days (Parrella 1987). The flies become active at sunrise and they are most active during the morning. Multiple mating is needed for maximum egg production and unfertilized females lay no viable eggs. The number of eggs laid per female depends on the host plant and on environmental conditions. *Liriomyza trifolii*, for instance, lays up to 300 eggs on chrysanthemum but only up to 80 on tomato (Parrella et al. 1983), generally values between 50 and 160 eggs per female at 20–25 °C are common (Minkenberg 1990; Wang et al. 2014; Mujica et al. 2017). *Liriomyza bryoniae* and *L. huidobrensis* pass through diapause and can overwinter outdoors in temperate climates, unlike *L. trifolii* and *L. sativae*.

4.2.10.3 Damage

Adult female leafminer flies puncture plant leaves with their ovipositor and then feed on the exuding plant fluids. This causes a small wound, which is called a "feeding spot" but is of little concern except under high population pressure or in ornamentals where the aesthetic value is compromised. The major damage is caused by the larvae hatching from the eggs which are also laid into a hole made by the ovipositor, usually on the upper side of the leaf. These larvae mine in the spongy mesophyll between the upper and lower leaf surface. The size of the mine depends on the stage of development of the leaf, the species of host plant and the leafminer species. Older larvae make wider tunnels. The mining causes a reduction of photosynthesis and can also lead to desiccation, premature leaf-fall and cosmetic damage. Loss of leaves also reduces yield. The actual impact on the plant is related to the position of the leaf. Younger leaves are more important for the metabolism of the plants than older leaves. In full-grown plants of fruiting vegetable crops, a considerable quantity of foliage can be lost before the harvest is affected. Seedlings and young plants can be completely destroyed by leafminers. Besides the direct damage by larval mining and adult feeding, leafminers may cause severe indirect damage by providing entry points for fungi and bacteria via the feeding spots (Brødsgaard and Albajes 1999; Gao et al. 2017).

4.2.10.4 Monitoring and Control

Adult leafminers can be monitored in greenhouses with yellow sticky traps (Parrella and Jones 1985). Leafminers are parasitized by a wide range of parasitoid species that normally control their populations effectively (Liu et al. 2009). They only tend to become pests of economic importance if their natural parasitoids are hindered, for instance through pesticide applications, or if crops are grown too early in the season for the natural populations of parasitoids to build up (Brødsgaard and Albajes 1999).

Chemical control of leafminers is complicated by the feeding of the larvae within the leaf and high reproductive capacity, although adults can be reached easily by insecticide applications due to their puncturing activity on the leaves. Resistance to insecticides has been frequently reported (Reitz et al. 2013). Furthermore, most insecticides are toxic for the complex of parasitoids that hold leafminers in check. When natural parasitism is not sufficient to keep leafminer population densities under economic thresholds, several parasitoid species are commercially available for seasonal inoculative releases in greenhouses (van der Ent et al. 2017, see Chap. 16).

4.2.11 Sciarid Flies

The economically important sciarid flies (fungus gnats) belong to the dipterous family Sciaridae. The species that cause most damage in greenhouses belong to the genus *Bradysia* whereas *Lycoriella* species are mainly found in commercial mushroom cultivations. Species identification is difficult. The species formerly named *Bradysia impatiens* (Johannsen), *B. paupera* (Tuomikoski) and *B. difformis* Frey have been recently synonimized under the name *B. impatiens* (Mohrig et al. 2013). Other important species are *B. ocellaris* (Comstock) and *B. coprophila* (Comstock). Their larvae feed on diverse organic materials, such as dead wood, leaf litter, humus and living plants (Cloyd 2015; Shin et al. 2015). Sciarid flies are usually found in damp, humid environments, and appear very commonly in greenhouses throughout the world. They generally do little harm to healthy plants but they can be particularly problematical in cuttings and other young growing plant material.

4.2.11.1 Life Cycle and Appearance

The life cycle of sciarid flies consists of egg, four larval instars, pupa and the adult. The adult insects are 1–5 mm long, grey-black midges with long antennae. They have relatively long legs, and their wings show very clear venation. The males are usually smaller than the females. The females are attracted to damp areas with high amounts of organic material and lay their minute eggs on the ground surface close to plant roots. The larval instars are morphologically identical, each a larger version of the previous one, although their color changes from transparent to milky white. The larvae can grow to between 5 and 12 mm in length, are legless and have a conspicuous brown or black head (van der Ent et al. 2017). Pupation takes place in a small hole in the ground. Pupae are 2–5 mm long and 0.3–1.5 mm in diameter. Initially they are white, but later they become yellow to brown. The posterior end of the pupa remains mobile.

4.2.11.2 Population Development

An environment that is humid and rich in dead organic material is ideal for the development of sciarid flies. They feed mainly on organic remains and the fungi that grow on them, although some species can also consume living plant material. The adults are attracted by a broad range of pathogenic and non-pathogenic microorganisms for oviposition. They are weak flyers but can build up huge populations in greenhouses when the conditions for the larvae are optimal. The females lay between 50 and 300 eggs on the soil. The development of *B. impatiens* from egg to adult takes approximately 50 days at 13 °C and 20 days at 25–29 °C (Wilkinson and Daughtery 1970; Marín-Cruz et al. 2015). The life-span of an adult is about 1 week.

4.2.11.3 Damage

Sciarid flies show no particular preference for plant species, as long as they can exploit a humid, humus rich environment. Damage often appears when plants grow poorly or when conditions are too moist. Large, healthy plants are usually not harmed. Sciarid flies can cause damage both directly and indirectly. Direct damage is the immediate result of larvae feeding on roots and root hairs. The lesions caused by feeding larvae provide invasion routes for various soil born pathogenic fungi, for instance *Fusarium* spp., *Botrytis* spp. and *Verticillium* spp. Adults can also spread pathogens from diseased to healthy plants (Cloyd 2015). Because the larvae move very little, plant death is generally local. Young plants that are kept humid and well watered are particularly at risk. Furthermore, the number of fungus gnats in greenhouses may build up to such large numbers that the flying adults are a major nuisance to the greenhouse workers.

4.2.11.4 Monitoring and Control

Sticky traps have been recommended to monitor adult sciarid flies (Rutherford et al. 1985) but Harris et al. (1995) did find no correlation between adult catches on sticky traps and larval densities and recommended to use potato discs placed on the potting medium as a more reliable monitoring method. If used in high densities, the sticky traps can also be used to reduce adult populations by mass-trapping. Chemical control of fungus gnats has been increasingly difficult due to the development of insecticide resistance and the decreasing number of registered insecticides (Cloyd 2015). To reduce the chance of sciarid flies developing into a large population, the growing substrate should be kept as dry as possible and the growth of algae should be avoided as much as possible. Nematodes and soil dwelling predatory mites can be used for biological control (van der Ent et al. 2017, see Chap. 16). Biological control based on a combination of these agents and a high hygienic standard in the greenhouses are normally effective.

4.2.12 Beetles

There are several species of beetles that can damage greenhouse crops (see e.g. van der Ent et al. 2017). The most important one is the pepper weevil, *Anthonomus eugenii* Cano. Another species, which is mainly a problem in ornamentals like, for instance, azalea, rhododendron and cyclamen is the black vine weevil *Otiorhynchus sulcatus* (Fabricius). *Anthonomus eugenii* is the most harmful insect pest of pepper species cultivated in the south of the United States, Mexico and Central America. It belongs to the family Curculionidae, and is native to Mexico and Central America, but now also distributed widely in southern USA and also occurs in some northern states and Canada (Ingerson-Mahar et al. 2015). In Europe, it has been reported in the Netherlands, where it has now been eradicated (NVWA 2013), as well as in Italy, where it has been officially declared transient, under eradication (EPPO 2014; Speranza et al. 2014).

4.2.12.1 Life Cycle and Appearance

Pepper weevil necessarily requires a host plant to complete its life cycle because the development of the larva and pupation occurs inside the fruits. The adults live outside the fruits. The eggs are small, approximately 0.5 mm long, and of oblong-oval shape. They are inserted into the reproductive parts of the plant: flower buds, flowers and fruits. There are three larval instars. The larvae are cylindrical and curved, legless, creamy-white, with a light brown head and dark jaws. They feed within the fruits and reach a length of up to 6 mm. The pupa is white when formed, turning yellowish with brown eyes later, and of similar shape to the adults. The adult emerges from the fruit through a round hole. It is about 3 mm long, dark mahogany to black and sparsely covered with small yellowish or whitish hairs. The snout is approximately half the length of the body (Capinera 2008; Torres-Ruíz and Rodríguez-Leyva 2012).

4.2.12.2 Population Development

Pepper weevil females make a cavity with their mouthparts into the reproductive parts of the plant before depositing the egg, and seal the puncture containing the egg with a light brown fluid that hardens and darkens. They prefer to oviposit in uninfested fruits. In the laboratory, adult longevity has been up to 90 days, and the adults can survive without food for up to 3 weeks. A female can deposit more than 350 eggs during its life time, with a maximum of nine eggs per day (Torres-Ruíz and Rodríguez-Leyva 2012). The duration of the life cycle of *A. eugenii*, and the number of annual generations, mainly depends on the availability of host plants and temperature. It takes around 2 weeks at 27 °C and 42 days at 15 °C from oviposition to adult emergence (Toapanta et al. 2005). The pepper weevil does not enter diapause, but does survive temperatures just above zero.

4.2.12.3 Damage

The adults feed on fruits and flower buds. Feeding on very small fruits and flower buds normally causes their drop, feeding on larger fruits can form scars. However, the most important damage is produced by larvae feeding and developing inside the fruit. They usually feed on the placental tissue and seeds inside the immature fruits, causing a darkening of the seeds and associated tissues and fruit abscission, resulting in loss of production. The pepper weevil has also been implicated in the transmission of *Alternaria* spp. in peppers (Bruton et al. 1989).

4.2.12.4 Monitoring and Control

Pepper weevil is mainly present in the uppermost parts of the plant where the flower buds, flowers and small fruits are present. Scouting should be carried out in this parts of the plants. They can fly and disperse into the greenhouse, but normally do not move much if food is available. This leads to an aggregated distribution (Capinera 2008). Monitoring can be carried out with yellow sticky traps (Riley and Schuster 1994). Male pepper weevils produce an aggregation pheromone that attracts both males and females. Traps baited with synthetic formulations of this pheromone can also be used for monitoring (Eller et al. 1994; Bottenberg and Lingren 1998). Mass trapping with large sticky sheets is also practiced in Mexico. Several parasitoids of pepper weevil are known (Rodríguez-Leyva et al. 2012). One of the more promising species is *Catolaccus hunteri* Crawford. Because of its wide host range, *C. hunteri* can be reared on factitious hosts and a rearing system has been developed using *Callosobruchus maculatus* (Fabricius) as host (Vazquez et al. 2005). However, so far it has not been possible to develop an effective and economic biocontrol strategy based on the use of this parasitoid. One of the problems is that the wasps cannot reach pepper weevil larvae with their ovipositor in larger fruits (Corrales 2002; Schuster 2007).

4.3 Prospects for the Future

In the first edition of this book, Brødsgaard and Albajes (1999) wrote: “The increasing globalization of international trade in vegetable and particularly ornamental crops will probably result in an acceleration of the establishment of exotic insect and mite pests in old and new greenhouse areas. …. Despite efforts devoted to preventing or reducing the entrance of exotic phytophagous species, the catalogue of new pests in greenhouses becomes longer every year. A global distribution of all important greenhouse pests in the future seems difficult to avoid." This trend has continued during the last two decades with probably the most significant species *T. absoluta*, but also *T. evansi* or more recently *Thrips setosus* Moulton, an Asian species that was found on *Hydrangea* plants in the Netherlands in 2014 (Vierbergen and Loomans 2016), and has since then also been reported from Croatia, France, Germany an the United Kingdom. Globalization of pest occurrence seems to be particularly prevalent in protected cultivation. The ever increasing international trade in ornamentals and the favorable conditions of greenhouse environments for a rapid population increase explain the special relevance of the problem in protected cultivation. In recent years, efforts to minimize the risk of introduction have been intensified and guidelines for risk and impact assessments for pests and diseases, as well as more generally invasive species, have been developed (EFSA 2011; EPPO 2011; Carboneras et al. 2018; Roy et al. 2018). Despite this, it will not be possible to completely avoid introductions of pests in an ever more closely connected world.

Due to rapid resistance development of many greenhouse pests to synthetic pesticides and increasing demands of legislators, supermarkets and consumers for residue-free products, biological control will play a key role in the management of these pests. Development of new exotic biocontrol agents has become more complicated due to Access and Benefit Sharing procedures under the Convention on Biological Diversity (Mason et al. 2018); however, there are still plenty of possibilities (van Lenteren et al. 2018). Furthermore, the rapid developments in the fields of genetics and genomics and the associated decrease in costs of molecular methods open new possibilities, like for instance the use of intraspecific variation to optimize biocontrol agents for certain purposes and conditions (Lommen et al. 2017).

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Chapter 5
Nematodes

Francisco Javier Sorribas, Caroline Djian-Caporalino, and Thierry Mateille

Abstract Plant-parasitic nematodes (PPNs) represent an important constraint for plant production worldwide. They are widely distributed around the world and are able to parasitize every plant species. Furthermore, the current restrictions on the use of chemical nematicides have increased the problems caused by PPNs, irrespective of the production system. Intensive vegetable production under protected cultivation is the system most vulnerable to PPN, especially to root-knot nematodes. Despite the high frequency of occurrence of root-knot nematodes, other PPN species occur in nematode communities, whose structure and composition are influenced by the plant species, the environmental conditions, the agronomical practices and the level of specificity of the control methods used to manage them. Integrated nematode management strategies must therefore be designed using a holistic approach that considers all the interactions between PPN species in the nematode communities, plant species and biotic and abiotic environmental conditions. The use of specific management tactics against a key PPN species only leads to changes of this species for others without solving the problem. Long-term studies that consider all of these complex relationships are therefore needed to manage the pathogenicity of the whole PPN community.

Keywords Cyst nematodes · Integrated nematode management · *Meloidogyne* · Nematode community shifts · Population dynamics · *Pratylenchus* · Sustainable management · Tolerance limit · Vegetable crops · Yield losses

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5.1 Introduction

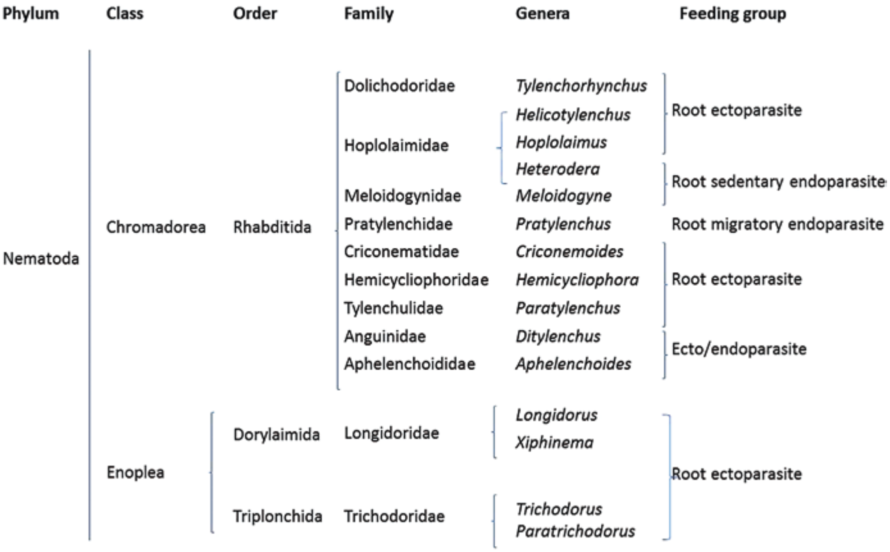
Nematodes are poikilothermic, worm-like animals that inhabit aquatic and terrestrial environments. They are the most abundant and diverse invertebrate group on the Earth, representing more than 80% of metazoan taxonomical and functional diversity in soils. The variety of reproductive modes (amphimixis, meiotic or mitotic parthenogenesis and hermaphroditism), along with several mechanisms for surviving adverse environmental conditions (cryobiosis, thermobiosis, anoxybiosis, osmobiosis and anhydrobiosis) and their diverse trophic behaviours (bacterivory, fungivory, predation, omnivory, and plant or animal parasitism) are key factors to their success. Most nematodes are active components in the cycling of organic matter. Furthermore, they have different degrees of vulnerability to pollutants and other environmental disturbances, so the composition of their community is a bioindicator of environmental quality that can be assessed according to its maturity index or other indices based on community composition and metabolic footprints (Wilson and Kaouli-Duarte 2009). In agriculture, insect-parasitic nematodes are beneficial for biological management of insect pests. Conversely, plant-parasitic nematodes (PPNs) are responsible for annual yield losses of around 10% of life-sustaining crops and 14% of economically-important crops (Sasser and Freckman 1987), varying greatly between growing areas according to specific nematode-plant-environment interactions. Among all PPNs, the sedentary parasites (root-knot and cyst nematodes) are considered the most damaging worldwide (Jones et al. 2013).

5.1.1 Plant-Parasitic Nematodes

PPNs are filiform, usually 0.5–2.0 mm in length and a few microns in width. Some adult females have swollen body shapes, as for example in cyst or root-knot nematodes. Information on the general morphology and anatomy of nematodes along with interactive diagnostic keys can be found in Decraemer and Hunt (2006), whose taxonomic classification of PPNs has been used in this chapter. These sources include the websites of the Nematode-Plant Expert information system of the University of California Davis (http://nemaplex.ucdavis.edu/Uppermnus/nematamnu.htm#Phylum_Nematoda) and the laboratory of Nematology of the University of Nebrasca-Lincoln (https://nematode.unl.edu/index.html).

More than 4100 described PPN species belong to one of the two classes: Chromadorea and Enoplea (Decraemer and Hunt 2006) (Table 5.1). PPNs can be categorized as ectoparasites, endoparasites or semi-endoparasites according to their relationship with the plant host. Ectoparasitic nematodes (e.g. Criconematoidea, *Paratylenchus, Tylenchorynchus, Xiphinema, Longidorus, Trichodorus, Paratrychodorus*) remain in the soil and feed from root cells. The type of plant tissue affected by ectoparasitic nematodes is related to the length of their stylet, the deepest affected tissue corresponding to the longest stylet. For example, species in

Table 5.1 Taxonomic classification of plant-parasitic nematodes (According to Decraemer and Hunt 2006) found on vegetable crops under protected cultivation



Phylum	Class	Order	Family	Genera	Feeding group
Nematoda	Chromadorea	Rhabditida	Dolichodoridae	*Tylenchorhynchus*	Root ectoparasite
			Hoplolaimidae	*Helicotylenchus*	
				Hoplolaimus	
				Heterodera	Root sedentary endoparasite
			Meloidogynidae	*Meloidogyne*	
			Pratylenchidae	*Pratylenchus*	Root migratory endoparasite
			Criconematidae	*Criconemoides*	Root ectoparasite
			Hemicycliophoridae	*Hemicycliophora*	
			Tylenchulidae	*Paratylenchus*	
			Anguinidae	*Ditylenchus*	Ecto/endoparasite
			Aphelenchoididae	*Aphelenchoides*	
	Enoplea	Dorylaimida	Longidoridae	*Longidorus*	Root ectoparasite
				Xiphinema	
		Triplonchida	Trichodoridae	*Trichodorus*	
				Paratrichodorus	

the genus *Tylenchorhynchus* (short stylet) cause limited necrosis in epidermal cells and root hairs, while species in the Longidoridae, with long stylets, kill epidermal and cortical cells as deep as the meristematic tissue near the root tips, from which the nematodes feed and induce galls. Endoparasitic nematodes entirely penetrate the plant tissue and migrate inside the plant. Migratory endoparasites such as *Pratylenchus* do so without establishing a permanent feeding site. Alternatively, sedentary endoparasites such as *Meloidogyne, Globodera* and *Heterodera* establish a permanent feeding site by inducing strong metabolic sinks and remain there for the rest of their lives, losing mobility and becoming globose. In semi-endoparasites such as *Rotylenchulus reniformis*, only the anterior part of the body penetrates the plant tissues, while the posterior part remains in the soil. Some PPNs can be categorized into more than one feeding group. For example, *Aphelenchoides* is a migratory endoparasite in leaves, but it also feeds ectoparasitically on leaf and flower buds, whereas *Ditylenchus* is a migratory ectoparasite and also an endoparasite of stems, bulbs, and tubers.

In their aboveground part, the plants parasitized by PPNs show a variety of non-specific symptoms that can easily be confused with those caused by other biotic or abiotic agents, such as damping-off, dwarfing, nutrient deficiency, wilt, necrosis and/or deformed organs, reduction in fruit size and marketable yield, plant decline and death of the plant. In the belowground parts of the plant, PPNs can produce root-knots or galls, necrosis, and root proliferations. Roots infected with PPNs reduce their ability to absorb water and nutrients. In addition, the mechanical injuries and/or physiological changes caused by PPNs in plant tissues facilitate infection by other pathogens, further increasing the disease severity and yield losses.

Examples of such pathogens include plant viruses transmitted by Longidoridae and Trichodoridae nematodes, fungi such as different species of *Verticillium, Fusarium, Pythium* and *Rhizoctonia*, and bacteria such as *Ralstonia solanacearum, Clavibacter* and *Pseudomonas*. Furthermore, PPNs can contribute to breaking down genetic resistance against certain soil borne fungal pathogens in specific nematode-fungus-plant interactions (Agrios 2005).

5.1.2 Life Cycle

PPNs usually pass through six development stages until life cycle completion: egg, four juvenile stages (J1 to J4) and adult. In some Longidoridae, three instead of four juvenile stages take place. Eggs may be laid singly in the soil or in plant tissues, and sometimes in masses in a gelatinous matrix secreted by the female (*Meloidogyne*). In cyst nematodes, the eggs remain inside the body of the female, which becomes a cyst when it dies. The egg is usually cylindrical, with an eggshell comprising an outer vitelline layer composed of lipoprotein, a middle chitinous layer formed by a chitin-protein complex responsible for the structure, and an inner lipid layer composed of lipoprotein that confers impermeability. Some microorganisms able to produce proteases and chitinases (e.g. *Pochonia chlamydosporia*, *Purpureocillium lilacinum*) are potential antagonists of PPNs. After embryogenesis, the formed J1 hatches from the egg in the class Enoplea, but in the class Chromadorea the J1 moults and the J2 hatches from the egg. Egg hatching occurs when environmental conditions, soil temperature and water content are conducive. In addition, root exudates are required for some PPNs with a narrow host range, such as species of *Globodera.* Nematodes move by undulating movements in the thin water layer around soil particles or aggregates with 25- to 100-μm pores. In general, sandy textured soils facilitate nematode locomotion more than clayey soils. Nematodes are attracted to their host plant by external stimuli (root exudates and existing gradients of amino acids, ions, pH, temperature and CO_2 around physiological active roots) (Robinson and Perry 2006).

Depending on the PPN species, the juvenile moults two or three times before reaching the adult stage. Most PPNs retain the same shape in their adult form as in the juvenile stages, with the exception of sedentary female root-knot and cyst nematodes, which become progressively swollen from post-infective J2 to adult female, whereas the males of these species are also vermiform. Reproduction is mainly done by two mechanisms: amphimixis, in which sex pheromones are produced by the female to attract males; and parthenogenesis, in which the female starts laying eggs when it reaches maturity. In the latter case, males are rare, appearing when environmental conditions are unfavourable for population development (e.g. scarcity of food or a stressed plant) as a way to regulate the size of the population by avoiding intraspecific competition. The duration of the life cycle is strongly influenced by environmental conditions such as soil temperature in irrigated crops and soil water content in non-irrigated crops. As crops grown under protected cultivation are all irrigated, the duration of the life cycle is expressed in terms of accumulated heat, known as physiological time. That is, the amount of accumulated heat between the lower and upper threshold temperatures for life cycle completion is constant for a given PPN-plant species combination and is expressed as accumulated degree days. Nematodes can survive adverse environmental conditions as eggs (embryo development, J1 or J2), as hatched juveniles (J4 of *Ditylenchus dipsaci*) and as adults (*Pratylenchus* spp.).

5.1.3 Population Dynamics and Yield Losses

The size of a PPN population depends on its life cycle, the plant host status and the environmental conditions, including the physicochemical characteristics of the biotope and the other components of the biocoenosis (summarized in Seinhorst 1970, Schomaker and Been 2006 and Greco and Di Vito 2009). In Nematology, the host plant status refers to (i) the ability of a nematode species to feed and reproduce on a plant species or genotype, and (ii) the tolerance of the plant to support nematode densities without suffering significant reductions in its productivity. A good host allows the build-up of nematode population densities. Conversely, a non-host does not allow the completion of the nematode life cycle. A resistant host or a poor host is used as a food source, but nematode development and reproduction on it are lower than on a good host. In a resistant host, the resistance is conferred by genes only present in some genotypes (e.g. resistant tomato cultivars bearing the *Mi1.2* gene and susceptible cultivars without it), while in a poor host all the plant species perform equally. The combination of these two criteria, reproduction and tolerance, form the host status of a plant species or germplasm.

In presence of host plant species and optimal environmental conditions, the nematode density at the end of the crop (final population *Pf*) is proportional to the density at planting or sowing (initial population *Pi*), that is $Pf = a\ Pi$, where a is the maximum multiplication rate. However, as Pi increases, the multiplication rate (Pf/Pi) decreases due to the scarcity of food and the competition, tending to stabilize around an equilibrium density (E) at which the plant can supply enough food to maintain the population density at planting ($Pf = Pi$; $Pf/Pi = 1$). Both parameters are indicators of the host status for a given set of conditions. That is, high values of a and E correspond to good hosts, while low values correspond to resistant or poor hosts. Plant growth and yield are also related to Pi, and the relationship is mathematically described by the Seinhorst damage function model, which provides indicators of plant tolerance (T) and yield losses ($1\text{-}m$) (Fig. 5.1). For a given PPN-plant combination, the damage caused by the nematode depends on the nematode density at planting, the plant tolerance and the number of generations that the nematode can complete during the cropping period.

In absence of a host plant, the survival forms of PPNs can remain in soil or plant debris, though not all individuals survive. For example, the mortality rate of the potato cyst nematode is greater the first year after a potato crop (69%) than in

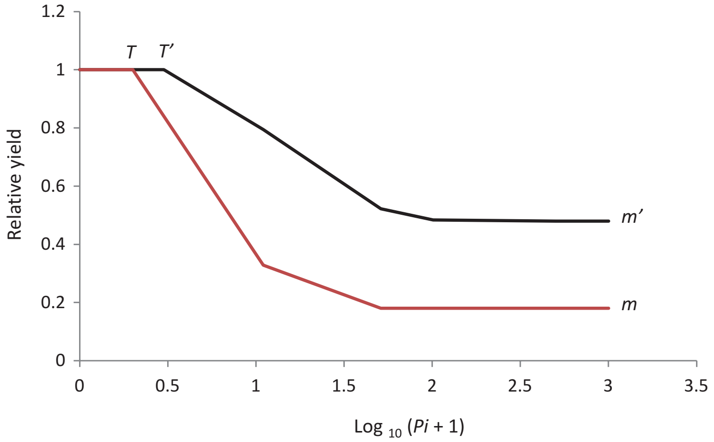


Fig. 5.1 The Seinhorst damage function model [($y = m + (1\text{-}m)\ 0.95^{(Pi/T\text{-}1)}$ when $Pi \geq T$, and $y = 1$ when $Pi < T$, where T = tolerance limit (the nematode density below which there is no yield loss), y = the relative yield and m = the minimum yield) that provides indicators of plant tolerance (T) and yield losses (1-m); T and m for cucumber; T' and m' for tomato]

subsequent years (20%–30%) (Schomaker and Been 2006). Regarding the survival rate of the sensitive stages of PPNs, it is inversely related to the accumulated soil temperatures in the range from the base to the optimal temperature, because the physiological activity, and thus their reserve consumption, is proportional to the soil temperatures in this range. The water content of soil also affects nematode survival in non-irrigated soils.

5.2 Plant-Parasitic Nematodes on Vegetable Crops Under Protected Cultivation

Several PPN genera have been reported on vegetable crops under protected cultivation (Table 5.1) (Verdejo-Lucas et al. 2002, 2013b; Chandel et al. 2010; Djian-Caporalino 2012; Anwar et al. 2013; Aydinli et al. 2013; Giné et al. 2013). Among them, root-knot nematodes (RKNs), *Meloidogyne* spp., are the main cause of crop yield losses (Sikora and Fernández 2005) and increasing operating costs to manage them. RKNs are mostly the only PPNs infesting the soil if fumigation or steam sterilization is frequently used (Verdejo-Lucas et al. 2002, 2013b; Djian-Caporalino 2012). Otherwise, other PPN species occur in addition to RKNs in both integrated and organic farming (Giné et al. 2013), although RKNs, lesion (*Pratylenchus*) and cyst nematodes are the most damaging ones (Briar et al. 2016). The prevalence of PPNs is related to the plant species included in the crop rotation schemes. In vegetable production, solanaceous and cucurbitaceous species generally favour the build-up of RKN populations. These crops are alternated in rotation more often in integrated production systems than in organic ones, in which a wider range of crops are included in the rotation sequences, such as French bean, lettuce, spinach, chard, radish and celery. In organic production systems, in addition to RKNs, other PPNs such as lesion and cyst nematodes can occur, but the problems caused by PPNs do not differ from those in integrated or conventional systems (Briar et al. 2016). In fact, an increasing perception of problems caused by nematodes has been reported by farm advisors after the restriction or prohibition of chemical nematicides (Djian-Caporalino 2012; Talavera et al. 2012).

5.2.1 Sedentary Endoparasitic Nematodes

5.2.1.1 *Meloidogyne*

There are around 100 described RKN species at present, but only three are responsible for most of the damage to vegetable crops under protected cultivation: *M. arenaria, M. incognita* and *M. javanica*. These species are widely distributed around the world because of (i) their wide range of host plants, which include common weed species growing during and between crops (Ornat and Sorribas 2008), and (ii) their parthenogenetic mechanism of reproduction. Other RKN species that can potentially be dangerous to vegetable crops have been found under protected cultivation. They include *M. ethiopica* (Aydinli et al. 2013), *M. luci* (Geric et al. 2017) and *M. enterolobii* (Kiewnick et al. 2008). Despite their low occurrence, these RKN species can parasitize solanaceous and cucurbitaceous crops, which are the main ones under protected cultivation. Moreover, *M. enterolobii* is not affected by the resistance genes that are present in several crops, including those in tomato, bell pepper and sweet pepper (Castagnone-Sereno 2012). Information on the geographic distribution of RKN species, plant hosts, impact, prevention and control can be found at http://www.cabi.org/isc.

The life cycle of RKNs comprises three steps: (i) infection, in which second-stage juveniles (J2) penetrate the roots of a host plant and migrate to the vascular cylinder to establish a permanent feeding site, and the J2 become sedentary and increase in width; (ii) development, in which, under favourable conditions, J2 moults three times to achieve the mature adult female stage, and under unfavourable conditions (high nematode density, scarcity of food or stressed plants) the juveniles develop into males; and (iii) production and emergence of a new inoculum, in which the females reproduce parthenogenically, laying large numbers of eggs in a gelatinous matrix, the egg mass, located on the surface and/or inside the galled roots. Most eggs develop to full-formed first-stage juveniles that moult once within the egg. The J2 emerge from the egg and leave the egg mass to search for a root.

The length of the life cycle is related to the thermal requirements of each RKN species and crop. For example, the thermal requirements of *M. incognita* and *M. javanica* are similar on cucumber and zucchini, but not on watermelon (Giné et al. 2014; López-Gómez et al. 2014; Vela et al. 2014) (Fig. 5.2). Ferris et al. (1985)

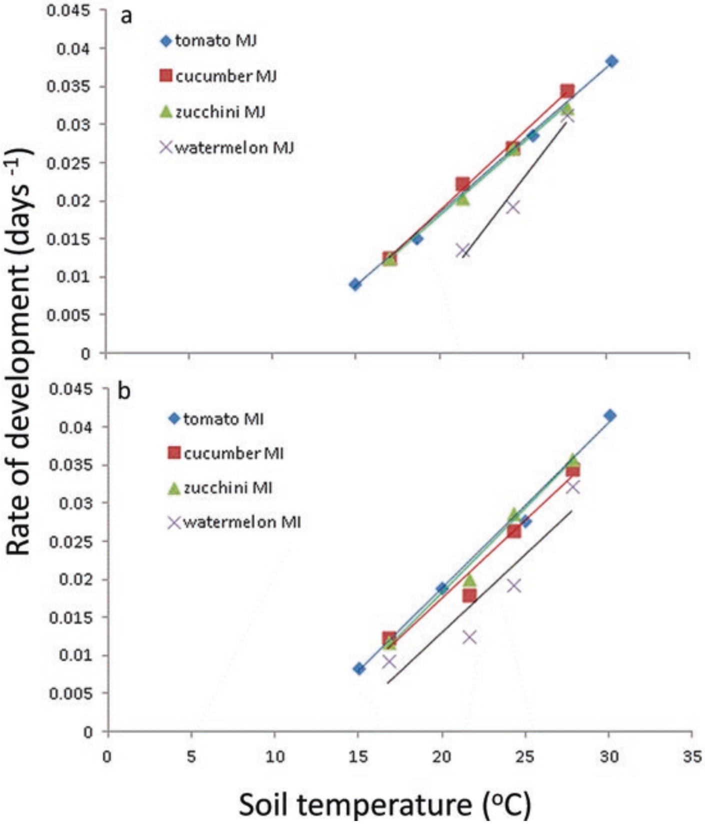


Fig. 5.2 Thermal requirements of *M. javanica* (**a**) and *M. incognita* (**b**) on cucumber, zucchini-squash, watermelon and tomato

Table 5.2 Thermal requirements for life cycle completion of *Meloidogyne* spp. on tomato (summarized in Maleita et al. 2012)

Meloidogyne spp.	Base temperature (*Tb*; °C)	Thermal constant (*S*)[a]
M. incognita	10.1	400
M. javanica	13.0	345
M. hapla	8.3	553
M. hispanica	10.4	526

[a] Accumulated degree days (°C) over Tb

proposed a single model for life cycle completion of the most frequent RKN species on tomato (thermal constant *S* between 600 and 700 accumulated degree days over a base temperature of 10 °C), though differences seem to occur between *M. incognita, M. javanica, M. hapla* and *M. hispanica* on tomato (summarized in Maleita et al. 2012) (Table 5.2). Several recent studies have demonstrated that there are no differences between the thermal requirements of *M. incognita* and *M. javanica* on susceptible tomato cultivars, irrespective of their (a) virulence to the *Mi 1.2*-resistance gene. Knowledge of the thermal requirements of RKNs on selected crops allows phenology models to be created for predicting planting date and trap crops (see Sect. 5.3.2), and for comparing crop yield losses for a given crop, because they are influenced by the number of generations that the nematode can complete on it. For example, in southern Spain, *M. javanica* can complete one or two generations on zucchini when it is cultivated in winter-spring or spring-summer in plastic greenhouses, respectively (Vela et al. 2014). The phenology models obtained on these crops are being validated in commercial plastic greenhouses across the Mediterranean coast of Spain, and the results have so far been encouraging.

The growth of the RKN population on a given plant species depends on the host status (see Sect. 5.1.3), the environmental conditions and the number of life cycles that the nematode can complete during the cropping period. It is known that the RKN population growth rate and crop yield losses are higher in sandy than in clayey textured soils. The maximum multiplication rate (*a*), equilibrium density (*E*) and tolerance limit (*T*) on Solanaceae and Cucurbitaceae cultivated in plastic greenhouses have been determined (Table 5.3). Additional information on tolerance limits and minimum relative yield obtained through pot or microplot experiments is available for some vegetable crop–RKN species combinations (summarized in Schomaker and Been 2006; Greco and Di Vito 2009; Giné et al. 2014; López-Gómez et al. 2014 and 2015) (Table 5.4). This information will help design crop rotation sequences to minimize the growth of the RKN population and prevent yield losses in the following crop (see Sect. 5.3.2). For example, cropping resistant

Table 5.3 Maximum multiplication rate (*a*), equilibrium density (*E*; eggs+J2 250 cm^{-3} of soil) of RKNs on tomato and cucurbits cultivated in plastic greenhouses, and tolerance threshold (*T*) and minimum relative yield (*m*) (Talavera et al. 2009; Giné et al. 2014, 2017; López-Gómez et al. 2014, 2015; Vela et al. 2014)

Meloidogyne spp.	Crop[a]	*a* (x100)	*E* (x1000)	*T*	*m*
M. incognita	Tomato (S)	82–98	13–15	2–4	0.44–0.48
	Tomato (R)	1–6	2–4	nf	nf
	Cucumber (summer-autumn)	11	0.6	< 0.4	0.12–0.34
	Cucumber (spring-summer)	10–23	4.3–10	1.3–6.7	0.18–0.26
	Cucumber (G) (spring-summer)	93–118	13–2 3	1.3–5.2	0.25–0.37
	Zucchini-squash (winter-spring)	0.16–0.96	0.3–0.5	8.1	0.61
	Zucchini-squash (autumn-winter)	2.7–23	0.8–1.2	1.5	0.69
M. javanica	Tomato (S)	35	2.8	–	–
	Tomato (R)	1.6	0.05	–	–
	Zucchini-squash (spring-summer)	31	1.5	0.1	0.48
	Watermelon	0.7	0.033	20	0.63

[a] S, without *Mi 1.2* resistance gene; R, with *Mi 1.2* resistance gene; G, grafted onto cucurbit hybrid rootstock. *E* and *T* of *M. javanica* on zucchini-squash and on watermelon are expressed as J2 100 cm^{-3} of soil; nf, Seinhorst damage function model not fitted

Table 5.4 Tolerance limit (*T*) of vegetable crops cultivated in pots or microplots to *Meloidogyne* spp. and minimum relative biomass or yield (*m*) (summarized in Schomaker and Been 2006 and Greco and Di Vito 2009; Giné et al. 2014; López-Gómez et al. 2014 and 2015)

Meloidogyne spp.	Crop[a]	*T*[b]	*m*[c]
M. incognita	Aubergine	0.05*	0.05*
	Pepper (S)	0.3	0.16*
	Pepper (R)	0.3	0.5*
	Pepper (S)	0.74*	0.1
	Pepper (R)	0.74*	0.4
	Tomato (S)	0.55	0*
	Tomato (S)	4*	0
	Tomato (R)	0.5*	0.7
	Melon	0.19	0*
	Cabbage	0.5	0.05
	Parsley	0.17	0.5
	Chard	1.1*	0.1
	Spinach	0.25	0
	Common bean	0.25	0
	Artichoke	1.1	0
M. javanica	Tomato (S)	0.28	0
	Pepper (S)	0.36	0
	Cucumber	0.01	0.36
	Zucchini-squash	4	0.82
	Watermelon	0.7	0.65
	Common bean	0.6	0

[a] susceptible (S) or resistant (R) cultivar; [b] data followed by * are expressed as nematodes g^{-1} of soil and otherwise as eggs cm^{-3} of soil; [c] data followed by * indicate relative crop yield and otherwise aboveground plant biomass

tomato cultivars or watermelon instead of susceptible tomato or cucumber in spring-summer can suppress the nematode population build-up and also reduce yield losses in the following summer-winter or autumn-winter crop (Talavera et al. 2009; Giné and Sorribas 2017b).

At the end of the crop, in the absence of a host plant, RKNs can survive as eggs in the egg masses for some time depending on environmental conditions such as soil moisture, soil aeration and soil temperature. Some eggs can stop their development at any stage (embryo, J1 or J2) when adverse conditions occur, and this can be reversed as favourable conditions return. This late development or *tardicultus* is important for RKN survival in field conditions. Detailed information on RKN survival can be found in Evans and Perry (2009). The gelatinous matrix protects every developmental stage inside the egg (embryo, J1 and J2) from desiccation. This is mainly important for J2 because of changes in the eggshell layer before hatching. In dry soils, dehydration of egg masses inhibits egg hatching. The percentage of J2 hatching decreases proportionally to soil moisture between −1.1 and − 3.0 bars

(Goodell and Ferris 1989). In moist soils, the emerged J2 consumes its own reserves at a rate related to environmental temperature because of its poikilothermic nature. Indeed, Goodell and Ferris (1989) reported a reduction of J2 survival related to the accumulated degree days over 10 °C (DD10) when it was incubated at 29 °C and assessed J2 recovery at 100 DD10 intervals. The rate of J2 survival in soil was related to DD when it was assessed in a range of soil temperatures between 15 and 30 °C (Ornat and Sorribas 2008). In agricultural soils, in which the greatest proportion of nematode inoculum is in the egg stage, the density of J2 in soil at the end of the crop in wet soils increases with time until the proportion of hatching is significantly reduced or arrested. Subsequently, the J2 density in soil decreases in relation to accumulated DD. At soil temperatures higher than 38 °C, the exposure time plays a significant effect on J2 and egg survival. Wang and McSorley (2008) found that 100% of J2 were dead when exposed at constant soil temperatures of 39, 40, 41 and 42 °C for 47.9, 46.2, 17.5 and 13.8 h, respectively. At these soil temperatures, egg hatching was completely suppressed after 164.5, 32.9, 19.7 and 13.1 h, respectively. This information is helpful to assess how long a given control method, such as solarization (see Sect. 5.3.1), should be maintained to reduce the nematode density below the economic threshold.

5.2.1.2 Heterodera

Several species of cyst nematodes can parasitize the main crops belonging to the families Solanaceae (tomato, pepper and aubergine) and Cucurbitaceae (cucumber, melon, zucchini and watermelon), as well as other crops that are sometimes included in the rotation sequences under protected cultivation, such those belonging to the families Compositae (lettuce), Chenopodiaceae (chard and spinach), Cruciferae (radish), Leguminoseae (French bean and pea) and Umbelliferae (carrot, celery, parsley and fennel). Among cyst nematode species, *Heterodera schachtii* has the widest range of hosts among the crops mentioned above (Evans and Rove 1998). Plants parasitized by the sugar beet cyst nematode show white-to-brown, lemon-shaped females or cysts adhered to the feeder roots. Eggs in cysts are the survival stage of the nematode. An average annual survival rate of 56% has been reported following the cultivation of an annual non-host crop or fallow (Roberts et al. 1981). Egg hatching occurs mostly in the presence of host root exudates but 10% to 50% of eggs can hatch in water (Zheng and Ferris 1991). The J2 penetrates the root and, after establishing a feeding site, becomes sedentary. After three consecutive moults, the nematode achieves the adult stage. A larger part of the female's body stays outside the root, while the male is vermiform and moves attracted by sexual pheromones to reproduce by amphimixis. Each female can produce 200–300 eggs. Life cycle completion occurs at 344 DD10 (Greco et al. 1982). Spinach yield losses of 29% and 49% were recorded at nematode densities at planting of 6 and 18 eggs+J2 g^{-1} of soil, respectively (Olthof et al. 1974).

5.2.2 *Migratory Endoparasitic Nematodes*

5.2.2.1 Pratylenchus

Several species of the lesion nematode have been found attacking most vegetable crops (Sikora and Fernández 2005), which show necrotic lesions in the belowground parts of the plants. Eggs laid in plant tissue or in soil can survive suboptimal environmental conditions, and juvenile and adult stages can enter in an anhydrobiotic state for more than one year (Castillo and Vovlas 2007). After the J2 has developed inside the egg, it can hatch under optimal conditions, irrespective of the root exudates, and it penetrates the root feeding on the root cortex. The J2 moults three more times before achieving the adult stage. Some *Pratylenchus* species reproduce by amphimixis and others by parthenogenesis. In the latter case, males are scarce. The length of the life cycle depends on soil temperature and moisture. *P. penetrans* needs 564 DD5.1 for life cycle completion (Mizukubo and Adachi 1997). The tolerance limit to *Pratylenchus* species of several crops, including vegetable crops, is summarized in Castillo and Vovlas (2007) (Table 5.5).

5.2.3 *Ectoparasitic Nematodes*

Nematode vectors of plant viruses belonging to the genera *Xiphinema, Trichodorus* and *Paratrichodorus* have been reported to cause yield losses on vegetables, particularly when they are cultivated in sandy soils (Sikora and Fernández 2005).

Table 5.5 Tolerance limit (*T*) of vegetable crops to *Pratylenchus* spp. (summarized in Castillo and Vovlas 2007)

Pratylenchus spp.	Crop	*T* (nematodes cm^{-1} of soil)
P. crenatus	Carrot	0.3–1.8
P. neglectus	Broad bean	2
P. penetrans	Aubergine	0.45
	Bean	0.5
	Brussels sprouts	0.45
	Cabbage	6
	Carrot	1–1.4
	Cauliflower	6
	Celery	0.6
	Cucumber	0.45
	Broad bean	6.2
	Lettuce	6
	Onion	0.67
	Tomato	0.45
P. scribneri	Bean	0.5
P. thornei	Broad bean	2.2

All of these nematodes parasitize a wide range of plant species, including vegetables and weeds, by feeding on root tips, where they induce galls (Longidoridae), or on root hairs and epidermal and subepidermal cells (Trichodorids). Some Longidoridae and Trichodoridae species are vectors of nepo- or tobraviruses, respectively. The retention of viral particles occurs on the inner surface of the odontostyle (*Longidorus*), in the cuticular lining of the odontophore and the pharynx (*Xiphinema*) or in the pharyngeal region (Trichodorids) (Taylor and Brown 1997). Most of these viruses are also transmitted by seeds of several weed species, which are important for their spread to susceptible crops (Taylor and Brown 1997). The economic importance of nematode-transmitted viruses for vegetable crops under protected cultivation is low (Tomlinson 1987). Both Longidoridae and Trichodoridae nematodes are characterized by a slow rate of increase in population density and relatively long adult survival.

There is little information on the population dynamics and effects on crop yield of the other ectoparasitic nematodes found on vegetable crops under protected cultivation (Table 5.1). However, information about the host range of a given PPN species and about the host status of a given plant species to PPNs is available at the Nematode-Plant Expert information system hosted by the University of California Davis (http://nemaplex.ucdavis.edu/Nemabase2010/Nemabase%20Search%20Menu.htm). Despite the lack of information, the increasing frequency of co-occurrence of the most damaging PPNs indicates the importance of studying their role in PPN communities and in crop yield.

Regarding the relationship between cohabiting PPN species, there is some evidence of antagonistic effects, as summarized in Castillo and Vovlas (2007). Examples of these effects include the suppression of tomato infection by *Pratylenchus* spp. in presence of *M. incognita*, which, in turn, produce smaller galls and reproduce more slowly than in absence of *Pratylenchus*, and the reduction of *Pratylenchus* infection when a high proportion (75%) of *Heterodera* co-occur. Other studies involving *Heterodera* and RKNs gave contradictory results. Recent transcriptomic studies have shown that the plant-nematode interaction results in a variety of plant responses that could differentially suppress the infection by other PPN species co-occurring in the same field (Kyndt et al. 2012; Islam et al. 2015). Long-term studies in commercial field conditions are needed to understand the relationships between PPN species in nematode communities and how these relationships influence crop yield before consistent and durable integrated nematode management strategies can be designed. In addition, the relationships between PPN species and other plant pathogens should be considered.

5.3 Control Methods and Strategies

Control methods and strategies for specific PPN management in intensive crops, including vegetables, have been reviewed (Guerena 2006; Ornat and Sorribas 2008; Nyczepir and Thomas 2009; Collange et al. 2011). Most of the current control practices (e.g. chemical nematicides, solarization and biofumigation) are non-specific and reduce nematode densities in the soil at planting or sowing (*Pi*), irrespective of the nematode taxa. Their effect on PPN communities may be high. Some more specific methods (e.g. nematode antagonists, plant resistance and cover crops), when available, may affect the *Pi,* the population growth rate, or both. Some of them may lead to shifts in the species composition in the nematode communities.

5.3.1 General Methods of Reducing Nematode Density in the Soil

5.3.1.1 Sanitation, Fallowing and Escape Cropping

In greenhouse crops, zones infested with PPNs are often found close to shelter entrances and along plant rows. They usually result from the introduction in the greenhouse of contaminated material, water or people. It is therefore recommended to prioritize the tillage of healthy areas before infested ones, and to clean tools, shoes and tractor wheels when passing from infested to uninfested plots. It is advised to avoid sprinkle irrigation because it may scatter eggs and juveniles (Mateille et al. 2005). It is also essential to ensure the sanitary quality of seedlings from nurseries and from planting soil. To reduce the risks of over-infestation and dissemination of nematodes on infested plots, contaminated cropped plants and host weeds (Amaranthaceae, Chenopodiaceae, Compositae, Graminaceae and Polygonaceae), which are reservoirs of infection, must be uprooted and eliminated, even if this is technically very difficult (Rich et al. 2009). Fallowing, tillage and changing of planting date to escape infection in cooler periods are also efficient for keeping PPN populations at lower levels (Ornat and Sorribas 2008). However, these practices are not primary tactics in intensive crop production systems because they may reduce income, increase the cost of weed control, and lead to soil erosion and loss of organic matter through oxidation (Ingham 1996). Similarly, a technical reorientation towards soil-less cultivation would technically solve the problem (Hallmann et al. 2005), but this practice remains expensive and unprofitable in cold shelters.

5.3.1.2 Chemical Methods: Fumigant and Non-fumigant Nematicides

Until recently, fumigant chemical nematicides or fumigant precursors for soil disinfection or liquid or granular products with systemic action were commonly used. All these products are extremely toxic to humans and animals, destructive of the biocoenosis and polluting for the groundwater, and some of them had a role in ozone depletion (Madhava and Gilbert 2000), so their use has been gradually restricted (MBTOC 2006; EPA 2007; EC Directive 1107/2009). The current authorization status of these products is presented in Table 5.6.

Table 5.6 Situation of nematicides according to European Directive 91/414/EC, Regulation 1107/2009 (Annex 1)

	Chemical nematicides		European status
Fumigants	Methyl bromide (organohalogen)	Not approved since 2008	Prohibited
	Enzone (tetrathiocarbonate)	Not approved since 2007	Prohibited
	1,3 dichloropropene(l,3-D) or 1,2-dibromo-3- chloropropane (DBCP) (organohalogen)	Not approved 2007. New authorization requested in 2013	Approval expected for 2018; derogations
	Chloropicrine (trichloro-nitromethane)	Not approved 2011. New authorization requested in 2013	Prohibited
	Metam sodium (thiocyanate)	Approved 2012. New authorization request for dose increase)	Employment restrictions
	Dazomet (thiocyanate)	Approved. In the process of re-evaluation 2011	Employment restrictions
	Dimethyl disulfide (DMDS)	Pending. Authorization requested in 2012 (marketed in the US since 2010)	Approval expected for 2018
	Fluorure de sulfuryle (oxyfluorure)	Approved 2010. Expiry 2020	Employment restrictions
Systemic non-fumigants	Fosthiazate (organophosphorus)	Approved 2004. Expiry 2016. In the process of re-evaluation since 2013	Employment restrictions
	Ethoprophos (organophosphorus)	Approved 2007. Expiry 2018	No longer produced since 2011
	Fenamiphos (organophosphorus)	Approved 2007. Expiry 2018	Employment restrictions (prohibited in France)
	Oxamyl (carbamate)	Approved 2006. Expiry 2018	Employment restrictions
	Aldicarbe (carbamate)	Not approved since 2007	Prohibited
	Carbofuran (carbamate)	Not approved since 2008	Prohibited
Non-fumigant new products	Fluopyrame (pyridinyl ethyl benzamid) / VELUM^{R}	Approved 2014. Expiry 2024	Employment restrictions
	Fluensulfone (fluoroalkenylthioether) / NIMITZ^{R}	Pending. Authorization requested in 2016	Approval expected for 2018
	Furfural (aldehyd)/MultiGuard Protect^{R} ou Crop Guard^{R}	Not approved	Prohibited
	Cinnamaldehyd (cinnamon oil) with diallyl disulfide (DADS) / RESET^{R}	Not approved	Prohibited
	Abamectin (avermectin) / AVICTA^{R}	Not approved	Prohibited

5.3.1.3 Physical Methods: Tilling, Steaming and Solarization

Freckman and Ettema (1993) and Lenz and Eisenbeis (2000) observed that various tillage treatments (with a cultivator or a two-layer plough) affected both the structural (taxonomic) and functional (trophic groups) characteristics of nematode communities, reducing the density of PPNs and increasing the populations of bacterivorous and fungivorous nematodes. Similar results were reported by Parmelee and Alston (1986), comparing conventional versus non-tilling systems. Deep tillage practices are therefore often recommended before fallowing, steaming or solarization to bring nematodes back to the surface. However, Gallaher et al. (1988) showed that the effect of tillage was far less important than the effect of crops in the rotation sequence. Soil sterilization using steam heat under pressure may be efficient for controlling PPNs in glasshouses (Runia and Greenberger 2005), but its use is limited because it involves high costs of heating fuel, changes the soil pH, promotes soil compaction and has a lethal effect on beneficial microorganisms (McSorley et al. 2006). Solarizing moistened soils in areas of high sunlight using thin, single- or double-layered transparent polyethylene tarps is currently a widely used alternative method, particularly in Southern and Eastern European countries (summarized in Wang and McSorley 2008).

5.3.1.4 Organic Methods: Soil Amendments, Biofumigation and Biopesticides

Many literature reviews have focused on the use of suppressive organic amendments to control PPNs (synthetized in McSorley 2011). These amendments include poultry and cattle manures, green manures from cover crops or crop residues, industrial wastes (oil seed cakes and defatted seed meal) and composted and uncomposted town wastes, which are applied on top of the soil as mulches or incorporated into the soil. Three major biological processes acting in combination are involved in PPN control methods: (i) improvement of the soil capacity for holding nutrients and water, which improves plant vigour and therefore increases plant tolerance to PPNs; (ii) stimulation of microbial activities in the soil (including nematode antagonists); and (iii) release of specific toxic compounds during the decomposition of plant tissues in the soil.

Some biocides such as isothiocyanates and hydrogen cyanide (HCN) are involved in a process known as biofumigation. Isothiocyanates are released during biodegradation of the glucosinolates or S-alk(en)yl cysteine sulfoxides present in the Brassicaceae (López-Pérez et al. 2010) and Alliaceae (Rakesh and Sharmaj 1991), respectively. HCN is released by the hydrolysis of dhurrin, a cyanogenic glycoside typically present in sorghum (Curto et al. 2012). The efficacy of biofumigation is variable, but interest in it has recently increased (Curto et al. 2016; Goillon et al. 2016; Djian-Caporalino et al. 2019). Technological improvements such as virtually impermeable plastic foils that are able to hold in the gaseous breakdown products (Gamliel and Stapleton 1993) and soil resetting may improve the fumigation-like effect of biofumigation (Chellami et al. 1997). Many nature-based compounds (plant extracts from *Crotalaria*, garlic, onion, leek, neem, sesame, *Cucumis*, *Asparagus*, *Tagetes*, yucca and hundreds of other plants, or bacteria and mycotoxins from *Bacillus, Erwinia, Muscodor, Streptomyces, Purpureocillium, Trichoderma*, etc.) have also been tested against PPNs, often with good nematostatic or nematicidal activity *in vitro* (synthesized in Chitwood 2003; Rich et al. 2004; Djian-Caporalino et al. 2005). The rate of degradation of the products in the soil and the intensity of infestation of the sites may explain their poor results under field conditions.

5.3.2 Specific Methods for Reducing the Rate of Population Growth

5.3.2.1 Biological Control

Various specific natural antagonists, including nematophagous or parasitic fungi, bacteria and mycorrhizae, have been known for a long time, and several microbial pathogens have been developed into commercial formulations, but very few are approved in Europe (Table 5.7). Moreover, though good efficiencies are found *in*

Table 5.7 Situation of different biocontrol agents (BCA) according to European Directive 91/414/EC, Regulation 1107/2009 (Annex 1)

	Biocontrol agent	Mode of action	European status
Fungi	*Arthrobotrys irregularis, A. conoïdes, A. oligospora*	Nematophagous	Not approved
	Purpureocillium (Paecilomyces) lilacinus	Female of sedentary nematodes and egg parasite	*PL251* approved 2008 (Expiry 2018). Marketed in USA, England, Portugal, Italy, Spain, Morocco, South Africa. Brazil (Bayer Co.)
	Pochonia (Verticillium) chlamydosporia	Female, cyst and egg parasite	Not approved. Marketed in Italy, Portugal, USA, Cuba, Africa, China (several Co.)
Bacteria	*Pasteuria penetrans, P. thornei, P. nihizawae, Candidatus pasteuria*	Juvenile parasite	Not approved Marketed in USA (Syngenta Co) for soybean cyst nematodes
	Bacillus firmus	Ovicidal	*Bf CNCM I-1582* ('Flocter') approved and marked since 2012 (Bayer Co.). Authorization requested for *Bf CNCM I-1562* ('Votivo' and Poncho') for wheat, soy, and cotton seeds
Endomycorrhizae	*Funneliformis (Glomus) mossae, Rhizophagus (Glomus) intraradices, R. (Glomus) fasciculatus, Glomus tenue, Gigaspora margarita*	Under study	Not approved as BCA. Marketing authorization as fertilizer (several Co.)

vitro, some antagonists (e.g. *Pasteuria*) show high host specificity, and results in the field are often disappointing, in particular because of the difficulty in developing stable formulations that allow these antagonists to be installed and act effectively in a variety of pedoclimatic and cultural conditions (Stirling and Smith 1998; López-Llorca et al. 2006; Giné and Sorribas 2017b). Actively managing soil biology using minimum-tillage practices, soil amendments, cover crops and crop rotations can help promote the growth of beneficial PPN antagonists, including bacterivorous and fungivorous nematodes (Freckman and Ettema 1993; Akhtar and Malik 2000) to achieve soil suppressiveness (Giné et al. 2016). Increasing the amount of chitin in the soil (e.g. with crushed crustacean shells) is a way to increase the population of some fungi that attack chitin-containing nematode eggs (Escudero et al. 2016, 2017). Rhizobacteria, mycorrhizae and other microorganisms such as *Trichoderma* may also induce systemic host resistance to PPNs (Barker and Koenning 1998; Veresoglou-Stavros and Rillig Matthias 2012; Vos et al. 2013; Martínez-Medina et al. 2017; Medeiros et al. 2017). Some microorganisms adhered to the cuticle of endoparasitic nematodes might induce plant defence or tolerance mechanisms or affect the development of PPNs, but their specific role in fostering soil suppressiveness is still unknown (Elhady et al. 2017).

5.3.2.2 Cover crops: Trap Crops and Buried Green Manures

There is increasing interest in the use of cover crops grown within or between cash crop cycles to improve sustainable agricultural systems in PPN management strategies (Barker and Koenning 1998; McSorley and Porazinska 2001). They are used as trap crops or through a biofumigation effect (Djian-Caporalino et al. 2005). They exhibit tremendous variability in their susceptibility to PPNs, demonstrating the importance of identifying the nematode species before planning a cover cropping strategy. Any short-cycle susceptible crop (carrot, lettuce or radish) could be used to attract and trap sedentary endoparasites (e.g. root-knot or cyst nematodes) if it is destroyed or uprooted before the nematodes are able to reproduce, i.e. 2–3 weeks after planting (Cuadra et al. 2000; Slosson Final Report 2007–2008). This method should nevertheless not be recommended without the support of phenology models, because the problem can worsen if the plant is not uprooted or destroyed on time. For example, *M. javanica* reproduced at the end of a lettuce crop when it was transplanted in mid-September but not when it was transplanted in mid-October or mid-November in a plastic greenhouse, because the nematode did not accumulate enough DD to achieve reproduction (Ornat and Sorribas 2008).

When phenology models are not available, plant species that allow nematode infection but not reproduction are preferred. For example, arugula (*Eruca sativa* L.) and some resistant peppers have been proved to be efficient as trap cover crops in the greenhouse, strongly decreasing RKN infestation in soil (Melakeberhan et al. 2006; Djian-Caporalino et al. 2014; Navarrete et al. 2016). The well-known marigold (*Tagetes* spp.) could also be used as a cover crop. It produces alpha-terthienyl, an allelochemical active on 14 PPN genera, including root-knot and lesion (*Pratylenchus* spp.) nematodes (Hooks et al. 2010). However, to be efficient, plants must be used as intercrops planted just before or immediately after the termination of the cash host crop (when nematodes are active rather than dormant) or close to the cash crop roots (nematodes cannot migrate long distances on their own) (McSorley 2001). Some poor host plants can also be used as cover crops under shelters and incorporated as biofumigant green manure (Kruger et al. 2013). For plots free in the summer (e.g. after melon or zucchini crops), the most frequent species used are Sudangrass (*Sorghum sudanense*) and Sudangrass hybrids (*S. bicolor x S. sudanense*) (Goillon et al. 2016). If the cash crop is still present in the summer (e.g. tomato or sweet pepper), cover cropping can be carried out in the autumn with Brassicaceae (e.g. forage radish or white mustard) (Giné et al. 2016). Their efficiency depends on the developmental stage of the plants when they are buried and the variety used.

5.3.2.3 Plant Resistance and Crop Rotation Management

In addition to crop rotation with a poor host or non-host that reduces the rate of population growth, the main aspect of crop management is the use of genetic resistance, which determines the level of PPN reproduction in the plant. Breeding for PPN resistance has become a major challenge in most crop improvement programmes, which are engineered through new molecular techniques (Williamson and Kumar 2006; Fuller et al. 2008). However, the introgression of PPN resistance genes (R genes) into commercial cultivars or rootstocks has several limitations. Firstly, this strategy is more effective against sedentary endoparasitic species, which are trapped within the roots if the specialized feeding cells on which they rely fail to develop, than against ectoparasitic species (Williamson and Kumar 2006). Secondly, although sources of resistance have been reported for tomato, pepper, eggplant, cucumber and lettuce (Boiteux and Charchar 1996; Walters et al. 1996; Maluf et al. 2002; Barbary et al. 2015), few R genes have been identified and only two of them are widely available in commercial varieties, i.e. *Mi1.2* and *N* in tomato and pepper, respectively. Moreover, some sources of nematode resistance are complex traits that are inherited polygenically, and the genes involved in the resistance mechanisms have rarely been identified (Barbary et al. 2016). Thirdly, constant soil temperatures above 28 °C suppress the expression of some resistance genes (e.g. *Mi1.2* in tomatoes) (Devran et al. 2010), but the expression is not affected when soil temperature peaks over 28 °C at some time in a day, a situation that is frequently encountered in soils under shelters (Verdejo-Lucas et al. 2013a). Finally, major R genes may be highly specific (to one single PPN species or even to one or a few isolates from one species) and tend to be overcome in the long run (Thies 2011; Djian-Caporalino et al. 2011; Castagnone-Sereno 2012; Giné and Sorribas 2017a; Expósito et al. 2019). Nevertheless, RKN R-pepper cultivars with the *N* gene (such as Charleston Belle) or in which two R genes are pyramided (such as *Me1Me3* hybrid) are already useful tools for managing *M. incognita* in double-cropping systems with cucurbit or lettuce crops (Thies, et al. 2004; Djian-Caporalino et al. 2014), or in double-cropping systems with RKN R-tomato cultivars (Ornat and Sorribas 2008; Giné and Sorribas 2017b). The use of these cultivars requires a constant hierarchy of management strategies to preserve their durability, with pyramiding > alternating > mixture of R genes > sequential use of a single R gene introgressed in a susceptible background (Djian-Caporalino et al. 2014). Because virulent RKNs have poor intrinsic dispersal ability and exhibit a reduced fitness on susceptible crops (Djian-Caporalino et al. 2011), combining resistant and susceptible plants in crop rotation over cropping seasons can also help increase the efficacy and sustainability of resistance-based nematode control.

A model was developed to describe plant root infection dynamics by PPNs and to minimize a proxy of nematode damage to crops, taking into account virulent cost and fitness of virulent nematodes (Nilusmas et al. 2016). This model gave optimal periodic crop rotations with rather few resistant plants, e.g. one resistant plant followed by three susceptible plants or by five susceptible plants on a 10- or 20-season temporal horizon, respectively. However, the efficacy of this strategy could depend on the specific interaction between the RKN species, the plant germplasm and the environmental conditions. In fact, two consecutive resistant tomato crops before cropping a susceptible tomato were needed to reduce nematode densities and to increase crop yield, in comparison with growing only one resistant cultivar followed by, or inserted between, two susceptible ones or with growing three consecutive susceptible cultivars (Talavera et al. 2009). A possible strategy for avoiding selection for virulence is the alternation of non-related sources of resistance. However, the main constraint is how long must elapse between cropping cultivars with the same R gene. Recently, a potential cucurbit rootstock was shown to be resistant to RKN populations, irrespective of their (a)virulence status to the *Mi1.2* resistance gene in tomato, and without conferring undesirable traits to melon fruits (Expósito et al. 2018). Nonetheless, the alternation of resistant tomato with melon grafted onto *C. metuliferus* did not prevent virulence selection to the *Mi1.2* gene, but the level was reduced (Expósito et al. 2019).

The control methods described against PPNs have all shown their limits when used individually (Collange et al. 2011). Several studies of RKNs in vegetable greenhouse cropping systems have shown the beneficial effect of integrated strategies deployed on pluri-annual crop sequences, resulting in a reduction of parasitic pressure in the soil and thus in an increase in the durability of R genes and a sustainable management of nematode problems (Navarrete et al. 2016; Djian-Caporalino et al. 2019). The current challenge for PPN control, quite innovative in Europe, is to co-design new cropping systems with stakeholders, focusing on the strategy of the "systems approach" instead of on one or several plant-pathogen model cases, and taking into account environmental and socio-economic impacts to avoid shifts in dangerous PPN species and increase their potential for adaptation.

5.3.3 Ecological sustainability of management strategies

Agronomic approaches for PPN control have always emphasized plant-parasite interactions involving a plant species and a PPN species (population scale). They have thus identified emblematic PPN species for each type of crop (Evans et al. 1993;

Luc et al. 2005), such as RKN species for vegetables. However, PPNs are everywhere detected as species communities. Moreover, it has been established that the plant production could depend on the diversity of the PPN communities (Lavelle et al. 2004). Consequently, the development and application of species-specific alternative control practices raises the question of their ecological sustainability, because the control of a species in a community may induce diversity shifts without necessarily solving the long-term nematological risk of the residual community.

5.3.3.1 Potential Shifts Between *Meloidogyne* species in Communities

Some resistance genes are very specific and confer resistance to a single *Meloidogyne* species, such as *Mech1* or *Mech2* against *M. chitwoodi* in *Capsicum annuum* (Djian-Caporalino et al. 2007). *M. hapla* and *M. enterolobii* are also not controlled by the *Mi* or *Me* genes (Djian-Caporalino et al. 1999; Castagnone-Sereno 2012). Obviously, such variability in the specificity of the available resistance genes limits the use of RKN-resistant cultivars. For example, a wide survey conducted in Senegal revealed that vegetable crops are infested by four *Meloidogyne* species (Trudgill et al. 2000): *M. arenaria, M. enterolobii, M. incognita* and *M. javanica*. Species mixtures were detected in 26.9% of the samples (1.3% with four species, 6.4% with three species and 19.2% with two species). In Senegal, *Mi*-resistant cultivars account for 95% of the seeds used. These cultivars were inefficient in providing protection in 15.4% of the mixture cases and, of course, when pure *M. enterolobii* populations occurred (19.2% of the samples), because no gene resistant to this species exists.

Similarly, the efficiency of nematicidal plants used as green manure or cover crops are highly PPN species-specific. For example, the paralysis of second-stage juveniles of *M. enterolobii, M. incognita* and *M. javanica* by aqueous root extracts of 15 West African *Crotalaria* species (Fabaceae) containing toxic alkaloids was analysed (Jourand et al. 2004). *M. incognita* was susceptible only to *C. gorrensis* extracts, *M. enterolobii* only to *C. atrorubens*, and *M. javanica* only to *C. pallida* and *C. perrottetii*. It was concluded that it will be problematic to select a *Crotalaria* species for controlling mixtures of *Meloidogyne* species.

Complex vegetable cropping systems including good, poor and resistant host crops and solarization were assessed in the French Mediterranean region in order to control mixed populations of *M. arenaria* and *M. incognita*. Solarization, resistant pepper and corn salad selected *M. incognita*, while susceptible pepper, salad and parsley increased *M. arenaria* (Djian-Caporalino et al. 2015).

The same observations can be made with biological control. In the predation of PPNs by nematophagous fungi, the host preference and the prey recognition are very specific (Askary and Martinelli 2015). When assessing the trapping efficiency of several West African strains of the fungi *Arthrobotrys oligospora* and *A. conoides* on second-stage juveniles of *M. enterolobii, M. incognita* and *M. javanica*, Duponnois et al. (1996) found that the *M. javanica* juveniles were trapped by one *A. oligospora* strain only, and another strain was able to trap *M. enterolobii* exclusively. With regard to parasitic bacteria, all the isolates of *Pasteuria penetrans* tested to date appear very specific to nematode hosts (Davies and Spiegel 2011). It has been observed that the attachment of a *P. penetrans* strain (PP1) to different RKN field populations showed different attachment rates depending on the origin of the RKNs (Davies et al. 2001). However, isolates maintained in contact with various *Meloidogyne* species showed a wider host range than isolates maintained on the same nematode strain for several generations (Davies et al. 1988). It will therefore be difficult for a biocontrol agent producer to develop a single generic bio-agent to control communities hosting mixed *Meloidogyne* species.

5.3.3.2 Potential shifts between different PPN taxa in communities

Shifts in PPN communities impacting PPN coexistence are likely to result from the application of natural control alternatives in cropping systems (Stirling 2014), especially when these alternatives are species-specific. Moreover, strong shifts would be expected because coexisting species exhibit different biological properties, including (i) life-cycle duration; (ii) fecundity; (iii) reproduction by amphimixis and mitotic and meiotic parthenogenesis (these three modes can be found among a same genus, such as RKNs or *Pratylenchus*; (iv) and parasitism strategies such as ecto-, endo- and semi-endoparasitism, and migratory or sedentary species. As an example of such shifts, a study conducted in Southern France compared the kinetics of different taxa in PPN communities including and excluding *M. incognita* and subjected to technical itineraries involving susceptible and resistant crops and a nematicidal cover crop (Mateille et al. 2019). In communities that harboured RKNs, the cropping system that was targeted for controlling RKNs led to the continuous long-term replacement of RKNs by Dolichodoridae nematodes. This would mean that, contrariwise, when a crop succession is susceptible to RKNs, the Dolichodoridae are excluded by competition. In communities without RKNs, the competition between Tylenchulidae and Dolichodoridae seems to be more cyclic, with a long-term increase in both PPN families, meaning less dependence on the cropping system. It seems that competition of RKNs and Dolichodoridae with Tylenchulidae and Dolichodoridae corresponds to hierarchic and cyclic models, respectively (Begon et al. 2006). Considering that the Tylenchulidae and Dolichodoridae could be pathogenic on vegetables (Potter and Olthof 1993), the replacement of RKNs by these taxa must be considered in control strategies. Partly as a consequence of the alternative strategies developed against RKNs, it is now very clear that Tylenchulidae nematodes are gradually invading the vegetable production area in Southern France.

Therefore, the sustainability of soil suppressiveness should be considered not only in terms of managing specific antagonisms (i.e. PPN species vs. resistance, service plants, biocontrol agents, etc.) but also in terms of managing the biodiversity and pathogenicity of the whole PPN communities (i.e. ecological sustainability) (Mateille et al. 2008).

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Part II
Tools for IPDM in Greenhouses

Chapter 6
Integrated Pest Management Methods and Considerations Concerning Implementation in Greenhouses

Joop C. van Lenteren and Philippe C. Nicot

Abstract We consider IPM as a combination of durable, environmentally, toxicologically and economically justifiable farming practices which prevent pest damage primarily through the use of natural factors limiting pest population growth and disease development, and which resort only if needed to other, preferably non-chemical, measures. IPM is not simply a combination of various control methods. We give an overview of IPM measures used in greenhouses and refer to specific chapters in this book for examples. In IPM, each practical situation dictates a number of special aspects for consideration, and IPM methods need continuous adaptation, making IPM knowledge intensive and interactive. Successful IPM programmes for greenhouse crops have a number of characteristics in common: (a) their use was promoted only after a complete IPM programme had been developed, (b) intensive support by the extension service was essential during initial implementation, (c) the costs of crop protection with IPM should not be higher than those of a chemical control programme, and (d) non-chemical management methods, such as biocontrol agents and resistant plant material, should be as easily available, as reliable, and as constant in quality, as chemical agents. IPM research and implementation in greenhouses during the past 50 years has taught us the lesson that the development of an IPM programme needs to be discussed in a very early stage with all stakeholders, including growers, pest management specialists, extension services and researchers. Such a meeting often results in a pragmatic design of a draft, very pragmatic IPM programme, which is continuously adapted during later meetings, based on growers' experience and new research results.

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Keywords Pest prevention · Pest reduction · Cultural control · Curative control · Host-plant resistance · Natural biocontrol · Classical biocontrol · Conservation biocontrol · Augmentative biocontrol · Semiochemical control

6.1 Introduction

Integrated pest[1] management (IPM) has been defined in many ways, from very pragmatic (the use of a combination of all kinds of management techniques to reduce pest problems) to ecologically and philosophically based ones (the use of ecosystem services and non-chemical management techniques and only in very exceptional cases selective chemical control as a last resort) (Radcliffe et al. 2009). The original meaning of IPM, also expressed in the definition given below, has often been corrupted, and is sometimes even used to denote Integrated Pesticide Management, Intelligent Pesticide Marketing or pesticide-dominated control programmes with the addition of a single non-synthetic pesticide. In this chapter, we will use a definition (adapted from Gruys, P., in van Lenteren 1993) that reflects our concern for biodiversity and the environment, but takes the economics of crop production into account: IPM is a combination of durable, environmentally, toxicologically, and economically justifiable farming practices which prevent pest damage primarily through the use of natural factors limiting pest population growth and disease development, and which resort only if needed to other, preferably non-chemical, measures.

From the time agriculture developed some 10,000 years ago until 1945, farming was based on a systems approach and crop protection programmes relied first of all on prevention methods of pests and diseases based on natural factors, because chemical control measures were not abundantly available. Thus, for ages crop protection was based on IPM and included, among others, periods of fallow, planning of crop combinations, crop rotation, tillage, use of resistant or tolerant crop cultivars, choice of the right planting and harvesting periods, biological, mechanical and physical control, etc. Due to developments in plant genetics, and the production of synthetic fertilizers and pesticides, agricultural research changed from a systems approach into an extremely reductionist science where pests are controlled by preventive calendar sprays and curative treatments with chemical pesticides. However, during the past decades it has become clear that reliance on pesticides may give rise to all kinds of problems, such as the development of resistance to pesticides by pests resulting in a pesticide treadmill with ever increasing treatment frequencies or volumes, the enhancement of secondary pests because of a decimation of natural enemies by pesticide treatments, the pollution of water, soil and air, the reduction of biodiversity and the interference with ecosystem services such as water and soil cleaning, pollination and crop protection, the production of food with pesticide residues and a variety of direct and indirect negative impacts on human health (Bourguet

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[1] The word pest is used in this chapter as defined by FAO/IIPC (1997), and includes weeds and animal pests as well as causal agents of diseases.

and Guillemaud 2016; Erisman et al. 2016; Pimentel and Burgess 2014; Tillman et al. 2012). Nowadays, consumers and in a number of cases also governments, are stressing the need for a drastic reduction in the use of chemical pesticides and plea for healthier food and a cleaner environment (Buurma et al. 2012; EC 2009). In this chapter we will illustrate that there are many non-chemical alternatives for pesticides even in the setting of crop production in greenhouses, and that a shift from pure chemical control to IPM is occurring worldwide (Pérez-Hedo et al. 2017).

Before we present these alternatives, we want to express that we are not advocating dogmatic, one-sided pest control approaches for greenhouse crops. Instead, we propose to combine the sustainability gain from all types of horticulture and pest prevention/control methods, including modern plant breeding. The fact that more creativity, knowledge and ecological insight are needed to be able to apply such pesticide-free/poor IPM crop management schemes should not be an excuse to keep using easier synthetic pesticide programme. Actually, IPM programmes for various greenhouse crops, including ornamentals, have shown to lead to higher yields and better quality of produce, and thus, a much better profit for the grower (see examples in Chaps.16 and 23).

6.2 Methods Used in Integrated Pest and Disease Management in Greenhouses

A wide variety of methods is available for IPM in the greenhouse (Table 6.1). They will be presented in relation to the timing of their implementation in the cropping season.

6.2.1 Measures Taken Before the Cropping Season to Prevent Infection of the Crop

The first line of defense is to try to *prevent the introduction of new pests* into a production area, but this is easier said than done. International organizations and national institutions have set up networks, regulations and inspection systems to prevent accidental introduction of new pests (see e.g. www.FAO.org, www.IIPC.int, www.efsa.europa.eu), but despite this, the number of new pests accidentally introduced is exponentially increasing and also forms a serious problem for greenhouse crops (Bacon et al. 2012; Seebens et al. 2017). In order to control invasive invertebrate pests, it was, until very recently, possible to collect potential biological control agents in the country of origin of the pest, and evaluate, mass produce and release them when an effective agent was found. But today, under the Convention on Biological Diversity (CBD 1993) countries have sovereign rights over their genetic resources, and agreements governing the access to these resources and the sharing of benefits arising from their use need to be established between involved parties

Table 6.1 Methods to prevent or reduce pest populations in greenhouses

IPM method	Use in Greenhouse IPM	Chapter treating this issue
Measures taken before the cropping season to prevent infection of the crop		
Prevent introduction of new pests (e.g. inspection and quarantine)	+	1
Apply cultural control (e.g. crop rotation)	+/−	10, 17–22
Start with clean seed and plant material (e.g. thermal disinfection)	+	11, 17–22
Start with pest free soil (steam sterilization, solarization and biological control (e.g. *Trichoderma*))	+	12, 17–22
Prevent introduction from neighboring crops (e.g. netting)	+	10, 17–22
Use plants which are fully resistant or tolerant to pests	+	9, 17–22
Measures taken during the cropping season to reduce infection of the crop		
Apply cultural control (e.g. trap crops)	+/−	5, 10, 17–22
Use plants which are partly resistant or tolerant to pests	+	9, 17–22
Exploit natural classical, conservation and augmentative biocontrol	+/−	14, 17–22
Apply one of the following curative control methods		
Mechanical control (mechanical destruction of pest organisms, vacuum cleaners, hand/machine removal of weeds)	+	10
Physical control (heating, UV treatment; colour traps)	+	10, 17–22
Control with attractants, repellants and antifeedants	+/−	14
Control with pheromones (mass trapping, confusion techniques)	+	14, 16–22
Control with other semiochemicals (repel pests, attract beneficials)	+/–	14, 16, 18
Control with hormones (disrupt development, prevent reproduction)	−	14, 19
Genetic control (sterile insect technique)	−	–
Conservation and augmentative biological control	+	13, 14, 17–22
Selective chemical control	+/−	15
Non-selective broad spectrum chemical control	+	15
Guided or supervised pest management: control based on sampling and spray thresholds	+/−	7
IPM: control based on the integration of methods which cause the least disruption of ecosystems	+	7, 16

(i.e., Access and Benefit Sharing (ABS) (https://www.cbd.int/abs/); Cock et al. 2010)). Today, permission to sample biological control agents must first be granted by the country where one intends to collect new natural enemies, and practically it has become impossible to do so in many cases due to unclear and very time consuming bureaucratic procedures (Mason et al. 2018). The consequence is that one of the main sources to combat invasive species, i.e. by classical biological control, may have been cut off.

Another method to prevent pest development is to *start with clean seed and plant material*, and this is used frequently in greenhouse IPM. For details about the many methods to obtain pest free seeds and plants, we refer to Chap. 11.

A start with a *pest free growing substrate* is also important and production on various soilless substrates is common, particularly in high-investment heated glasshouses. For greenhouses with plants grown on soil, the presence of soilborne pathogens is usually detrimental, with the exception of "suppressive soils" for which the resident microbiome is able to prevent disease development (Schlatter et al. 2017; Mazzola and Freilich 2017). When needed, a variety of non-chemical methods can be applied to reduce or eliminate soilborne pests. These methods include crop rotation, the use of trap plants, biofumigation, anaerobic soil disinfestation and stimulation of beneficial microbial communities through the cultivation of cover crops as green manure or the application of soil amendments or microbial biocontrol agents (Pannacci et al. 2017; Katan 2017; Shrestha et al. 2016; Mazzola and Freilich 2017). Soil solarization and biosolarization offer increasing possibilities against soilborne pests, with progress in mulching technology and synergistic combinations with various organic amendments or biocontrol agents (Katan 2017; Oka et al. 2007; Pane et al. 2012; Öz et al. 2017; Butler et al. 2014). Solarization and biosolarization are also increasingly noted for their possible role in decontaminating soil tainted with pesticide residues (Fenoll et al. 2017; Vela et al. 2017).

Mulching (with polyethylene film or organic matter) can also contribute to the protection of the crop by affecting the survival and development of soilborne pests (including weeds) through its many physical effects on the soil and the soil microbiota and by preventing direct contact between aerial plant organs and pests present at the soil surface.

To avoid the carry-over of pests from one crop to the next in the greenhouse (for example virus-vectoring insects, inoculum of plant pathogens as free propagules or embedded in plant debris or soil particles), it may be necessary to respect a *plant-free period between successive crops* and to clean thoroughly and *disinfest the greenhouse structures*. Disinfestation can be achieved by heat (steam or keeping the greenhouse closed during a hot weather period) or with the help of chemical disinfectants. Finally, growers can use completely closed glasshouse structures with advanced climate management, or glass or greenhouses where all openings at windows are covered with fine mesh netting to *prevent entrance of pests*.

6.2.2 Measures Taken During the Cropping Season to Reduce Infection of the Crop

Host-plant resistance is one of the important cornerstones of IPM and its role could become even more important for many greenhouse crops in the near future because of new genetic techniques (Chap. 9). Selection of plant resistance has been widely focused against diseases and it has remained less significant against arthropods, but we expect increasing interest for selection of arthropod resistance in crops. While full resistance is most commonly sought, partial plant resistance can also be quite useful in IPM. This is particularly true for pest control, as a slowdown in pest population development may greatly facilitate the beneficial effect of natural enemies. Both classic and modern plant breeding, including CRISPR-Cas and RNAi, will help us design robust IPM programmes. Changing plant characteristics by breeding can help pest and disease prevention in different ways: by making a plant less sensitive, repellent or even poisonous to a pest, but also by producing attractants for biological control agents after pest attack (Dicke 2016; Kappers et al. 2011), or by harbouring microbiomes that foster natural biocontrol. Plant architecture may also be selected for features which foster accessibility for natural enemies or render canopy structure and microclimate less conducive to disease or pest development (Grumet et al. 2013; Tivoli et al. 2013). Finally, susceptible varieties can be grafted on rootstock with resistance to various soilborne pests (Katan 2017; Louws et al. 2010; Gamliel and van Bruggen 2016), and resistance of the rootstock to airborne pathogens can sometimes also be of benefit to the grafted variety (Albert et al. 2017). Most varieties used as rootstock are also known to improve agronomic traits of the crop, including tolerance to abiotic stress (Schwarz et al. 2010). For several vegetable crops this practice is implemented on a large percentage of the acreage (Kyriacou et al. 2017; Louws et al. 2010) (Chaps. 17–19).

A wide array of *cultural control methods* may also be mobilized for IPM in the greenhouse (Chap. 10). These practices can render the physical environment of the crop less conducive to pest development, decrease the physiological receptiveness of a susceptible crop to its pests or have a direct suppressive effect on those pests. Avoiding periods of high humidity, dew formation on the plants and guttation is a key to limiting the incidence and the impact of most airborne fungal and bacterial diseases. Although cost may be an issue, this can be achieved through (often computer-controlled) climate management in heated glasshouses. Some level of climate management can also be achieved through ventilation in unheated greenhouses; in Mediterranean climates, moderate high temperatures in summer months is a key issue to extent cropping season. Microclimate within the canopy can be further modulated to be less favourable for the pests by adjusting row spacing, planting density, type and timing of irrigation, N-fertilization and by adapting plant architecture, for example through leaf pruning (Decognet et al. 2010). Fertilization and water supply may also affect the physiological receptiveness of the plants to pathogens and the development of plant feeding pests (Datnoff et al. 2007; Han et al. 2014; Ximenez-Embun et al. 2017; Achuo et al. 2006; Nicot et al. 2012). However, the design of fertilization schemes for IPM purposes may be complicated by opposite effects for different pests and the need to take into account possible impact on yield (Nicot et al. 2012; Hoffland et al. 2000; Xu et al. 2013). Plant susceptibility may also be influenced by the application of a variety of compounds and microorganisms that stimulate its natural defence system. These typically include biopesticides (Chap. 13) and plant biostimulants, two types of products that are gaining increasing interest in horticultural production, for use as foliar or root treatments (Colla and Rouphael 2015; Le Mire et al. 2016; Pappas et al. 2017). Biostimulants comprise a great variety of compounds with numerous underlying biological processes and combined properties of fertilizers and plant protection products, a situation which complicates the definition of a clear regulatory framework for their registration (La Torre et al. 2016; Yakhin et al. 2017).

All types of *biological control* – natural, classical, conservation and augmentative – can be used to prevent population increase of pests to densities where they become damaging (Chaps. 13 and 14). Recent experience in Spain has shown, for example, that naturally occurring natural enemies in combination with growing nectar-and pollen-providing plants between greenhouses enhances biological control inside greenhouses. Another example is natural control of leafminers in the Netherlands; in the 1980s after invasions of different leafminer species into northern Europe we found that they are kept below damage levels as soon as the weather necessitates regular opening of windows for cooling and native parasitoids can enter the glasshouse. Also, preventative releases with natural enemies – a form of augmentative biological control – are increasingly made in young plantings of vegetables and ornamentals, even before the pest has been seen, in order to guarantee immediate reduction of pest populations when they enter the greenhouse (Calvo et al. 2012a). This is often done in combination with the use of banker plants so the natural enemies can establish on alternative food (Messelink et al. 2014). While virtually absent from the greenhouse 20 years ago, biological control agents and biopesticides are now increasingly available for the management of airborne plant pathogens (Nicot and Bardin 2012; van Lenteren 2000; van Lenteren et al. 2018). They include microorganisms with a variety of modes of action (Chap. 13), as well as plant extracts and other natural compounds. Commercial products are registered against the major pathogens of important vegetable crops, but there is still a large discrepancy between countries and some increasingly prevalent diseases such as downy mildew (late blight for tomato) are not well covered. Similarly, greenhouse crops include a large gamut of “minor” (mostly ornamental) crops, for which registration of biocontrol products is lagging behind.

Next to reduction of pests in an early phase of development, there are also many methods that can be used curatively. *Mechanical control* has been applied since the origin of agriculture in many different ways, starting with simple hand weeding, and hand removal of pest individuals or diseased plant parts. Mechanical removal of weeds is now also used and large “vacuum cleaners” specially designed for use in greenhouses can be used over young and/or relative small plants to remove arthropods. Also *physical control* has been used since long in the form of burning of pest infected material, or by placing sticky colour traps in the greenhouse (a combination of mechanical and physical control). Currently interesting developments take place, whereby disease causing organisms are filtered (mechanical control) and killed by UV treatment (physical control) of the irrigation water in drip irrigation systems where water is recirculated (Scarlett et al. 2016; Prenafeta-Boldu et al. 2017). Recently, aerial treatment with UV has been applied in greenhouses to destroy plant pathogens or reduce their infectivity (Suthaparan et al. 2017) and some potential has been shown of using hormetic doses of UV light to decrease plant susceptibility

(Vargas-Hernandez et al. 2017). Many chemical *attractants, repellents and anti-feedants* are on the market for the control of arthropod pests, but their use is limited in greenhouses. A special group of attractants are *pheromones* (chemical compound(s) produced by an organism that trigger(s) a response in an organism of the same species) and these are regularly used in greenhouses to monitor pest presence, to mass trap pests or as a confusion technique by putting an overdose of a synthetic sex pheromone in the greenhouse with the result that males can no longer find their female partner that emit the natural sex pheromone (see Chap. 14 for examples); this technique for monitoring and control is only feasible and useful in cases of Lepidoptera mating inside greenhouse but not for those pests that mostly mate outside the greenhouse and go into already mated. Also *semiochemicals* (chemical compounds playing a role in communication between organisms of the same or other species) form a special group of attractants and repellents: greenhouse multitrophic systems consisting of plants, pests and biological control agents are interacting, among others, with chemical communication. Some of the volatile chemical compounds produced on attack by a pest (a disease-causing organism or nematode attacking roots in the soil, or an insect attacking leaves of the plant) do attract natural enemies, and the same or other compounds repel pests or induce defence reactions in the plants (Dicke 2016). Knowledge about semiochemicals has quickly developed since the 1970s (e.g. Nordlund et al. 1981), but although there are now thousands of scientific publications and many claims have been made about their potentially positive contribution to pest management in IPM programmes, their practical use is still very limited in the greenhouse. We know of one published example showing, in a test with eight cucumber varieties equally infested with the spider mite *Tetranychus urticae*, that (1) these varieties emitted different compositions and quantities of volatiles, (2) the composition of the blends of emitted volatiles was more important than the volume, and (3) that amounts of 4 specific volatiles correlated positively with attraction of predatory mites. These results imply that foraging success of natural enemies can be enhanced by breeding for crop varieties that release specific volatiles after pest attack (Kappers et al. 2011). In some cases, pest control with synthetic *growth hormones* had been applied. These hormones disrupt development of the pest, prevent reproduction and are rather pest specific so can be integrated with other non-chemical management methods. *Genetic control*, for example by introducing large numbers of sterile males into the greenhouse so that females mate with these sterile males and do not reproduce, has been proposed for control of several pests, among others for whitefly, but is not popular in greenhouses. Augmentative biological control through the repeated release of beneficial organisms has been applied in greenhouses since the 1920s and is now a popular method for control of pests and diseases worldwide. Many biological control agents (parasitoids, predators, pathogens) are commercially available (Chaps. 13 and 14) and have shown to be as reliable as or better than chemical control (e.g. van Lenteren et al. 2018). Biological control has in several cases even saved the greenhouse sector, because chemical control of several key pests was no longer effective (e.g. Calvo et al. 2012b). Specific cases of biological control are mentioned in many of the following chapters, but a good recent example showing the large array of biocontrol agents available for almost all key pests in tomato is presented by Pérez-Hedo et al. (2017). Because of the high sensitivity of biological control agents for all groups of pesticides, including herbicides and fungicides, *non-selective broad spectrum chemical control* can not be used in IPM, unless their application is on selected spots and in low doses (Chap. 15). In IPM, *selective chemical control* can be used under strict conditions. First of all the grower should determine whether chemical control is necessary based on reliable sampling for pests in the crop. Next, a suitable selective chemical control method should be selected. An extensive overview of potential candidates to replace conventional synthetic pesticides can be found in Benuzzi and Ladurner (2017). Generally, when using biological control, the grower should try to delay spraying as long as possible to avoid killing beneficial organisms such as biocontrol agents and pollinators, and to prevent causation of secondary pests (pests that develop as the result of killing their natural enemies or antagonists and which normally do not cause problems when no or very selective pesticides are used; an example of a secondary pest is leafminers). If spraying is inescapable, it is recommended for arthropod control to spray only at pest foci, spray with lower than advised volumes of active ingredients, and use those selective pesticides that have limited negative effects on beneficial organisms. Spraying with lower than advised doses of fungicides for disease control is also increasingly done, but care should be taken not to increase concomitantly the frequency of treatments, as for certain pathogens this could foster the development of resistance (Jørgensen et al. 2017). Pesticide side-effect and selectivity data have been determined for many years by the working group "Pesticides and beneficial organisms"of IOBC-WPRS (www.iobc.wprs.org) and information on side effects can now be accessed on the internet (e.g. www.iobc-wprs.org/ip_ipm/IOBC_Pesticide_Side_Effect_Database.html), websites of producers of beneficial organisms or via app's provided by producers of beneficial organisms on a smart phone.

6.3 Making Implementation of IPM a Success

In this chapter we will not discuss implementation of IPM in detail, this topic will be treated in Chap. 16. From behind a desk it is rather easy to develop a set of guidelines for implementation of IPM. Each practical situation dictates, however, a number of special aspects for consideration, which we will present below. We have experienced during the past decades that implementation of IPM in greenhouses in some crops and regions (e.g. vegetables in temperate climates) is much easier than in others (e.g. vegetables in semi-tropical climates, and ornamentals in all climates) because of differences in attitudes of growers, in climate, in greenhouse design, in culture methods and in composition of the pest complex. When considering to start working on an IPM project from scratch it is important to formulate targets for research. In Table 6.2, the targets for research are formulated for new and already running IPM programmes.

Table 6.2 Targets for IPM research

A. Targets for research if IPM is not yet in use
Verify if biological control and other non-chemical methods have a chance of implementation (attitudes of growers and policy makers, possibilities for production of natural enemies, availability of other non-chemical control methods, etc.)
Make an inventory of pest, disease and weeds problems the specific crop
Check whether supposed status (importance) of the pests is estimated correctly, exaggerated or underestimated, and estimate economic threshold densities
Find out (through literature search and correspondence) which of the pests can be controlled by existing non-chemical control methods, exploring the entire spectrum from cultural methods, host-plant resistance and mechanical control to biological control, based on the overview of Table 6.1
Determine which pests can be controlled only with regular applications of broad spectrum pesticides. If these are key pests, their control will interfere with the use of biocontrol and IPM. A solution for the management of these pests must be found before introduction of biocontrol agents will be possible. If no short-term non-chemical solution for management of such key pests can be found, these pests will become priority targets for biological control research
If biological control methods or other non-chemical or selective chemical control methods are available for all pests and diseases, an IPM programme can be designed and tested under semi-commercial conditions. An extension programme will have to be implemented and a reliable delivery programme for control agents should be developed
B. Targets for research in ongoing IPM programmes
Identify potential pests which might be introduced into protected crops from elsewhere and become invasive. Make an inventory of available control strategies which are compatible with the ongoing IPM programme. Such studies of anticipated invasive pests can prevent panic actions which disrupt biological control of the previously established pests
If key pests are all under non-chemical control, start to evaluate natural enemies or other selective control methods for secondary pests
Start to develop biocontrol for pests which are presently controlled by selective pesticides that will be removed from the market
Further develop the toolbox of biocontrol solutions against diseases, especially those still poorly covered by currently available products, both in major and in minor crops
Increase the resilience of the total IPM system, e.g. by using polyphagous natural enemies, by preventative release or inoculation methods, and by increasing the diversity of tools available in the IPM toolbox

Successful IPM programmes for greenhouse crops have a number of characteristics in common. First of all, their use was promoted only after a complete IPM programme had been developed, covering all aspects of pest control for a crop. Secondly, an intensive support of the IPM programme by the advisory/extension service or by the provider of biological control agents was necessary during the first years. Next, the total costs of crop protection in the IPM programme were not higher than in the chemical control programme, or, if the management methods of IPM were more expensive, these costs should be more than compensated by a higher yield, a higher price for the produce, and better produce quality. Finally, non-chemical management methods (like biological control agents and resistant plant material) had to be as easily available, as reliable, as constant in quality and their deployment had to be as well guided as for chemical agents (van Lenteren 1993).

Below we describe how success was obtained in northern Europe by forming voluntary working groups of researchers, extension agents and growers. Similar results have elsewhere been obtained by study groups formed by growers.

An implication in IPM research and implementation in greenhouses for several decades has taught a number of essential lessons on ways to obtain success, which were earlier presented in van Lenteren (2009). One of these lesson is that the development of an IPM programme needs to be discussed in a very early stage with all stakeholders, including growers, pest control specialists (all kinds of control methods), extension service and researchers (e.g. plant breeders, entomologists, phytopathologists etc.). The initiative for a start-up meeting can be from any group of stakeholders. It could result, for example, from an interest in applying IPM in a new setting or to adapt an existing programme threatened by the recent emergence of a new pest. The conclusion of such a meeting might be that IPM is the best solution or not. A major point is always that a complete pest management programme should be available, covering all aspects of pest management. If, for example, one of the chemical pesticides used for arthropod, disease or weed control is having a strong negative side effect on a new natural enemy, biological control is not realistic until an alternative for this pesticide has been found. What follows from these initial meetings is a pragmatic design of a draft IPM programme, for example for the management of the new emerging pest mentioned above, including an overall IPM programme for the other pests and diseases. This is then discussed in follow-up meetings with the stakeholders until agreement has been reached about the applicability of the programme. Next, the IPM programme is continuously adapted during later meetings, based on growers experience and new research results. Often, the development of these IPM programmes was made possible thanks to intensive cooperation within, and provision of essential information by, the European and North American Working Groups of the International Organization for Biological Control (see www.IOBC-WPRS.org for working group details and publications).

Also, it is crucial to cooperate with the most progressive growers. To our initial surprise, they were keenly interested, took up the knowledge quickly, suggested many improvements concerning release of biological control agents and sampling methods for pests, saw possibilities to advertise crops produced under IPM, and they were able to convince other less progressive growers how useful IPM was. It was these growers who allowed us to do experiments in their commercial greenhouses, and who invited other growers and the extension service to demonstrate how well biological control and IPM worked. We could not have found better advocates for implementation of IPM!

Often at the start of introducing IPM, growers had a wrong perception of IPM or had even never heard about it. It was necessary to develop teaching material for vocational schools, high schools and universities. Teachers of science and biology were often happy that they could link the development of an applied ecological method that was beneficial for the environment to general biological issues. The result was that teaching of biological control and IPM took off quickly and had a clear impact on changes in thinking about crop protection: children and students taught their parents how biological control worked within an IPM approach.

We also realized that it was necessary to retrain the personnel of the extension service. Next, and often together with the extension service, we organized free courses on IPM and biological control to train the farmers in recognizing the natural enemies and pests, and in sampling and release methods. In addition to training, we started to publish about IPM in journals that the growers use primarily for obtaining the newest information on production and crop protection techniques.

During initial periods of implementation of IPM we were confronted with the fact that many small companies sold IPM products, including biological control agents, of poor quality and without providing sufficient guidance. The danger of selling IPM materials without guidance is that if they do not work, the grower is disappointed and will speak negatively of IPM. Therefore, producers of biocontrol agents and IPM materials should preferably provide a guidance information system that is sold to the growers for a certain price, including provision of the biocontrol agents and other crop protection materials. For control of insects and mites, this is now an accepted way of work, but it seems to be more difficult for disease control.

Biocontrol researchers should realize that pushing for biological control as the only solution to control pests might not always be realistic, because sometimes biocontrol is not the best solution. An example is pest control in short-term crops, like lettuce, which is produced during 6-week cycles. One of the main pests is aphids, a notoriously quick developing pest which is difficult to control in all greenhouse crops. In the 1980s we were able to keep aphids under biological control with frequent releases of great numbers of a whole array of natural enemies in lettuce, but it was too expensive and complicated to apply to be of practical use. At that time, we had to conclude that development of host-plant resistance to aphids was a better approach for developing IPM in lettuce, and when this was realized and became a success, we could advise to apply biocontrol for other pests, like leafminers (de Ponti and Mollema 1992). Recently, the situation has changed and lacewing (*Chrysoperla carnea*, see Chap. 20) are increasingly used for aphid control in lettuce, for example in France (Chambre d'Agriculture des Bouches-du-Rhône 2017).

And finally, it may be most important to try to get IPM accepted as an official plant protection philosophy at national and international level. This happened for example in Indonesia for a specific crop, rice (Röling and van de Fliert 1994). In other cases it included all crops, like in The Netherlands (Dutch Ministry of Agriculture 2005) or in France with the National Action Plan "Ecophyto" (Cerf et al. 2017). Currently, at an international level, the European Union is strongly supporting implementation of IPM both by providing grants to develop IPM programmes, as well as by supporting policies that lead to a quicker registration of alternative pest control methods needed in IPM programmes (EC 2009). The establishment of farmers groups is also a very powerful tool to foster progress in IPM development and adoption, as experienced for example in the "DEPHY Ferme" network of 1900 growers recently set up in France in the framework of the "Ecophyto" National Action Plan (http://www.chambres-agriculture.fr/ recherche-innovation/dephy-ecophyto/).

6.4 Concluding Remarks

IPM in greenhouses is currently well developed and applied in many countries worldwide. IPM in protected cultivation was initially limited mainly to the control of arthropods (van Lenteren and Woets 1988) and the majority of arthropods can now be controlled with biological control agents. In parallel with the development of biological control for arthropod pests, diseases were basically controlled with crop plant resistance and it was likely the main reason of the slower development of biological control of plant pathogens. Plant pathogens are creating frequent problems in greenhouses, but only some fungicides can be integrated with the use natural enemies (www.iobc-wprs.org/ip_ipm/IOBC_Pesticide_Side_Effect_Database.html). As problems of fungicide resistance are strongly increasing, fewer "relatively safe" fungicides remain available. Thus, serious negative effects of fungicides on natural enemies of insects and widespread resistance of foliar pathogens to fungicides demands for alternatives. As a result, disease management is now evolving towards strategies relying on the use of resistant cultivars and manipulation of the environment, in particular relative humidity. During the past decades several initiatives have led to research in non-chemical control, such as the effect of soil solarization on nematodes and fungi, and the potential use of antagonistic leaf fungi (Albajes et al. 1999). For an overview of recent successes and practical applications with disease suppressive soils, biological control of soil-borne pathogens and root, stem or foliar diseases, we refer to Chaps. 12 and 13. Several microbial products now are registered and used for disease control in greenhouse vegetables and ornamentals Europe, and other bacterial and fungal products for control of fungi are in the last phase of the registration procedure.

IPM programmes are more complicated than pure chemical control, ask continuous attention and need to be adapted regularly, depending on changes in the production system, the crop cultivars used and emergence of new pests. However, the greater demands for IPM solutions from researchers and growers will result in a cleaner environment, a richer biodiversity and a better health.

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Chapter 7
Epidemiology and Population Dynamics: Modelisation, Monitoring and Management

Geneviève Marchand, Philippe C. Nicot, Ramon Albajes, and Odile Carisse

Abstract Understanding how populations of microbial pathogens and arthropod pests develop over time is critical for timely and effective intervention to control disease epidemics and pest infestations in agricultural production systems. Various elements including the pathogen or pest, host plant, natural enemies or competitors, environment, and human activity interact in complex ways, and some of these elements can be factored into mathematical models for pest population increase and disease progress. Greenhouse production affords a level of control over climate and growth environment, as well as the opportunity to release biological control agents, and thus the potential to influence pathogen and arthropod pest populations and their development to a much greater degree than in field production. To this end, thresholds for intervention must be derived based on the relationship between losses and yields weighed against the cost of intervention. In the context of integrated pest management, monitoring of pathogen and pest populations, as well as of the environment and the development of resistance to chemical pesticides such as fungicides and insecticides, is necessary to estimate the risk to the crop posed by these diseases and pests and to select the optimal method for their control.

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7.1 Introduction

Epidemiology and population biology study the development and spread of plant diseases and arthropod pests, and the factors affecting these processes. The level of disease or pest infestation is the result of many interacting factors, and this level determines the yield loss that the grower suffers from the pathogen or pest. Plant disease epidemiology can be defined as the "change in disease intensity in a host population over time and space." Several terms were used to describe epidemiology including 'ecology of disease', or 'science of disease in populations' (Vanderplank 1963). In other words, epidemiology is the science of populations of pathogens in populations of host plants, and the resulting disease as influenced by the environment and human activities. The ultimate objective of epidemiological research is to increase our understanding of how diseases develop in order to develop sustainable and effective management strategies. When we are interested in changes in the abundance of pests, most of which are herbivorous arthropods, we need to understand how and why fluctuations of their densities occur; this is the subject of population dynamics. Although plant disease epidemiology and pest population dynamics are apparently two different approaches to the study of changes in the abundance of organisms and their effects on plants, both are concerned by populations, whether of pathogens, diseased plants, or of pest individuals. In the greenhouse, human activities are much more intensive than in field production, and the environmental controls present unique opportunities to influence not only the growth and development of host plants, but also that of arthropod pests, pathogens, and biocontrol agents used to control these noxious organisms. This chapter will explore basic epidemiological concepts such as the relationship between host plants and their pests and pathogens, as influenced by time and human activities, as they relate to the production of commercial crops in greenhouse environments. Modelling the development of pathogens and pests, establishing thresholds, and monitoring of pest populations will facilitate the implementation of integrated pest management (IPM) in greenhouse production systems.

7.2 Development of Disease Epidemics and Pest Populations

7.2.1 Elements of an Epidemic

Disease development is a dynamic process occurring in two physical dimensions: time and space. Because here we are concerned with the epidemiology of diseases in greenhouse crops, this chapter will focus mostly on the development of epidemics over time. Plant disease is the result of the interaction between a pathogen population, a population of hosts, and the environment. This simplified conception of an epidemic can be represented by the disease triangle proposed by Zadoks and Schein (1979) (Fig. 7.1). However, these interactions are also influenced by time so that the disease triangle can be modified to become the disease tetrahedron (Fig. 7.1). In the context of disease management, it is also important to include human activities, mostly management practices (disease pyramid). Knowledge of the interactions between these five components should be used to select best strategic (long term), tactical (middle term), and operational (short term) management decisions. Also, a thorough knowledge on how the five components interact to cause loss is used to design integrated disease management programs. The three basic components of the disease triangle (pathogen, host, and environment) and human activity will be discussed below, and the influence of time discussed under the Sect. 7.3 (Disease progress and pest population increase).

7.2.1.1 The Pathogen

Bacteria, viruses, fungi, and oomycetes (fungus-like eukaryotic microorganisms) can incite disease on greenhouse crops. Nematodes (microscopic worms) also cause disease-like symptoms on their hosts and for that reason have historically been considered plant pathogens (Agrios 2005). It's intuitive that pathogens from such a wide taxonomical range will have varied life cycles, which will impact their popula-

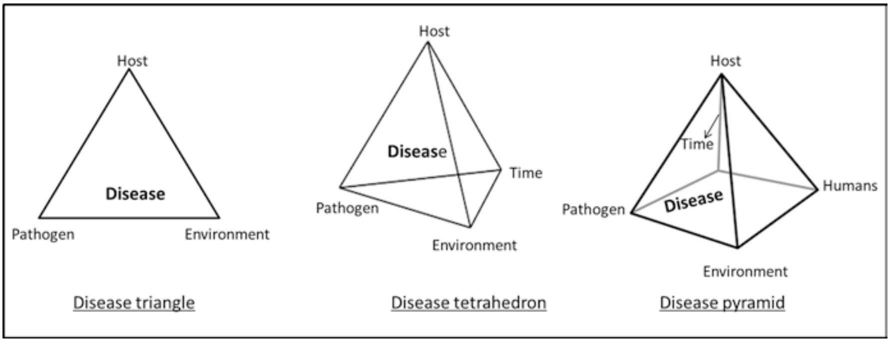

Fig. 7.1 Representation of the disease triangle, disease tetrahedron, and disease pyramid

tion dynamics and the epidemiology of the disease incited on host plants. In general terms, pathogens will take several seasons (polyetic disease), one season (monocyclic disease) or few days or weeks (polycyclic disease) to complete their life cycle. The infection process starts with inoculum of the pathogen coming in contact with the host and initiating infection, if the interaction is compatible (see Chap. 9 and below). Inoculum may be airborne (e.g. powdery mildew, gray mould), soilborne (e.g. wilts caused by *Fusarium* and *Verticillium* spp., seedling damping off caused by *Pythium* spp.), or vector-borne (e.g. viruses vectored by plant-feeding insects such as aphids). In greenhouse production systems that that do not use soil such as hydroponics or aeroponics, the concept of "soil" as it relates to plant pathology should be extended to commonly-used growing substrates such as rockwool or cocoa coir, and the nutrient solution used to feed the plants. Once they have infected the host, pathogens may reproduce on the surface of aerial plant parts or within infected plant parts in soil or growing media. This will impact the initiation of secondary infection cycles, or of further primary infection cycles depending on the nature of the pathogen. In either case, crops debris may serve as a reservoir of inoculum, hence the importance of proper "cleanout" sanitation practices between cropping cycles.

Primary inoculum is the initial source of infection. For polycyclic diseases, secondary infection cycles are initiated by secondary inoculum, produced on or within the host as the result of the primary infection cycle. Disease progress within and beyond a crop will depend on the aggressiveness of the pathogen, and the means of dispersal. For example, soilborne pathogens such as those causing damping off can be very aggressive, meaning that they usually kill susceptible hosts relatively quickly, but they tend to occur in patches and their dispersal through soil is usually limited. These diseases are also typically monocyclic. At the other end of the spectrum, airborne pathogens such as powdery mildews are disseminated readily by air movement. With powdery mildews, secondary cycles of infection happen rapidly in these polycyclic pathogens as they rapidly sporulate on leaves under conducive conditions, but these pathogens tends to be less aggressive and will usually reduce photosynthetic capacity in their host without killing it off rapidly (Jarosz and Davelos 1995). Infections can also be bimodal; for example, infection by grey mould (*Botrytis cinerea*) can occur first on stems during vegetative growth, and be followed by flower infections once the host transitions to reproductive growth.

7.2.1.2 The Host

A fundamental tenet of plant pathology is that there must be compatibility between a virulent pathogen and a susceptible host for infection to occur (Agrios 2005). If a plant species resists infection by all isolates of a pathogen species, this is known as non-host resistance (Nürnberger and Lipka 2005). Other forms of resistance are termed qualitative (or vertical) and quantitative (or horizontal) resistance. These presuppose a compatible interaction between the host and the pathogen, at least in some instances. In the case of vertical resistance, single resistance genes confer complete resistance to different races or pathotypes of the pathogen. A virulent race of the pathogen can infect a host lacking the corresponding resistance gene, in a gene-for-gene concept first described by Flor (1955). This type of resistance has historically been attractive to plant breeders as it's a relatively simple process to ingress one resistance gene into a commercial cultivar. However, this type of resistance applies a strong selective pressure on pathogen populations, especially with genetically uniform populations of host plants in regards to resistance genes. This is the most common situation in commercial greenhouse operations, where the same variety is often grown over a large area. Pathogens can overcome this resistance by acquiring mutations or adapting to the host varieties, with potentially devastating consequences. The use of multilines (a mixture of lines with different resistance gene alleles to a specific pathogens) is one way of maintaining genetic diversity within pathogen populations and has made headways in some field crops (Finckh and Wolfe 2006), but not yet in the greenhouse. By contrast, horizontal resistance is usually understood to confer partial resistance to all isolates of a pathogen. This type of resistance is more durable than vertical resistance, but can be overcome under high disease pressure and disease-conducive conditions. Nonetheless, it should be an essential component of any IPM program, as genetic resistance built into commercial cultivars comes at no additional cost to greenhouse operators or potential negative impacts on human health or the environment.

The life cycles of crops will also influence the development of disease over time. Most greenhouse crops are annuals, although some semi-perennial crops such as strawberries are gaining in popularity. In the greenhouse, sanitation practices between cropping cycles can very effectively interrupt the life cycle of pathogens if done efficiently, and thus avoid polyetic disease development. Disease control then becomes a matter of controlling the development of pathogens until the end of the current cropping cycle. On the other hand, pathogens typically develop more rapidly on genetically uniform cultivated annual crops than on more genetically diverse wild perennial relatives (Cox et al. 2006).

The age of the host can be an important factor affecting disease development. Some pathogens like *Pythium* spp. can be devastating when causing damping-off on and rapidly killing emerging seedlings, but will be less damaging to and tolerated to a certain degree by adult plants; this is termed ontogenic resistance (Develey-Rivière and Galiana 2007). Tomato plants become more resistant to infection by the causal agent of bacterial canker, *Clavibacter michiganensis* subsp. *michiganensis*, as they age (Sharabani et al. 2013). On the other end of the spectrum, vascular wilts caused by *Fusarium oxysporum* can remain latent (Kuldau and Yates 2000) in vegetative plants, but rapidly cause damage once plants become generative due to the added reproductive stress on the host. The relative age of the various organs of host plants can also influence susceptibility to pathogens, especially given the long cropping cycles for fruits and vegetables grown in the greenhouse. For example, leaves of strawberries acquire ontogenic resistance to powdery mildew rapidly after they unfold and thus become more resistant as they age (Asalf et al. 2014; Carisse and Bouchard 2010), while in tomato and pepper, older leaves are more susceptible to powdery mildew (De Souza and Café-Filho 2003; Lebeda et al. 2014). There is also evidence that senescing leaves of tomato are more susceptible to infection by *B. cinerea* than their younger counterparts, and that infection by this pathogen may accelerate the senescence of infected leaves (Swartzberg et al. 2008).

7.2.1.3 The Environment

The physical environment is the third side of the disease triangle (Fig. 7.1). Environmental conditions such as moisture, temperature, air movement and light will influence the growth and dissemination of pathogens. Compared to field production, greenhouse production offers the advantage of more control over some or nearly all environmental conditions, depending on the level of sophistication of the greenhouse covering materials and climate control systems used, as well as the cost of energy inputs (heating fuel, electricity) (Castilla et al. 2004). Environmental moisture is a key factor for the germination of spores of pathogenic fungi. For fungal pathogens directly infecting aerial plant parts (leaves, stems, fruit), free surface water or high relative humidity in the air is required for spores to germinate and initiate infection (Baptista et al. 2008; Miller et al. 2003). Because relative humidity is dependent on temperature and pressure, the concept of vapour pressure deficit (VPD, the difference between the amount of water held in the air and the maximum amount of water that could be held before condensation occurs) is usually employed in North America to manage the greenhouse climate (Prenger and Ling 2001). Specific recommendations are made to manage disease using the vapour pressure deficit, but must take into account the use of arthropods or micro-organisms as biological control agents, as these live organisms will also be impacted by the vapour pressure deficit. Nevertheless, the concept of vapour pressure deficit illustrates the impact of heat on relative humidity, as warm air can hold more moisture so heat can be used to dehumidify a greenhouse and thus manage aerial pathogens in cold weather. In warm weather, venting can help lower both temperature and humidity in the greenhouse, but this will be limited by the conditions outside of it. Evaporative paths, shade cloths, ground coverings, and geothermal systems can also lower the temperature inside a greenhouse. For greenhouse crops grown in soil, soil moisture will influence the infection process of soilborne pathogens in the same way that it does for field crops. Roots that are starved of oxygen by standing water may be more vulnerable to infection, and the zoospores of oomycetal pathogens can swim through water. Spores of oomycetal and fungal root pathogens are attracted to roots of their hosts by exsudates (Nelson 2004). The need to control soilborne pathogens was one of the drivers for the development of soilless growing systems (Vallance et al. 2011), yet some soilborne pathogens can still be an issue if introduced into recirculating nutrient solution systems used in the greenhouse. Disinfestation of the recycling nutrient solution is one avenue to control the pathogens that may contaminate it (Ehret et al. 2001b). The use of beneficial microorganisms as inoculants in the soil or growth substrate is another. Steam sterilization (Preece 2003), solarization (Gullino and Garibaldi 2012) and biofumigation (Guerrero et al. 2005) can be used to disinfest the soil.

It's difficult to generalize about the impact of temperature on pathogens, given their great diversity and vastly differing lifestyles and reproductive cycles. Even within a single pathogen species, temperature can affect different life stages or infection processes differently. With grey mould caused by *B. cinerea*, the optimal temperature for sporulation is between 15 and 20 °C. Raising the temperature to 25 °C will lower stem infection, but increase flower infections (Eden et al. 1996).

Air movement is an important consideration as it will contribute to the dispersal of numerous foliar and stem pathogens. In the greenhouse, ventilation systems may thus contribute to the dispersal of these pathogens. On the other hand, management of the canopy by thinning or de-leafing is recommended in some greenhouse crops (e.g., tomato) to improve air circulation, modify the microclimate around the host plants and lower the relative humidity of the air, and thus contribute to managing infection by air borne pathogens. The spectral quality and quantity of light available will influence the host plants, the pathogens, and even the outcome of plant-pathogen interactions (Bechtold et al. 2005; Canessa et al. 2014; Roden and Ingle 2009). In the greenhouse, natural light may be supplemented to lengthen the photoperiod or augment the amount and spectral quality of available daylight. The recent availability and rising popularity of light-emitting diodes (LEDs) affords an opportunity to manipulate the spectral quality of supplemental light by using different specific wavelengths (e.g. UV-A, blue, red and far-red), which wasn't possible with the high pressure sodium lamps that were previously used. Initial results show some impacts on pathogens of greenhouse crops, such as powdery mildew of tomato (Tokuno et al. 2012) and downy mildew of basil (Patel et al. 2016).

Other environmental factors will also influence the epidemiology of diseases in greenhouse crops. Enrichment with supplemental carbon dioxide (CO_2) is used in greenhouse vegetable crops to improve productivity. Most of the research on the direct impact of carbon dioxide enrichment on plant pathogens has been done in the context of global warming and on pathogens of forest trees or field crops. Impacts of higher carbon dioxide concentrations in the atmosphere are generally hypothesized to result in higher incidence and/or severity of plant pathogens (Garrett et al. 2009). However, it has also been shown that carbon dioxide enrichment will lower the required time to kill soilborne pathogen *Verticillium dahliae* when using soil solarisation (Al-Kayssi 2009). Some of the effects of carbon dioxide enrichment on pathogens will be indirect, through the direct impact on host plants. It seems intuitive that the acceleration of plant growth, enabled by carbon dioxide supplementation and the availability of sufficient nutrients and light, is likely to result in less damage from pathogens. Thus the effect of carbon dioxide supplementation on damage caused by pathogens is likely to be positive overall, although more research is needed to validate this assumption, and this will likely depend on the specific host, pathogen, and other environmental factors. Going back to the concept of the disease triangle, any abiotic factor causing stress to the host plant has the potential to make it more susceptible to pathogens. Examples could include insufficient irrigation, water salinity, and extremely high or low ambient temperatures. The sophisticated greenhouse climate controls in modern greenhouse systems should alleviate these if used correctly and functioning properly, however such factors may cause issues in older or simpler greenhouse systems, and in field tunnels.

Soil fertilization and fertigation of greenhouse vegetables will influence the biochemical environment of the plant roots. This may directly impact soilborne pathogens, or have an indirect effect on the host-pathogen interaction though the influence on the host. For example, levels of available nitrogen have been shown to increase or decrease host susceptibility to various pathogens in different crops (Hoffland et al. 2000; Mitchell et al. 2003; Snoeijers et al. 2000).

In addition to the physical environment, biotic parameters will influence the development of disease epidemics in the greenhouse, especially in relation to soil or growing media. For example, recent advances in Next Generation Sequencing (NGS) technology have shed some light on the complexity and diversity of soil microbiome that were only hypothesized about when using culture-based methods for such studies. These complex microbiomes will no doubt have an impact on soilborne pathogens of greenhouse crops grown in soil. Pathogens represent an infinitesimal part of total microbial communities, although this is still poorly understood and not yet fully considered within the context of IPM programs (Massart et al. 2015). It's possible that this technology may also result in the discovery and eventual commercialization of new microbial biocontrol agents.

7.2.1.4 Human Activity

Human activity will also influence disease epidemics in the greenhouse, and in the broad sense this could cover every intentional decision made, including the design of greenhouse systems, varieties to plant and other inputs to use, management and monitoring of the crop, harvest and marketing. Early detection of signs and symptoms of pathogens, followed by appropriate management control measures are crucial to successful management of disease from an epidemiological perspective. However, the unintended impact of human activities must also be considered. One example could be the transfer of inoculum from an infected plant to an uninfected plant through contact with workers' hands, tools or clothing, or the introduction of spores of soilborne pathogens in soil carried over under workers boots worn outside. To prevent these unintended consequences, proper training and protective equipment (coveralls, gloves) must be provided, combined with the use of appropriate sanitation measures (e.g. footbaths, disinfection of tools). Decisions about the design of greenhouse systems and implementation of IPM programs may also have unintended consequences. One example is the recommendation to allow leaves of greenhouse tomato crops removed by de-leafing operations to remain on the ground for a period of time to allow time for the arthropod biocontrol agents that they harbour to find their way back to the crop. While this can desirable from the perspective of the management of arthropod pests, there is also the potential for those leaves to serve as a reservoir of inoculum for pathogens, and thus to contribute to disease management issues. Another example could be the emergence of resistant populations of plant pests and pathogens, should recommendations about rotating the mode of action of pesticides not be followed (see Sect. 7.5.4 on fungicide and insecticide resistance).

7.2.2 *Factors Influencing Pest Population Dynamics in an Agricultural Ecosystem*

In a simplified scheme of a food web in agricultural ecosystems, as shown in Fig. 7.2, herbivorous arthropods that may cause damages and yield losses on their host plants are primary consumers that obtain energy from feeding on agricultural and non-agricultural plants and are, in turn, consumed by secondary consumers, especially predators, parasitoids and entomopathogens (the so-called pest natural enemies). Within primary consumers, as in the others steps, several organisms may compete each other (e.g. herbivore 1 and herbivore 2 in Fig. 7.2) for resources required for survival, development and reproduction.

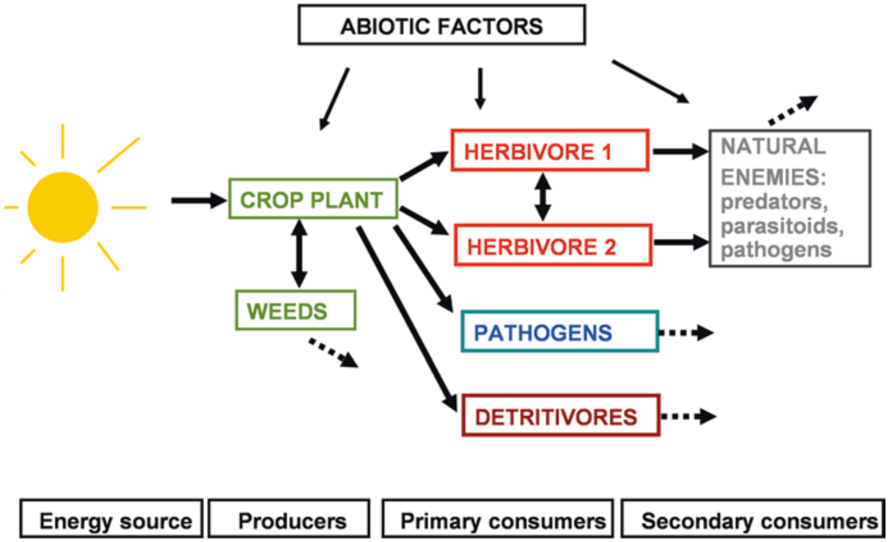

Fig. 7.2 Main components and relationships related to insect pests and their control in an agroecosystem food web. Arrows show the direction of energy flow between components of adjacent trophic levels. Double arrow shows competition between components within a trophic level. Dashed arrows show that energy flow continues but the further components involved are not represented. All biotic relationships in the agrosystem are influenced by several kinds of abiotic factors. Instability of agrosystems caused by the intrinsic nature of agriculture or by disruptive agricultural practices has been associated with reduced biodiversity so as to answer questions such as which kind of biodiversity and thus how the agrosystem has to be managed to prevent populations of herbivores building up damaging densities are the basis for designing efficient integrated pest management systems

Therefore, abundance and distribution of arthropod pests in agrosystems is the result of the action of biotic and abiotic factors shown in Fig. 7.2. Among the former, to what extent crop plants are accessible to or can defend themselves from pest attack and consumption, is crucial for pest population dynamics. Mechanisms and factors governing herbivorous arthropod-crop plants relationships are increasingly understood, although much more progress is still needed to reach the knowledge we have of the relationships between the pathogen and the host crop plant. Natural enemies are mainly responsible for maintaining most herbivorous arthropods in agrosystems under damaging densities and, vice versa, their removal by agricultural practices can contribute to an overabundance of many arthropod pests. Beyond tritrophic relationships (crop plant, herbivore, natural enemy), many other biotic agrosystem components, like non-agricultural flora, play a role in the pest population dynamics and thus in the occurrence or prevention of yield losses.

However, various abiotic factors also directly and indirectly affect pest densities. They include climate characteristics and others factors including physical and chemical soil or substrate properties, or air and water pollutants. In spite of the fact that greenhouses and soilless cultivation, as mentioned earlier, strongly alter abiotic conditions to which arthropods are submitted inside the greenhouse, abiotic conditions of the environment surrounding the greenhouse may determine pest population dynamics too, due to periodic population exchanges between the greenhouse interior and exterior. A more detailed description of how the greenhouse environment influences pests may be found in Berlinger et al. (1999).

7.3 Disease Progress and Pest Population Increase

7.3.1 Disease Progress Curves

As shown in Sect. 7.2, time influences the pathogen-host-environment interaction and the resulting disease. Intuitively, if a host population is exposed to a pathogen population under favorable environmental conditions, it is expected that disease will be severe and most probably crop losses important. Hence, the rate of disease development is one of the key parameters used to estimate risk of disease; the faster the disease will develop, the higher the risk and probability of crop losses. Temporal disease progress is generally measured by assessing disease several times during a cropping period. Disease data collected over time are used to build disease progress curves (DPC). Disease progress curves are the result of complex interactions between host, pathogen, environments and human activities (Fig. 7.3). Consequently, DPC are used to compare epidemics development under different conditions, such as crop susceptibility, environmental conditions, or control measures. In the mid 1940s to early1950s, Large (1945, 1952) proposed to use DPC and the rate of disease development to compare effectiveness of fungicide application for potato late blight (*Phytophthora infestans*) management. More formal quantitative DPC analy-

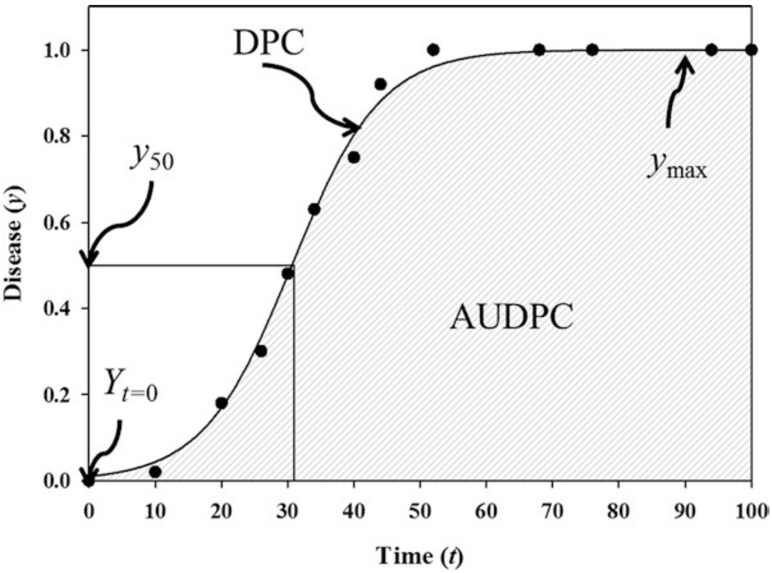

Fig. 7.3 Typical disease progress curve and parameters which could be readily obtained from disease data

sis was initiated by Vanderplank who introduced important concepts such as apparent infection rate and demonstrated the value of DPC parameters in comparing epidemics (Kranz 1974).

Analysis of DPC generally starts by fitting growth curve models to disease data collected over time (*t*) and then deriving parameters such as the rate of disease progress (*r*), maximum disease intensity (y_{max}), time to 50% disease intensity (y_{50}), or initial ($t = 0$) disease intensity (Fig. 7.3). The best model is selected based on the shape of the DPC and criteria such as the coefficient of determination (R^2), coefficient of variation (CV), standard error (SE), standard deviations of parameter estimates, and inspection of residual plots (Campbell and Madden 1990). Once the best model is selected, DPC parameters for different epidemics can be compared using analysis of variance to determine if there are significant differences between growth curve model parameters. However, as for any modeling procedure, there are basic assumptions when fitting growth curve models to disease data. Among others, it is assumed that they are no spatial aggregations of disease because spatial aggregation may influence temporal disease progress.

The most commonly used growth models are: monomolecular, exponential, logistic and Gompertz (Campbell and Madden 1990; Jeger 2004; Xu 2006) (Table 7.1, Fig. 7.4). The monomolecular model, also called negative exponential model, is generally appropriate when there is no secondary disease spread within a growing season. In other words, the pathogen completes only one infection-sporulation-dispersal cycle during one growing season. The exponential model, also called logarithmic or geometric model, is appropriate when newly diseased plants

Table 7.1 Summary of integrated expression, rate, and linearized expression of commonly used models to describe disease progress curves

Model	Integrated expression (y=)	Absolute rate (dy/dt=)	Linearized equation
Monomolecular	$1 - [(1 - y_o)$ exp. $(-r_M\, t)]$	$r_M\,(1 - y)$	$\mathrm{Ln}[1/(1 - y)] = \ln[1/(1 - y_o)] + r_M\, t$
Exponential	(y_o) exp. $(r_E t)$	$r_E y$	$\ln(y) = \ln(y_o) + r_E\, t$
Logistic	$1/[1+[(1 - y_0)/y_0]$exp. $(r_L t)]$	$r_L y\,(1 - y)$	$\mathrm{Ln}[y/(1 - y)] = \ln[y/(1 - y_o)] + r_L t$
Gompertz	exp$[\ln(y_o)$ exp. $(-r_G t)]$	$r_G[-\ln(y)]$	$-\ln[-\ln(y)] = \ln[-\ln(y_o)] + r_G t$
Richards	$[1 - B\exp(-r_R t)]^{1/(1-m)}$	$r_R y(1 - y^{m-1})/m-1$	$\mathrm{Ln}[1/(1 - y^{(1-m)})] = -\ln(B) + r_R t$
	If $m>1$, $B=(y_0)^{1-m} - 1$		If $m<1$ $B=1 - (y_0^{(1-m)})$; if $m>1$ $B=(y_0^{(1-m)}) - 1$

y is disease intensity; t is time; r is the rate parameter and r_M, r_E, r_L $r_{G,\text{ and}}$ r_R are the rate for the monomolecular, exponential, logistic, Gompertz, and Richards models, respectively; y_o is a constant of integration, corresponding to y at $t = 0$, B is an asymptote parameter; and m is a shape parameter (Campbell and Madden 1990).

or plants parts produce more diseased plants or plant parts. The logistic model was proposed by Vanderplank (1963), to model polycyclic diseases for which there is a secondary development within a growing season. Polycyclic disease progress curves can also be described by the Gompertz model. As opposed to the logistic model, the rate of disease progress reaches a maximum more rapidly and declines more gradually. These models can be used to represent a range of curve shapes (Fig. 7.4), however, some epidemics observed in the field showed other shapes of progress over time. Richards (1959) proposed a model named after his name with a shape parameter (m) that ranges from 0 to infinity. In the Richards model, when $m = 0$ the model is equivalent to the monocular model, when $m = 2$ it is similar to the logistic model, while when m approaches 1, it is similar to the Gompertz model. There are numerous other models that can be fitted to the DPC however, it is important to select model with parameters that have biological meanings (Carisse et al. 2000).

In most situations, simple growth models with few parameters are sufficient to describe temporal disease progress. However, there are situations where these simple models do not satisfactorily describe disease dynamics. This could be because they do not consider some disease characteristics such as host growth, the variable rate of disease progress, or the influence of environmental conditions on the length of the pathogen's latent and infectious periods. In these situations, more complex models or other modeling procedures, including time series analyses, could be used. Nevertheless, the degree of reliability in describing a disease progress curve depends on the purpose of modeling. If the objective is to gain knowledge on influence and interaction among various variables, then more sophisticated modeling may be required. However, if the purpose is to compare epidemics under different conditions and to identify good management practices, simple models are generally sufficient.

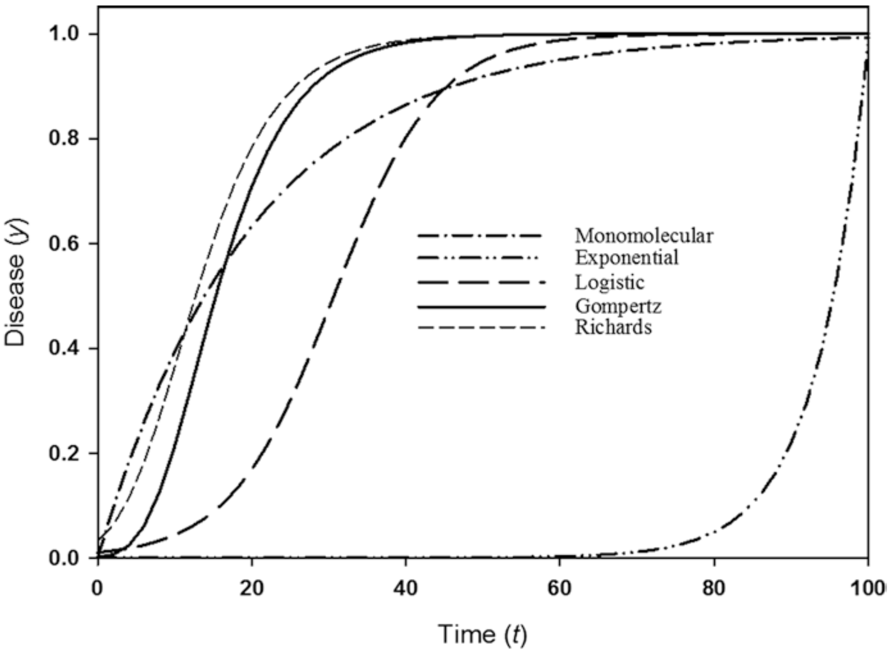

Fig. 7.4 Example of disease progress curves represented by the most commonly used growth models

7.3.2 Area under the Disease Progress Curve

Sometimes, it is not possible to fit a growth curve model, or a parameter representing the whole epidemic is required. The area under the disease progress curve (AUDPC) represents the amount of disease integrated between two assessment times and can be calculated irrespective of the curve shape (Shaner and Finney 1977). Analysis of AUDPC is useful when crop injuries are proportional to the total amount of disease during a cropping period. However, when crop injury occurs at a specific period, for example during bloom, the use of AUDPC may not be appropriate for the prediction of damage. The AUDPC can be used to compare epidemics. It is calculated using the following equation:

$$AUDPC = \sum_{i=1}^{n-1} \left(\frac{DIS_i + DIS_{i+1}}{2} \right) \times \left(t_{i+1} - t_i \right)$$

where n is the number of assessments and DIS_i is the disease intensity at time t_i. When disease data for different epidemics are not collected during the same duration, the AUDPCs can be standardized by dividing each AUDPC by the total duration of the epidemics in days (AUDPCstd). The AUDPC can also be used for testing

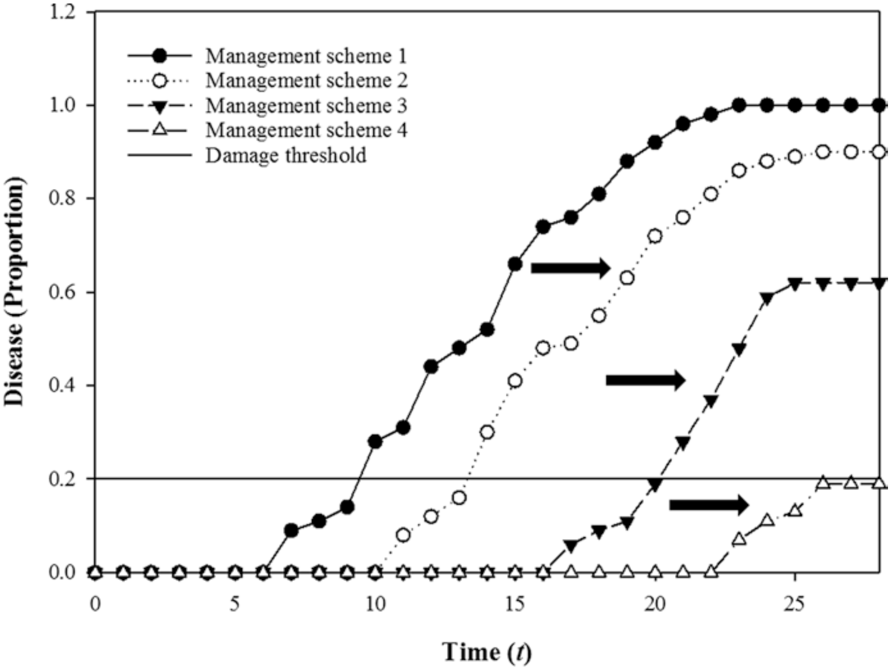

Fig. 7.5 Example of disease progress curve for different management schemes

hypotheses about the efficacy of different disease management options using regression and variance analyses.

7.3.3 *Comparison of Disease Progress Curves*

Analysis of DPC can be used to compare epidemics under different conditions and to select best management practices. In the example below, four management schemes were evaluated for the management of strawberry powdery mildew under greenhouse conditions. From Fig. 7.5, it can be seen that only management scheme 4 allowed for maintaining disease under the damage threshold. In this example, maximum disease varied from 0.19 to 1, and the rates of disease progress based on the Gompertz model were 0.26, 0.22, 0.20, and 0.13 for management schemes 1–4, respectively (Table 7.2). Similarly, the AUDPC was lower for the management scheme 4 as compared to the other management schemes.

Table 7.2 Example of disease progress curve parameters for different management schemes (Fig. 7.5)

	Management scheme 1	Management scheme 2	Management scheme 3	Management scheme 4
Maximum disease (Y_{max})	1.00	0.90	0.62	0.19
Gompertz rate of disease progress	0.26	0.22	0.20	0.13
AUDPC	0.50	0.45	0.31	0.09

7.3.4 *Pest Population Increase*

Malthus' equation, initially developed to describe human population growth, was soon adopted by entomologists to study insect demography. The equation predicts that a population will grow exponentially according to:

$$N_t = N_0 \, e^{rt}$$

where N_t is the number of pest organisms at a specified time, N_0 is that number at an initial time (0), e is Euler's number (used as the base of Napierian logarithms), r is the rate of population increase, and t is the elapsed time. If r is assumed to be constant and independent of conditions that affect pest development, survival and reproduction, population growth is unlimited. This rate of increase r is also called intrinsic or maximal rate of increase and as such is referred to as r_m and depicts the rate at which the population would increase under permanently favourable conditions and if resources are unlimited. In nature, however, favourable conditions are never indefinitely maintained and several (usually many) factors limit or retard population growth, and resources are increasingly limited as population increases. To reflect this, the so-called Verhulst' or logistic model predicts that populations will grow until reaching a maximum following a logistic or sigmoid curve that can be mathematically expressed by:

$$N_t = K / \left\{1 + \left[\left(K - N_0\right) / N_0\right] \mathrm{e}^{-rt}\right\}$$

where K, called *carrying capacity* (the maximum population size that the environment's resources can sustain), is the asymptote of the sigmoid curve and the other parameters are as in the formula of exponential growth. The parameter K is a measure of the global effect of all environmental factors that limit the growth of a population, the so-called environmental resistance. The shape of population growth in Verhulst' model is represented in Fig. 7.6. Note that it can also represent the logistic model of Vanderplank and, although biologically unrealistic, it demonstrates how pest control procedures may prevent pest populations from reaching damaging densities. As for disease control, pest population growth may be reduced by decreasing or delaying immigration of the first pest individuals into crop plants (lowering N_0 or

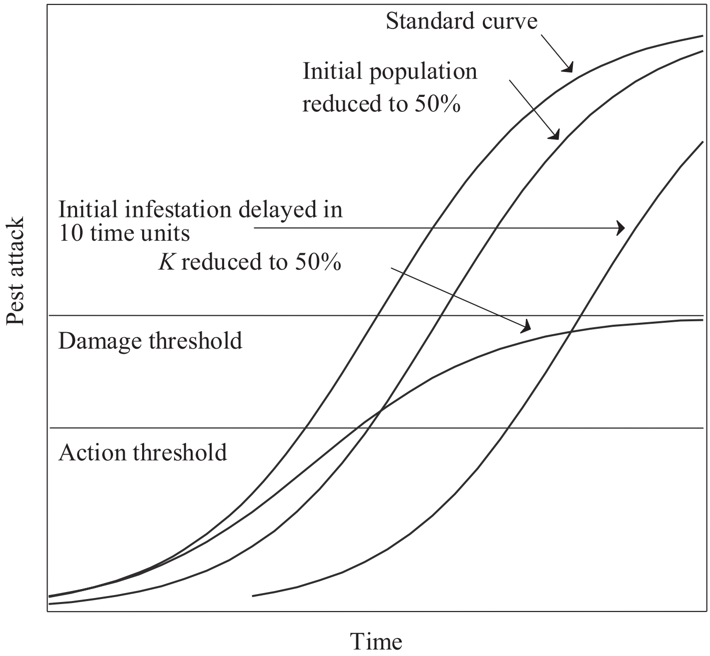

Fig. 7.6 The logistic curve of population increase and different procedures to prevent a pest population from reaching the damage threshold. Initial population can be reduced (e.g. by planting uninfested seedlings) or *K* can be lowered (e.g. host-plant resistance or biocontrol) or initial infestation delayed (e.g. sanitation)

t), or by decreasing the rate of population increase via integrated enhancement of environmental resistance, for example by the release of natural enemies (lowering *K*). In some of the coming chapters, the reader will find a discussion on how different effects on pest development and reproduction influences r_m.

7.4 Losses, Damages and Thresholds

To maintain profitability, growers must avoid losses. Hence, the ultimate objective of disease and pest management is to maintain pathogens and pests below a pre-established threshold. Therefore, accurate information on yield and losses is essential for growers and agronomists to establish decision thresholds for determining when control measures should be deployed. Despite an intuitively close relationship between disease or pest density and resulting losses, relating losses to diseases or pests is a complex endeavor. Nevertheless, quantitative information on crop losses and factors that influence them is essential to assess the efficacy of disease management programs, and to make improved management decisions.

7.4.1 Definition of Losses and Yields

The first obstacle when studying disease-yield (or losses) relationship is to agree on the terminology (Table 7.3). **Injury** is defined as the impact of a pathogen/pest on its host, such as the development of lesions on leaves, stems, flowers, fruit or roots. In an agricultural context, injury is not equal to **damage** or **losses** because there are situations where the injuries do not engender significant reductions in the amount or quality of the commodity that the farmer seeks to harvest. Depending on the host and pathogen or pest relationship, it is possible that a pathogen or pest population injures the host without causing much harm. For example, a low density of a leaf or stem pathogen or pest affecting a fruit crop such as tomato may not necessarily reduce the yield (number and quality of fruits harvested). Larvae of leaf mining *Liriomyza* spp. flies feed on leaf tissue between the adaxial and abaxial surfaces, destroying a number of chloroplasts and thus reducing photosynthetic assimilates, but this does not necessarily cause yield losses at low pest densities. On the other hand, the opposite situation may occur where significant harm is caused at apparent low levels of damage by pests or pathogens. For instance, a single stem wound caused by *B. cinerea* on greenhouse tomato may engender the death of an entire plant, resulting in the loss of fruit production over several months (Carisse and Van der Heyden 2015). In ornamental production, a small speck on a flower (for example caused by *B. cinerea* on roses or other cut flowers) may suffice to make it improper for commercialization. Similarly, a single feeding or probing bite of a virus-carrying insect causes very little direct injury to the plant tissue but may lead to the development of a destructive viral infection. **Crop losses** include both quality (marketable) and quantity reduction in yield. Finally, **economic losses** include the value of the harvested product, and costs engendered by the disease such as additional harvesting or sorting costs.

Yield is always expressed or estimated in relation to the **maximum yield**, which is the theoretical yield that could be attained for crops grown under optimum environmental conditions, with the highest yielding cultivar, managed with the most effective disease or pest management practices (Fig. 7.7). In practice, however, we often refer to the **attainable yield** which is defined as the maximum yield that can

Table 7.3 Definition of crop loss terminology

Type of losses	Definition
Injury	Any observable deviation from the normal (healthy) crop; injury may lead to crop loss (damage)
Crop loss (damage)	Any decrease in quantity (yield loss) and/or quality of a crop output; damage may lead to loss. Note that crop loss encompasses yield loss
Loss	Any decrease in economic returns from damage, and the cost of agricultural activities designed to reduce damage
Attainable yield	The yield performance of a crop that has not been exposed to yield-reducing factors, especially pests

Adapted from Savary et al. (2006)

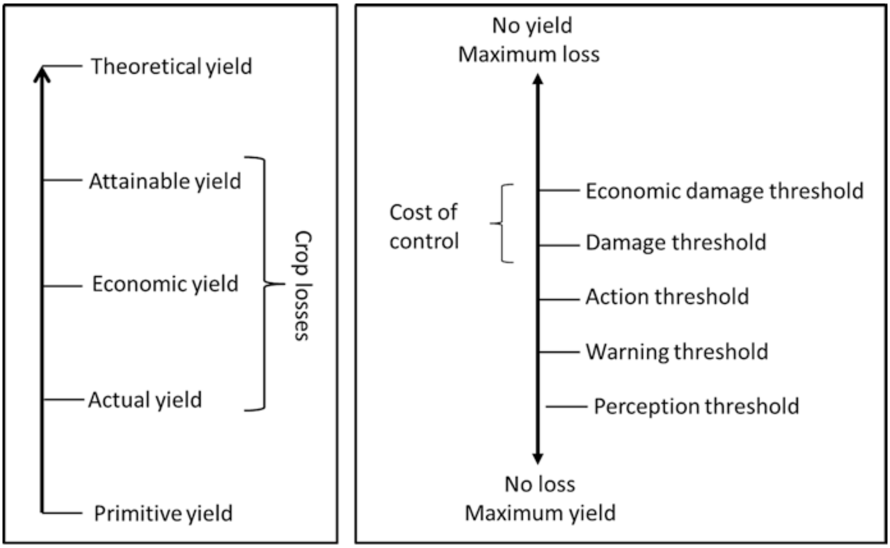

Fig. 7.7 Yield levels and crop loss (left, Adapted from Zadoks and Schein 1979) and Hierarchy of thresholds for decision making (right, Adapted from Nutter et al. 1993)

be obtained at a specific location or under specific growing conditions provided that the most effective disease or pest management programs were applied. Typically, attainable yields are achieved in well-managed greenhouses. In practice, there is a cost attached to using a large number of disease or pest management options to achieve attainable yield, and the cost of disease or pest management may be high in comparison to the value of the crop or make the production unprofitable. Also, trying to reach attainable yield might imply a cost to the environment. This is why the concept of economic yield was developed. **Economic yield** is defined as the achievable yield that provides the highest net return on expenses. In other words, when the cost of using a disease or pest management option is higher than the expected yield increase resulting from this action, it is not cost effective to use this management option, at least from the perspective of yield losses. **Actual yield** is defined as the yield obtained under the standard disease or pest management program, keeping in mind that several factors such as the environment may limit yield (Fig. 7.7). Finally, **primitive yield** is defined as the yield in absence of disease management. Thus, most disease or pest management options aim at reducing the gap between actual and attainable yield. Yield assessment can be used as a baseline for determining the best disease or pest management practices in each specific greenhouse.

7.4.2 Relating Disease and Pests to Losses

The relationship between disease severity or disease incidence and crop losses is difficult to establish because several factors other than disease influence yield (James 1983). For example, regardless of the amount of disease, water supply, fertilisation, or poor insect management may limit yield. Nevertheless, knowing the relationship between disease intensity and losses is essential to decide if control measures are needed. Hence modeling disease-losses relationship is closely related to the concept of threshold. One of the difficulties in establishing the disease-yield relationship is to decide how and when to measure both disease and yield. For example, in some greenhouse production systems, such as for tomato, slight defoliation may favor fruit maturity and quality. Similarly, the estimation of disease severity may not be related to crop losses in the same way when expressed as proportion of diseased leaf area or as lesion size. On several greenhouse crops, stem lesions generally have a greater effect on losses than leaf lesions (Carisse and Van der Heyden 2015). Also, there are situations where visible symptoms are poorly correlated with the extent of tissue colonization and consequent crop losses. For example, a low level of internal fruit rot of pepper often goes undetected until fruits are cut open (Choi et al. 2011). The time at which disease intensity is measured is also critical. High disease intensity early in the cropping season may indicate that yield will be reduced because plants will not reach maturity when expected. But in some cases, the expected yield may eventually be produced, if the plants compensate over time for damaged organs (for example by producing new shoots, roots or fruits). This has been demonstrated for the control of grey mould in greenhouse cucumber, which may not result in a net yield increase (Yunis et al. 1991). This explains why some scientists used healthy plant area rather than disease intensity to model yield losses (Bryson et al. 1995). Other scientists proposed that for modelling crop losses in relation to disease intensity, depending on the system, it might be important to considerer other factors such as healthy leaf area duration, radiation interception, spatial pattern of disease intensity and time of infection (Madden and Nutter 1995). Nevertheless, when relating yield or loss to disease intensity, we assume that there is a relation between yield (losses) and some of the parameters representing disease. As a general principle, disease-yield models should be developed using data collected over many seasons and locations, and other factors such as weather, crop susceptibility, and farming practice must be considered. Experiments may be designed to compare diseased and healthy plants, plants with different intensities of disease, crops not managed for disease with well managed crops, or healthy plants with plants that are artificially damaged (e.g. manually defoliated). If we represent yield by W, W_0 represents yield in the absence of disease; hence loss (L) is calculated as $L = W_0 - W$. Regardless of the methods employed to collect the disease-yield data, the type and complexity of models depend on the disease and crop, and on variables included in the model. Because, in general, disease-yield models do not include data on crop physiology they are empirical (descriptive) rather than mechanistic. Despite this, the descriptive models can be very useful for

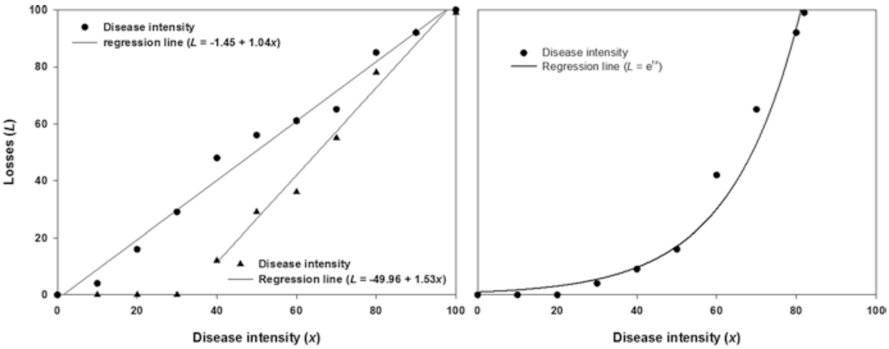

Fig. 7.8 Linear (left) and non-linear (right) relationship between loss and disease intensity measured at one point during an epidemic

disease management. Campbell and Madden (1990) proposed five descriptive models to relate disease to yield loss: (i) single-point or critical-point models, (ii) multiple-point models, (iii) response-surface models, (iv) integral models, and (v) generalized or non-linear models.

(i) The single-point models or critical-point models. In single-point or critical-point models, loss is modelled as a function of disease intensity measured at one time during the growing season. Generally, this time represents a critical point in the disease progress and is expected to have an influence on losses so that a good statistical relationship with losses is found at that one specific time. For example, critical points could be a specific growth stage (e.g. onset of flowering) or a number of days before harvest. Less frequently, these models have been developed with time variables, for example the number of disease-free days or the time until a certain level of disease is reached. Their use is limited in crops in which yield accumulates over a long period of time or harvesting takes place more than once, as for example in greenhouse vegetables. In single-point models the relationship between losses and disease can be linear or nonlinear (Fig. 7.8). Linear models can be expressed as: $Loss = \beta_0 + \beta_1 x$ in which β_0 and β_1 are regression parameters and x is disease data (severity, incidence, or other parameters, transformed or not). These models are simple, do not require a lot of data (observations) but are less appropriate for diseases with variable infection rates.

(ii) Multiple-point models. In multiple-point models, loss is modelled as a function of disease assessments made at several times during the growing season. Disease assessments can be made at fixed intervals or at specific times. In multiple-point models, the relationship between loss and disease is modelled as a function of disease measured at each assessment time or as a function of change in disease between assessments. These relationships are generally modelled using multiple regressions models such as: $Loss = \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \ldots \beta_n x_n$ where $\beta_1 \ldots \beta_n$ are partial regression coefficients for the first and nth disease assessments, respectively, and $x_1 \ldots x_n$ are the corresponding disease intensity or changes for the first and the nth assessments, respectively. This type of model is most useful in situations where disease progress can be highly variable, depending on the host plant or the environment. When both loss and disease are assessed at multiple time during a growing period, polynomial distributed lag regression can be used to model both variables expressed a time series (Carisse et al. 2013).

(iii) Integral models. These models use the summed disease pressure over a specific period of crop growth which is relevant to yield. This is determined by calculating the area under the disease progress curve (AUDPC). Integral models are a modification of the multiple-point model (Vanderplank 1963). In these models, losses are related to the area under the disease progress curve (AUDPC). Because the AUDPC represents the sum of the disease, it can be used to compare epidemics of different durations and with different shape of disease progress, provided that loss is proportional to the accumulation of disease (damage). Hence, this approach is mostly used for disease of short durations. However, these models cannot distinguish between an early moderate epidemic and a more severe epidemic which starts later with the same AUDPC. This can be overcome by assigning weighting factors to the disease assessments made on different times or by incorporating another factor, for example the number of disease-free days, into the model.

(iv) Response surface models. These models predict yield loss by using two different types of variables, for example disease severity and crop growth stage.

(v) Synoptic models or multivariate models. These models are appropriate for multiple diseases or when multiple disease parameters are needed to describe yield losses. In general, disease and crop data are collected at different sites or from surveys. Various multivariate techniques can be used to analyse these types of data, including principal components and correspondence analyses. Other approaches such as multi-criteria analysis were recently used to model multiple diseases expressed as injury profiles (Robin et al. 2013).

Several other variables representing disease progress (epidemics) such as time to symptom appearance, final disease severity, or rate of disease development can be used to model disease-losses relationships. For practical purposes, crop loss models are sometimes incorporated in crop growth models (Willocquet et al. 2000, 2008). This approach generates explanatory models, which are expected to have a greater predictive value than descriptive models. However, the development of simulation models requires a lot more basic information on the physiological processes underlying losses and on the effect of environmental parameters on epidemics, and they are therefore more difficult to develop than models based on regression or other statistical analysis.

Much of the conceptual framework to estimate the relationship between amount of disease and yield loss may be applied as well to damage relationship concerning arthropod pests. For decision-making purposes, a linear function of the amount of injury to pest density can be generally assumed. In case the crop is able to compensate for limited injury, there is a level of tolerance associated with low pest density.

Crop tolerance to pest attack may be relatively high when pests injure the leaves of fruiting vegetables like tomato, pepper, cucurbits or eggplants, and often even 30–40% of leaf injury does not result in yield reduction. Contrarily to situations in which crop plants may compensate for injuries caused by low pest populations, there is the opposite case when crop plants are very susceptible to a low level of injury. In this situation, crop losses increase abruptly at low injury levels but then, when injuries continue to increase, crop losses stabilize (Fig. 7.9) (Albajes and Madeira 2018). The consideration of more than one pest or disease and crop variables results in complex polynomial relationships (the synoptic models mentioned above), which are difficult to interpret and to use for decision-making. If a linear yield response may be assumed or derived, damage relationship can be "easily" found with field data as it has been mentioned above in single- and multiple-point models. When pests are multivoltine and their numbers are quite variable along the season, the use of insect∗days instead of seasonal mean insect densities may be more meaningful as noted in the above-mentioned integral models. Methods and techniques for this kind of studies may be found in Teng (1987) and Dent and Walton (1997).

7.4.3 Thresholds

Once the relationship between disease or pest and loss is established, the next step is to determine at which disease or pest level, or threshold, management action should be taken. In most cropping situations, complete eradication of a pathogen or pest is practically impossible, and is usually unwanted because it can imply the deployment of costly and environmentally harmful control measures. It is usually more cost effective to determine the level of pathogen/disease or pest that can be accepted without significant impact on yield. Applying control measures only when needed is the essence of integrated pest management.

However, there are distinctions to be made between thresholds. There is a hierarchy of thresholds (Fig. 7.7), with the "**perception (detection) threshold**" defined as the lowest pathogen or pest population density or injury level needed to detect a

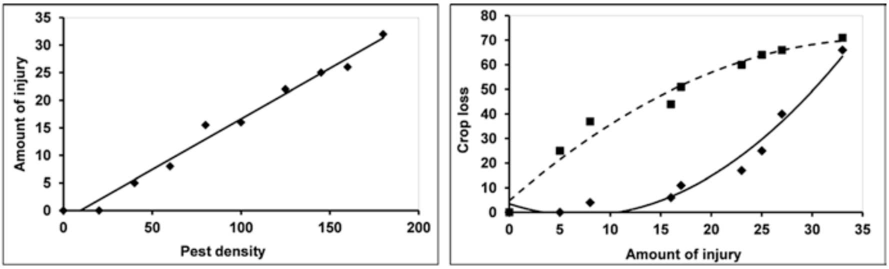

Fig. 7.9 Relationship between pest density and amount of injury (left) and two common relationships between the amount of injury caused by one pest and losses caused on the crop (right)

pathogen or pest. This threshold is largely influenced by the tools and methods used to quantify the pathogen population. With the advances in molecular biology and sampling methods, it is now possible to detect small pathogen populations in soil, water or air. Because taking action requires time, the **warning threshold** corresponds to a pathogen or pest population or disease level below the action threshold that can be considered as an alert. In other words, it could be considered as a 'preparedness threshold'. It follows that the action threshold should correspond to the size of the pathogen population or disease intensity at which action must be taken in order to prevent loss. The **action threshold** corresponds to the critical point where cost of control is below the cost of losses. The next level of threshold is the **damage threshold** which corresponds to the point where damage (losses) will occur regardless of the action taken. Finally, the **economic threshold** takes into consideration the cost of both losses and control measures. Regardless of the type of threshold used, they are closely related to the concept of risk and can be based on the pathogen population, disease intensity, or environment.

7.5 Monitoring Disease, Pathogen/Pest Populations, the Environment, and Pesticide Resistance

7.5.1 Monitoring Disease

Disease monitoring, assessment, measurement or quantification is the backbone of plant disease epidemiology and of disease management (Kranz 1988; Madden et al. 2007; Nutter et al. 1991). Without accurate and cost effective assessment of disease, it is not possible to conduct epidemiological studies, assess crop losses, estimate yield, establish thresholds, monitor disease, conduct surveys, and evaluate and compare effectiveness of disease management programs (Kranz 1988). Consequently, errors in disease measurement could have important consequences and lead to inappropriate decisions. As a first look, it may seem easy to measure disease, however, the task is not trivial and require some thoughts before collecting disease data.

There are several factors to consider for determining the best approach to the measurement of disease. Because diseases cause different types of symptoms, not all diseases can be assessed using the same approach. For example, to assess leaf spotting diseases, the number of lesions per leaves can be used while for vascular diseases, the number of wilting or dead plants may be more appropriate. In addition, most often, diseases must be assessed in a population of plants and is expressed as disease intensity, prevalence, incidence or severity. Therefore, disease assessment approaches must include both disease measurement per say and sampling methodology.

Disease intensity is a general term for the amount of disease present in a plant population which can be expressed as disease prevalence, incidence or severity (Nutter et al. 1991). Disease prevalence is the number of fields or greenhouses with diseased plants in a given geographic area and is generally expressed as the proportion of greenhouses with diseased plants (number of greenhouses with diseased plants divided by the total number of greenhouses sampled). Disease incidence is the proportion of plants or plant parts diseased from a sample of N plants or N plant parts. Disease incidence can be assessed at different scales such as proportion of leaflets, leaves, or plant diseased. Disease severity is the relative or absolute area of diseased plant part or tissue. Severity is often expressed as the proportion or percent area diseased. For some diseases, it is appropriate to measure disease using counts, for example the number of lesions per leaf or per other plant part.

In most cases, disease incidence is easier to assess than disease severity or count; it is easy to train the assessor and variations among assessors is generally low. Incidence is often considered the most objective assessment method because little judgement is required to declare a plant or a plant part as diseased or not diseased. However, incidence is more appropriate when the disease severity is low to moderate. When disease severity is moderate to high, incidence may reach 100% for a range of severities, resulting in inaccurate assessment. For some diseases, counting is easy and rapid when lesions are well defined and in small numbers without coalescences. Disease severity is thus the most challenging disease assessment. Disease severity can be estimated based on visual estimation without or with the aid of a disease diagram. In such case, each sample is assigned a severity value based on the perception of the assessor and closeness to one of the values in the diagram (pictorial representations of the host plant with known and graded amounts of disease (Barratt and Horsfall 1945)). Disease severity can also be estimated using disease scales with various degree of precision. The assessor assigns a sample to a class value, each class representing a range of severity values. In general, the use of a scale improves accuracy and speed of severity estimation. However, for some diseases, it is very difficult to estimate severity based on area diseased, or speed of estimation is more important than accuracy. In these cases, ordinal scales can be used. Ordinal scales represent categories or classes of severity such as: no, low moderate or high severity; or categories of symptoms such as: few dead leaves, beginning of defoliation, partially defoliated, or completely defoliated. Considering the challenges associated with disease severity assessment there are situations where severity can be derived from incidence data. Incidence for individual plant assessed is generally not related to severity of the plant assessed, however, for a population of plants assessed, for some diseases, there is a good relationship between incidence and severity (Fig. 7.10, Carisse et al. 2013). Disease severity can also be estimated using various types of sensors (remote sensing, image analysis) from multispectral, hyperspectral, thermal, chlorophyll-fluorescence to 3D sensors (Mahlein 2016).

In addition to the ease and speed of disease assessment, factors such as reliability and accuracy must be considered when choosing a method. The best method is both reliable and accurate (Madden et al. 2007). In the context of disease monitoring, reliability is defined as the extent to which the same measurements of individuals (diseased plants), obtained under different conditions, yield similar results (Madden et al. 2007). Hence, intra-rater reliability is the agreement between measurements made by the same assessor (rater) on the same sample following repeated assess-

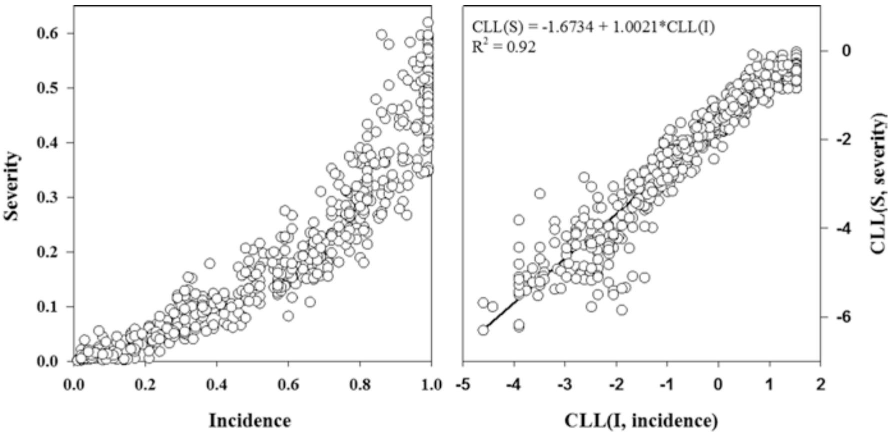

Fig. 7.10 Relationship between incidence and severity of strawberry powdery mildew caused by *Podosphaera aphanis* (left) and complementary log-log (CLL)-transformed data for the June-bearing cultivars 'Chambly', 'Darselect', and 'Jewel' grown in plastic tunnels (right). (Adapted from Carisse et al. 2013)

ments; while inter-rater reliability is the agreement between measurements made by two or more assessors on the same sample. Accuracy is a measure of how close the disease severity estimation is from actual disease severity (true severity). Least-squares regression can be used to determine if there is a significant linear relationship between disease assessments performed by different assessors, between related assessments performed by the same sample and whether there is a statistical relationship between estimated and actual disease severity. Regression parameters, such as the slope and the intercept, could be used to evaluate and compare the reliability and accuracy of disease assessments. Slopes that are significantly different from one indicate the presence of systematic bias among rates, whereas intercepts significantly different from zero indicate the presence of a constant source of error among assessors. The concordance correlation coefficient (CCC) can be used as a measure of accuracy. It is calculated as CCC = r × Cb, where r is the Pearson product-moment correlation between estimated and actual severity values and Cb is a bias coefficient representing the deviation of the best-fit line from the concordance line (perfect agreement between observed and predicted values), which is a straight line with an intercept of 0 and a slope of 1 (Madden et al. 2007).

7.5.2 *Monitoring Pathogen and Pest Populations*

Most commercial growers rely on regular scouting to monitor the incidence of and severity of damage caused by pests and pathogens, which can be performed by employees or specialized contractors. Professional scouts usually visit operations once a week, whilst monitoring by employees can be done more frequently, and larger operations may have employees dedicated to scouting and management for pests and diseases. Ideally, all greenhouse workers should be trained to identify pests and the damage that they cause, as well as signs and symptoms of diseases caused by pathogens, and to immediately report them as well as any unknown symptoms or damage-causing agents to management. From a grower's perspective, the ability to automatically monitor, in real-time, the populations of pathogens and pests, as well as biocontrol agents (both microbials and arthropods) to make management decisions would be utopian, especially if detection thresholds were below damage thresholds for the pathogens and pests. Molecular techniques for the identification of pathogens have evolved rapidly since the polymerase chain reaction (PCR) has become more affordable and ubiquitous in research and diagnostic laboratories. Further refinements, such as quantitative real-time PCR, allow for the quantification of the target. It's now possible for growers to submit plant and environmental (e.g. nutrient solution, soil) samples to diagnostic laboratories for rapid identification, and sometimes also quantification, of pathogens present in these samples via molecular means. While this can be very useful when there is a doubt about the identification of the pathogen based solely on symptoms and signs on the host, care must be taken not to jump to conclusions about the causal agents of disease, as Koch first formalized during the 1890s (Evans 1976). Samples must also be taken manually and shipped to off-site laboratories in most cases, although diagnostic systems for in-house use are being developed. For example, instant diagnostic kits based on serological methods are commercially available for some viral pathogens of greenhouse crops. Portable platforms, on based various molecular techniques such as microfluidic or isothermal DNA amplification, or next generation sequencing, are being developed for other diagnostic applications (Gardy and Loman 2017; Zarei 2017). In order to fully integrate such systems within greenhouse controls, methods must also be developed to automatically sample crops or the greenhouse environment. For airborne pathogens, this could be accomplished by spore traps. The development of spore traps for airborne spores began in the 1940s (Hirst 1952). Passive traps usually consist of a sticky surface laid out horizontally on which spore sediment, while active spore traps can be motorized or use other means of achieving volumetric air flow. While the first generations of spore traps relied on microscopic examination of their contents, traps have now been develop that can sample sequentially over time and capture samples separately, and that are compatible with molecular detection of pathogens. Such systems combining spore traps for sampling airborne pathogens and detection modules for identification and/or quantification are currently in development and use in other fields (West and Kimber 2015), and will make their way into greenhouses as technology improves, costs come down and they're optimized for the detection of plant pathogens. Recently an airborne inoculum-based threshold for de-leafing operations was developed to facilitate decisions making related to gray mould (*B. cinerea*) on greenhouse tomato (Carisse and Van der Heyden 2015). In this study, a quantitative PCR assay was used to monitor airborne inoculum of *B. cinerea* and to determine minimum airborne inoculum concentration for both stem wound and flower infections. The increasing use of automation in the greenhouse may provide an opportunity to automatically sample soil, recycling nutrient solution or crops for the detection and quantification of soilborne pathogens or those whose growth is restricted inside the host. Action thresholds would then need to be established to inform management decisions.

Arthropod population monitoring aims to identify and locate pest problems and quantify changes of population densities in order to determine when and where control measures have to be adopted. The identification of arthropod pests is still based mostly on morphological criteria although some serological and molecular tools are available for the identification of important pests of greenhouse crops. The tools for arthropod pest monitoring vary with the crop plant and arthropod species but generally, plant inspection, sticky and pheromone traps are the most commonly used techniques. Time and economic efforts for pest population monitoring have to balance costs and required precision. Unfortunately, reliability of early pest detection requires a high number of plants or traps but benefits may compensate for high monitoring costs when action thresholds are low and control measures have to be applied in first infestation foci. The most recommendable color of sticky traps depends on pest species to be monitored; whereas yellow traps are mostly suitable for whiteflies and aphids, blue traps are recommended for thrips. Pheromone traps are useful for some lepidopteran pests, an increasing problem in greenhouses, particularly those of warmer areas; knowledge of mating behaviour of the pest helps the selection of optimal location of traps, either inside or outside the greenhouse.

7.5.3 Monitoring of the Environment

The sophistication of greenhouse controls and monitoring systems varies greatly. Simple plastic tunnels usually lack any such monitoring systems, and adjustments must be made manually by opening and closing the sides of these structures, based on observations made empirically. Cultures may be grown in soil or in pots, and irrigation provided manually or via an automated system. On the other end of the spectrum, modern glass or polyethylene greenhouses may contain technologically advanced computer systems connected to sensors for temperature, relative humidity, light intensity, CO_2, electrical conductivity of the root zone, composition of the recycling nutrient solution, and control systems for heat, ventilation, supplemental lighting, CO_2 enrichment, and fertigation (Ehret et al. 2001a). There is interest in the development of wireless sensors and control systems, and although fully wireless systems aren’t commercially available yet, some of the components (e.g. LED lights from some manufacturers) can be controlled wirelessly. A reliable environment monitoring and forecasting system can support the implementation of correct greenhouse management practices for IPM.

7.5.4 Monitoring Fungicide and Insecticide Resistance

Because application of fungicides is a commonly used control option, determining the level of resistance is critical for disease management decisions. Subsequent to the introduction and extensive use of single-site fungicides, the development of resistance has become common in several pathogen populations (Gossen et al. 2014). Information of fungicide resistance level is essential for choosing the most effective fungicide, for fungicide resistance management, and to help identifying the cause of disease control failure. Fungicide resistance is a natural phenomenon related to fungal adaptation resulting in reduced sensitivity to one or many fungicides. Reduced sensitivity is caused by genetic mutations which initially are present at low frequencies. However, with repeated applications of fungicides with the same mode of action, the frequency of resistant individuals will increase. Hence, fungicide resistance is generally assessed as the proportion or percent of individuals that are resistant to one or more fungicides. The proportion of resistant individual in a fungal population should be monitored based on a large sample size (number of diseased plants assessed). When resistance is assessed using laboratory assays, the pathogen is first isolated from the diseased plant samples and then grown on culture media. To assess resistance, the individual pathogen isolates are exposed to different dose of fungicides or to a discriminatory dose. The discriminatory dose represents the fungicide concentration at which only resistant isolates grow, germinate or infect. Fungicide resistance is measured as the inhibition of fungus growth, spore germination, or plant infection (severity or incidence) for obligate parasites (the organism cannot be cultured). When several doses of fungicides are tested, the fungicide dose which inhibits growth, germination, or infection by 50% (EC50) is then calculated for each sample. When only one dose is tested (discriminatory dose), the samples are classified as sensitive or resistant based on growth, germination, or infection. Because fungicide resistance is the result of genetic adjustment, several DNA-based methods for monitoring were developed. For example, PCR based technologies such as RFLP-PCR, PIRA-PCR or CAPS can be used to assess resistance provided that the genetic mutations are known. Early detection of new resistance or of known resistance present at low frequency is important for selecting efficient fungicides and for implementation of anti-resistance strategies. However, when the proportion of resistant individual in a population is low, a large sample size is required (Van der Heyden et al. 2014). This issue will be resolved by DNA-based tools such as pyrosequencing which allow for assessing the proportion of several known mutations within a sample (Gobeil-Richard et al. 2016).

Most concepts exposed above for fungicide resistance also apply to insecticide resistance. Several of the most harmful arthropods in greenhouses like whiteflies, aphids, and thrips have developed insecticide-resistant populations worldwide (see information of insecticide resistant insects and mites in www.pesticideresistance.org) due to favorable conditions for that in greenhouses. The tools mentioned above for insect monitoring in greenhouses may be adapted for early detection of insecticide resistant individuals in order to implement resistance management strategies.

The increasing surface of greenhouse industry covered by biological control of insect pests has contributed to mitigate the quick evolution of insecticide resistance in past decades.

7.6 Disease Risk Estimation (Disease Forecasting), Decision Making

Because of the importance of greenhouse crop diseases, various control measures could be deployed to manage them. However, making a decision to apply them is complex and involves agronomic, environmental and economic considerations. Deploying control measures in absence of disease results in unnecessary costs in pesticides and impacts on the environment. On the other hand, crop losses will occur if control measures are not applied when disease is above the threshold. Informed and rational disease management decisions should thus be taken based on knowledge about the risk. Disease prediction models (forecasting models) are tools used to estimate disease risk based on conditions under which diseases develop (Gent et al. 2013). To develop reliable disease risk estimators, it is thus essential to understand the factors that trigger epidemics. Almost all disease risk models are based on the interaction of all or some of the factors that influence epidemic development: the host, the pathogen, and the environment (disease triangle). There is a wide variety of disease prediction (risk) models with an array of complexity that range from simple rule-based models to highly complex dynamic simulation models. Most disease prediction models can be classified as observational, empirical or mechanistic (Carisse et al. 2014).

The observational models are typically rule-based and the relationships between predictor variables (e.g. temperature, wetness,…) and disease cycle components (infection, sporulation, dispersal) are not represented mathematically. These models are generally structured as “if-then-else” rules. In other words, based on a set of conditions the disease component is classified either as a binary response (i.e., infection occurred or did not) or as a given a risk index. Shtienberg and Elad (1997) used current and 4-day weather forecasts to calculate grey mould (*B. cinerea*) severity values. In this system, for example when the forecasted amount of rain is 0.0–5.0, 5.1–10.0, 10.1–20, 20.1–30.0, or >30 mm/day, grey mould severity values are 0.2, 0.4, 0.6, 1.0, and 1.2, respectively. The knowledge used to build this type of models may be subjective or based on empirical and/or fundamental knowledge. With this type of model, disease risk is generally estimated based on accumulation of favorable days or disease index and the decision to act is based on predetermined thresholds (Shtienberg and Elad 1997).

The empirical models are based on statistical relationships between predictor variables and some intensity of disease cycle components, such as infection or sporulation. These types of models are often developed using controlled or field/greenhouse experiments data. In most empirical models, the intensity of disease component is expressed as a proportion of the maximum occurring under optimal conditions on a 0–1 scale, where 0 represents no disease risk and 1 the maximum disease risk (Carisse et al. 2000). Disease risk can be estimated based on one or several disease component model (infection, sporulation, dispersal) (Carisse et al. 2012).

In mechanistic models, disease risk is estimated from a series of sub-models describing the effect of predictor variables on different components of the disease cycle. Most often the objective is to 'mimic' disease development by modeling the most important phases of the disease cycle. Disease development is modeled trough a sequence of biological events such as dormancy, reproduction, dispersal, and infection. The quantity computed by the model could be the amount of inoculum, number of lesions, or diseased area (Carisse et al. 2014; Fall et al. 2016), in each stage at a given time. Each stage can be further detailed in sub-stages, for instance spore germination, penetration, and colonization, sporulation, spore removal, and dispersal and deposition to new infection sites. Sub-models are generally developed from both field and controlled experiments. When knowledge about a component of the disease is not available, then sub-models will be developed from assumptions about relationships between predictor variable and the disease component using 'best knowledge' or data from similar pathogens.

Each approach to predict disease risk has value and several good models are a combination of these approaches. Regardless of the risk determination approach, for most diseases, the predictor variables are micro or macro-environment conditions mostly temperature, relative humidity, and wetness (Shtienberg and Elad 1997). However, the reliability of environment-based risk models can be improved by adding information on pathogen inoculum, or host susceptibility (Carisse and Van der Heyden 2015). Once a model is developed, the relationship between predicted and observed disease should be established and an action threshold derived from this relationship and knowledge about potential losses. Finally, it is important to validate the model under different conditions and to establish its reliability (Carisse et al. 2014).

7.7 Integrated Disease Management: Selecting the Best Control Method

The greenhouse environment offers opportunities to control pathogens and arthropod pests that are much greater than what is possible for field crops. Methods to control pathogens can target the initial inoculum load or the rate of disease progress, and must be integrated within an IPM program. Management decisions are complex and must integrate elements from different approaches to be successful.

The first step in the fight against pathogens is to aim to start from a clean slate, by reducing or eliminating the initial inoculum load of the pathogen. The greenhouse environment can be sanitized between cropping cycles, and specific recommendations to this effect are made by extension specialists. Cleanout protocols usually involve the removal of the old crop and associated plant debris, followed by a detergent wash, and then by sterilization methods for the surface of the greenhouse structures. Recycling nutrient solution must also be disinfested, and several commercial systems are available, using heat, filtration, or oxidizing chemicals (Ehret et al. 2001b).

Reducing the rate of disease progress is the next level of intervention, and there are numerous avenues that should be used simultaneously or sequentially to maximize success. Resistant crop varieties may take longer to become colonized by pathogens, thus slowing disease development via secondary cycles of infection for polycyclic pathogens. The use of microbial competitors that colonize the growing media before the pathogens can establish can also help. Management of the crop canopy to optimize air flow and environmental controls to maintain sufficient vapour pressure deficit should also reduce both primary and secondary infection cycles. Biopesticides that directly target specific pathogens would be used next in an IPM program, with pesticides as a last resort should pathogens not respond to other control measures and the risk of damage to the crop be considered too great (Ehler 2006). However, the use of two control measure simultaneously has been demonstrated to achieve synergistic effects (Ben-Noon et al. 2003), where the total effect is greater than the sum of the individual effects, and it is in many cases possible to manage diseases in the greenhouse without requiring the application of conventional pesticides. As illustrated earlier (Sect. 7.2.1) with the example about recommendations for de-leafing and the impact of arthropod pests and pathogens, it is however possible that best practices and recommendations for managing a specific pathogen or pest may not be optimal for the management of other pathogens, arthropod pests or biocontrol agents. Fertilization practices that reduce the epidemiological development of certain pathogens may foster that of others. This is the case for example of high nitrogen levels, which reduce tomato grey mould and improves the efficacy of biocontrol agents against *B. cinerea* (Abro et al. 2013, 2014), but foster powdery mildew (Nicot et al. 2012) and the development of the white fly *Bemisia tabaci* as well as the attractiveness of the plants for these insects (Idriss et al. 2015; Islam et al. 2017). The decision-making process for disease and pest management is thus far from simple. While there are numerous intervention methods that can be employed against pathogens and pests of greenhouse crops, there are pragmatic reasons that will limit their use, cost being the foremost. Mathematical models have been developed to further our understanding of the epidemiology of pests and pathogens and assist in decision making (see Sect. 7.4.2). One issue is that few action thresholds have yet been developed for the control of pathogens in greenhouse crops, and this this is perhaps not surprising given the very nature of action thresholds. They will depend, among other factors, on the prices of biopesticides and pesticides and other associated costs (labour) versus the market price of commodities, and as a result are ever in flux (Zadoks 1985). The time required by a control method to be effective is another factor influencing action thresholds; for example, predators or parasitoids inoculated in the crop for biocontrol of arthropod pests need to be released when the pest is still at lower numbers than in the case of chemical application. Individual growers might have to set up their own action thresholds for pathogens and pests that are recurring issues in their operations, and this will require an in depth economic analysis. Local growers' associations or groups can sometimes pool resources and fund research to develop models that work locally, with individual growers inputting their own values for market prices and labour costs.

7.8 Concluding Remarks

Remarkable progress has been made in the field of epidemiology or population dynamics as applied to plant pests and diseases since the concept was first introduced and early mathematical models proposed in the 1950s. Basic concepts relating to the biology and interactions of host plants and pathogens, as well as the effects of time and the impact of human activities, still influence the development of epidemics of pests and pathogens in greenhouse crops. Although our understanding of epidemiology has evolved, the establishment of action thresholds remains a challenge for the management of pests and pathogens. Recent developments and decreasing costs of molecular technologies for diagnostics and quantification of pathogens in other fields should open up fascinating avenues for research into the epidemiology of pests and pathogens of greenhouse crops, and eventually new avenues for their control. The technological evolution of greenhouse climate control systems and increasing mechanization in greenhouse production should also afford opportunities to develop new and creative ways of managing pathogens and pests for greenhouse operators.

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Chapter 8
Diagnostics and Identification of Diseases, Insects and Mites

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Abstract Rapid and reliable diagnostic methods for arthropod pests and pathogens allow for a rational and efficient use of plant protection products. Traditional detection methods based on visual assessment of plant symptoms, isolation, culturing in selective media, and direct microscopic observation of pathogens are frequently laborious, time-consuming and require extensive knowledge of classical taxonomy. Molecular techniques are faster, more specific, sensitive, and accurate than traditional techniques. Plant viral and bacterial diagnostics have been traditionally based on serological methods, such as ELISA or Lateral Flow Devices. New molecular techniques (qPCR, digital PCR, microarray) have been developed, optimized and validated in the last years with different applications to pest and pathogen detection and identification. HTS technologies are having an enormous impact on biological sciences, allowing the determination of genome variation within a species or a population. The use of field techniques, such as LAMP and portable platforms, is a

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promising tool to early and quickly detect pests. One of the critical points of on-site detection consists in the use of simple and user-friendly nucleic acid extraction procedure, involving a low number of steps. The choice of the diagnostic technique depends on the balance between the reliability and the cost of the analysis.

Keywords Digital PCR · ELISA · High throughput sequencing · In field diagnostics · LAMP · Lateral flow devices · Microarray · Molecular markers · Phylogeny · Real time PCR

8.1 Introduction

Arthropod pests and diseases negatively influence greenhouse production of vegetables and ornamentals. Preventive measures to avoid planting contaminated material are of crucial importance in the context of an integrated pest management. Rapid and reliable diagnostic methods allow a rational and efficient use of plant protection products and constitute an important requirement for the development of the horticultural sector. The trend in the European Union for detecting plant pathogens, outlined in the European and Mediterranean Plant Protection Organization (EPPO) protocols, integrates phenotypic, serological, and molecular techniques. The present chapter provides information on new methods for fast, accurate, reliable, and early detection of arthropod pests and pathogens.

8.2 Plant Pathogen Diagnostics

The easy spread of fungal spores, virus and bacteria combined with the intense globalization are key factors to allow the movement of pathogens around the world, which can become invasive in new areas and even cause the total destruction of the crop. The traditional detection methods based on visual assessment of plant symptoms, isolation, culturing in selective media, and direct microscopic observation of pathogens are frequently laborious, time-consuming and require extensive knowledge of classical taxonomy. The observation under microscope or stereoscopic microscope is used to determine the causal agent of the disease taking into consideration pathogenicity tests and morphological features, such as size and shape of the conidia and colony characteristics, such as colour. However, many microorganisms can produce the same symptoms in the plant making difficult the correct identification of the causal agent. As many plant pathogens remain latent in the planting material, and in very low numbers, methods of high sensitivity, specificity, and reliability are required. The difficulty of culturing some species in vitro and the inability for accurate quantification of the pathogen are other limitations. Early detection of pathogens in seeds and plant materials is of key importance to avoid further spreading and introduction of new pathogens into growing areas where they are not present yet. These limitations have led to the development of molecular approaches with improved accuracy and reliability. Molecular techniques are faster, more specific, sensitive, and accurate than traditional techniques and they can identify non-cultivable microorganisms and facilitate early disease management decisions. The development of new instruments and platforms and the continuous increase of bioinformatics-data have been allowed the use of bioinformatics-based techniques as metagenomics, comparative genomics and genome sequencing as routine analysis. However, these techniques are associated with enormous quantity of information, which can only be managed by skilled personnel.

8.2.1 Immunological Methods

Advances in antibody production have boosted the development of new methods for the detection of plant pathogens. Polyclonal and monoclonal antisera are used to develop diagnostic systems to use in routine laboratories or for on-site detection. Plant viral and bacterial diagnostics have been traditionally based on serological methods, such as ELISA (Enzyme-linked immunosorbent assay) or LFD (Lateral Flow Devices) specific for the target organisms (Boonham et al. 2014). ELISA tests allow the diagnosis of the disease due to the use of specific antibodies against the target organisms. Commercial kits have been developed for the detection of phytopathogenic fungi, such as *Botrytis cinerea, Rhizoctonia solani, Pythium* spp. or *Septoria* spp., bacteria, such as *Acidovorax avenae* subsp. *citrulli, Clavibacter michiganensis*, *Pseudomonas syringae, Ralstonia solanacearum, Xanthomonas* spp., and a high number of virus.

On the other hand, the first LFD, designed by Danks and Barker (2000), based on the agglutination of only one band, simplify the interpretation of the results and the use on-site (Tomlinson et al. 2010a; Hodgetts et al. 2015). Despite the cost effectiveness of the serological methods, DNA-based methods have replaced antibody-based diagnosis analysis due to lower sensitivity of the serological methods, risk of false positives and negatives, and necessity of specific antibodies for each target.

8.2.2 DNA-Based Methods

DNA based methods are focused on the amplification of one or some regions of the DNA using specific primers and the comparison of the sequence with worldwide accessible databases, such as GenBank (https://www.ncbi.nlm.nih.gov/genbank/), databases of a specific genomic sequence, or databases of a genus, such as the Fusarium genome database hosted by the Broad Institute (https://www.broadinstitute.org/), to identify the causal agent of a disease. The main step includes an amplification of a target DNA or cDNA using primers or probes following a qualitative or quantitative polymerase chain reaction (PCR or qPCR). Both approaches require the assessment of the sensitivity and specificity of the primers, by using taxonomically closely related genera/species, morphological 'look-a-likes' isolates, or other species commonly found in the target host.

Fusarium oxysporum is a worldwide-distributed soilborne and seedborne pathogen, which can cause high losses in favourable conditions. It is a good candidate to explain the difficulty present in developing some diagnostics assay, to obtain specific assays. The species includes both pathogenic and non-pathogenic strains. Over 100 *formae speciales* have been identified within the pathogenic strains based on the host species. No morphological features can distinguish the *formae speciales* or the races (identified in function of the virulence patterns on different host cultivars). Many studies have been performed to determine molecular markers able to distinguish the *formae speciales* and the elongation factor 1-alpha, the LSU, IGS or polygalacturonases genes could be useful target regions (Mbofung et al. 2007; Hirano and Arie 2009). PCR based assays were developed for the detection of a specific *forma specialis* (*F. oxysporum* f.sp. *lactucae* on lettuce seeds) (Mbofung and Pryor 2010) or even for its quantification by qPCR (*F. oxysporum* f.sp. *melonis* on cucurbits) (Haegi et al. 2013). RAPD (Random Amplification of Polymorphic DNA) and other fingerprint assays have been used to determine monomorphic bands specific for a *forma specialis,* such as *F. oxysporum* f.sp. *niveum,* causal agent of Fusarium wilt on watermelon (Lin et al. 2010), *F. oxysporum* f.sp. *radici-lycopersici* or *F. oxysporum* f.sp. *radicis-cucumerinum* (Validov et al. 2011).

In addition, the high number of transposable elements on the *Fusarium* genome has also exploited to design specific assays within the species: *Foxy* transposable elements have been used to discriminate *F. oxysporum* f.sp. *fragariae* (Suga et al. (2013), *Fot1* to determinate the presence of a new *F. oxysporum* pathogenic on Paris daisy (*Argyranthemum frutescens* L.; Pasquali et al. 2004), or even the to discriminate races among *F. oxysporum* f.sp. *lactucae* using the *Skippy* and *Han*-solo retrotransposons (Pasquali et al. 2007; Gilardi et al. 2016).

Specific-primers assays for the diagnosis of *Phytophthora,* an important oomycete genus, have been designed and tested for *P. nicotianae* and *P. cactorum* (Li et al. 2011), *P. cactorum, P. megasperma, P. plurivora, P. pseudosyringae* and *P. quercina* from soil samples (Nowakowska et al. 2017), or *P. infestans* in potato (Hussain et al. 2017). Specific primers have also been developed for phytopathogenic bacteria, such as *Pantoea ananatis, Burkholderia* spp., and *Enterobacter* in onion (Asselin et al. 2016).

8.2.3 Barcode Sequences

One of the most critical points in the DNA-based methods is the selection of a correct genetic marker or barcode, which is informative enough to obtain a species-level identification or even sub-species identification. A barcode is a short and standardized DNA sequence in a well-known gene, which is useful for the identification of species. The Internal Transcribed Spacer region (rDNA ITS) has been proposed by the Consortium for the Barcode of Life (CBOL) as the primary fungal barcode (Begerow et al. 2010). The ITS region is part of the fungal ribosomal RNA genes and is present in a variable number of copies in the genome, ranging from 30 to 30,000 copies in eukaryotes (Prokopowich 2003), is composed by the conserved genes 18S (small ribosomal subunit), 5.8S, 28S (large ribosomal subunit) and 5S present only in some species. Two highly variable spacers flanked the 5.8S region, ITS1, and ITS2 are variable enough to determinate the species in the majority of the genera. The ITS region has been considered an optimal barcode due to the high number of copies, the easy amplification using universal primers such as ITS1 and ITS4 (White et al. 1990), the robust primers sites constructed in conserved regions of the 18S and 28S genes and the variability among species.

However, the ITS, due to its high variability among species, can cause problems in the identification of higher phylogeny ranks, such as families or orders, where other genetic regions should be used. On the other side, in many fungal genera the ITS is not decisive enough to differentiate the species and other molecular regions have been used. The elongation factor 1-alpha (EF1-α) gene, which codes for an elongation factor for protein translation, has been widely used to determine the species of *Fusarium.* In addition, the intergenic spacer region (IGS) of the nuclear ribosomal operon has been used as barcode for several *formae speciales* of *F. oxysporum* (Mbofung et al. 2007; Gherbawy et al. 2008; Srinivasan et al. 2010, 2012; Bertoldo et al. 2015). Other genes, such as beta tubulin, which codifies for the beta tubulin protein in the microtubules, have been demonstrated useful markers in other pathogenic and mycotoxigenic fungi such as *Penicillium* spp. (Frisvad 2014) and for some oomycetes.

In the case of oomycetes, the cytochrome oxidase subunit I and II were useful to identify species and sub-species with more resolution than the ITS within *Pythium* spp. pathogenic for leafy vegetables (Levesque and De Cock 2004). Other mitochondrial genes, such as *cox2, nad9, rps10* and *secY*, produced consistent results with the data from nuclear genes within *Phytophthora* genus (Martin et al. 2014).

A common approach is to combine different molecular markers for taxonomic purposes in a multilocus sequencing analysis (MLSA). In the MLSA analysis, the sequence of different gene sequences is concatenated and phylogenetic analysis could be carried out for species or sub-species identification obtaining a more accurate classification due to the higher amount of genetic information used.

In the case of bacteria, the 16S rRNA was used as universal barcode for bacteria identification. It is composed by 9 highly variable regions (V1–V9) ranging from 30 to 100 bp involved in the secondary structure of the small ribosomal subunit. The most common primers – 27F and 1492R – have been designed by Weisburg et al. in 1991.

8.2.4 Quantitative PCR

The quantitative PCR or real time PCR (rt-PCR) (Heid et al. 1996; Raso and Biassoni 2014) consists in a PCR amplification with the real time measure of the accumulated product, by using intercalating dyes, such as SYBR GREEN or EVA

Green, or probes, such as TaqMan probes or Scorpion. The intercalating dyes allow the DNA quantification by fluorescent measurement after each replication cycle and comparing the results against a standard curve of known concentration of the target DNA. The specificity of the assay could be increased by a TaqMan qPCR, where the primers are combined with a TaqMan probe, a short oligonucleotide designed internally in the amplification product and labelled in the 5′ with a fluorophore and a quencher in the 3′. The annealing of the TaqMan probe to the DNA does not produce any fluorescence due to the proximity between the quencher and the reporter, whilst the detection of the fluorescence occurs during the extension step when the DNA polymerase excides the TaqMan nucleotides and therefore the quencher and fluorophore. The fluorescence is measured after each cycle and is later related with the accumulation of the product using absolute quantification methods (with standard curve) or relative quantification methods (comparing the target gene with an endogenous gene). One of the most important characteristics of this technique is the high sensitivity, which allows the determination of a plant pathogen even at femtogram level. The real time has been also miniaturized to obtain real time portable instruments (Koo et al. 2013).

This technique permits the determination of the presence and quantity of plant pathogens (Schaad and Frederick 2002; Sanzani et al. 2014; Mirmajlessi et al. 2016; Amaral Carneiro et al. 2017). Several qPCR assays have been recently developed for ascomycetes, such as *Alternaria solani* and *A. alternata,* causal agents of potato early blight and brown spot (Leiminger et al. 2014; Kordalewska et al. 2015), or for oomycetes, such as *Bremia lactucae* (Kunjeti et al. 2016), *Plectospherella cucumerina* (Gilardi et al. 2016), *Pythium irregulare* and *P. ultimum* directly from soil samples (Schroeder et al. 2006). The diagnosis of quarantine pathogens has to be accurate and rapid and qPCR assays have been developed in the last years for several quarantine pathogens, such as Potato Spindle Tuber Viroid (PSTVd) (Boonham et al. 2004).

8.2.5 Droplet Digital PCR

Digital PCR (dPCR) has been introduced in the last decade as a highly sensitive, precise and accurate acid nucleic quantification technique (Hindson et al. 2011). Initially described by Sykes et al. (1992), the dPCR combines the advantages of the end-point PCR, which consists in a semi-quantitative analysis measured by gel electrophoresis, and the qPCR, which uses fluorescence measurements of the accumulated products compared with a control (standards curve or reference gene). It is based on the detection of fluorescent probes without the necessity of the qPCR controls. The sample is diluted and partitioned into 20,000 droplets to obtain single template molecules, and, in each droplet, single amplifications occur. Subsequently, the droplets are quantified as positive or negative for the target sequence in function of the detection of fluorescence or not. Poisson statistics analysis of the positive and negative numbers allows the absolute quantification of the target sequence. This technique overcomes the sensitivity issues and the difficulties in determining single nucleotide mutations and it is resilient to PCR inhibitors from plant, soil or water samples (Rački et al. 2014). dPCR assays have been developed for *Ralstonia solanacearum* causing potato brown rot (Dreo et al. 2014; Gutiérrez-Aguirre et al. 2015).

8.2.6 In Field Diagnostics Methods

The use of molecular techniques directly in the field on glass or plastic slides has been studied since the early 1980s. The first on-site test used in the diagnosis of plant pathogen was based on latex agglutination for the detection of plant viruses (Talley et al. 1980; Fribourg and Nakashima 1984). Since then, the objective has been to develop the fastest and more sensitive test, which produces results in short times without common laboratory tools and instruments.

One of the critical points of on-site detection consists in the use of simple and user-friendly nucleic acid extraction procedure, involving a low number of steps. The matrix rupture to extract the DNA usually combines enzymatic, chemical and mechanical methods to obtain the total cell disruption and a high extraction yield. However, the high yield with total disruption could be accompanied by the inhibition of downstream analyses. Post-extraction concentration and purification through a membrane or beads are widely performed. Many rapid, simple and easy protocols to extract the DNA in the field use membrane discs. However, the alkaline extraction is the most useful and easy technique for DNA extraction. Though it had been initially used for the extraction of plasmid from bacteria (Bimboim and Doly 1979), it has been recently optimized for a quick crude DNA extraction from plant material. Chomczynski and Rymaszewski (2006) used the polyethylene glycol-based method to lyse the cells and release the DNA to perform PCR. This type of nucleic acid extraction has been used to obtain a crude extract, which could be easily obtained by mechanical disruption of the cells directly in field.

Inexpensive but accurate tests should be used for routine programs including certification, breeding, plant quarantine or germplasm screening, or more diagnostics needs in the laboratory. The end-users are generally inexpert in molecular biology techniques, but the tests developed should maintain high specificity and sensitivity to avoid false positives and false negatives. The inspection in the fields requires easy techniques with a simple interpretation of the results. On-site testing is carried out in many cases with seeds without evident symptoms or plant material in pre-symptomatic infection stage where the pathogen is unnoticeable. The failure of an inspection test may allow the spread of the pathogen or the disease development until visible symptoms. A high sensitivity is a desirable characteristic in this type of tests.

Lateral Flow Devices (LFD) have been used for on-site testing, but the lower sensitivity compared to nucleic-acid methods as well as the difficult and long antibody production process is time-consuming and challenging, specially to detect species or lower taxonomical levels. Moreover, the multiple detection of pathogens in the same assay could be a problem using this type of method.

8.2.7 Isothermal Amplification in the Field

Despite the advantages of the PCR and qPCR as diagnostic tools, their field application requires a complex equipment. These techniques are widely diffused among routine centralized laboratories where diary samples arrive from inspections and certifications. On-site diagnostic methods developed based on an antigen-antibody reaction, such as LFD, have been overcome by DNA-based methods. In field detection methods need to be specific and sensitive, easy to be interpreted and simple for the end-user.

Isothermal methods, which require a less complex equipment, present some advantages in contrast to PCR-based methods. The use of an isothermal water bath to perform the amplification, instead of a thermal cycler, has been considered an advantage to develop loop-mediated isothermal amplification (LAMP). A wide number of molecular techniques based on isothermal conditions have been taken into consideration, such as NASBA (acid-sequence-based amplification), 3SR (self-sustained sequence replication) and SDA (strand displacement amplification). However, these amplification methods have some drawbacks that LAMP overcame such as the use of a precise instrument to detect the product due to the low specificity becoming useless in the routine diagnosis. SDA overcomes some of these shortcomings by using four primers but it produces a high number of background products and the modified nucleotide increase the total cost of the technique making it unaffordable for phytopathological diagnostics.

The LAMP assay is able to amplify few copies of the target DNA in less than 1 h with high specificity and low susceptibility to inhibitors from the host matrix. The combination with the crude extraction method based on alkaline disruption of cells showed great potential for on-site detection (Franco-Ortega et al. 2018a).

The visualization of the results includes colour change reactions with HNB or calcein and $MnCl_2$, which vary from violet to blue and from orange to green after the reaction, respectively. Positive amplifications can be detected also due to an increase in turbidity caused by the precipitation of magnesium pyrophosphate observable only after centrifugation. The above-mentioned methods are quite subjective among the different users, particularly around the detection limit. Another visualization procedure includes the addition of intercalating dyes, such as SYBR Green and PicoGreen at high concentration, however the risk of cross-contamination increases with the amount of DNA produced using this reagent. A lower number of manipulations reduce possible cross-contaminations, which can cause false positive reactions.

The easiest procedure to detect positive LAMP results is the Real Time LAMP using instruments such as the OptiGene Genie II® and Genie III®. These small size and battery-powered platforms have been designed as a suitable tool for on-site detection with closed-tubes to reduce post-amplification contaminations.

The conjunction of crude extraction procedures with the detection by real-time procedures to reduce the number of steps to analyse the samples and the risk of contamination is the most effective and suitable procedure to identify or confirm the causal agent of a disease in symptomatic material.

The high specificity of the LAMP assay has been exploited for the identification of the different *formae speciales* within *F. oxysporum,* such as *F. oxysporum* f.sp. *ciceris* using HNB (Ghosh et al. 2015), *Fusarium oxysporum* f.sp. *lactucae* (Franco Ortega et al. 2018b), or even races within a *forma specialis* as *F. oxysporum* f.sp. *lycopersici* race 1 (Ayukawa et al. 2016) using the portable Genie II®. LAMP assays for other Ascomycota as *Botrytis cinerea* (Tomlinson et al. 2010b; Duan et al. 2014), and Basidiomycota as *Rhizoctonia solani* (Patel et al. 2015) have been also developed and validated. Within the oomycetes, some LAMP assays have been designed in the last years for *Phytophthora nicotianae* (Li et al. 2015), *P. capsici* (Dong et al. 2015) and *Pythium aphanidermatum* in tomato (Li et al. 2011). For plant pathogenic bacteria, LAMP assays have been developed for '*Candidatus* Liberibacter solanacearum' (Ravindran et al. 2015) and *Ralstonia solanacearum* (Lenarčič et al. 2014) in potato.

The ease of using LAMP assays for the end users, has favoured the development of seed tests, overcoming the time consuming traditional approach of blotting, which is still recommended by the International Seed Testing Association (Abd-Elsalam et al. 2011; Franco Ortega et al. 2018b) or soil tests (Chen et al. 2013; Peng et al. 2014).

8.2.8 Microarray

DNA chips, DNA microarrays or macroarrays consist of a solid glass slide onto which dots of nucleic acid probes or primers have been printed. Each probe or primer is complementary to a target region in the genome of different genera/species, so the identification of the genus/species present in complex samples exploits the DNA hybridization, such as environmental samples, can be determined in a single assay (Zhou and Thompson 2002). Microarrays have been widely used in multiple gene expression studies, but they could be used to determine multiple bacterial or fungal species (Lievens et al. 2012), viruses (Boonham et al. 2007) or even mixtures of microorganisms, such as *Pantoea ananatis* and Maize Dwarf Mosaic Virus (MDMV) in maize (Krawczyk et al. 2017). This method allows a comprehensive vision of the population (Kristensen et al. 2007) or studying the population dynamics with high sensitivity, low reagent consumption, rapid and low cost approach. Miniaturized devices for DNA diagnostics, called 'lab-on-a-chip', have been applied to determine oomycetes species, such as *Phytopthora ramorum* and *Pythium* spp. (Julich et al. 2011).

8.2.9 High throughput Sequencing

In the last years, high throughput sequencing has become a feasible tool, which has been adopted across many biological fields, such as diagnosis of human, animal and plant diseases, population genetics and microbiology. Whole genome sequencing (WGS) approaches allow obtaining a comprehensive view of the genomics of a sample.

Since the first original Roche 454 platform, the innovation in the technologies has revolutionized the microbial ecology and the plant pathology diagnosis. High throughput Sequencing (HTS) platforms with long-read sequencing technologies are helping to resolve long repeated and complex sequences, which have been problematic to assemble with short-read sequencing platforms.

Unlike other DNA-based methods, in this case, the HTS opens the door to multiple detection of even unknown species of bacteria, fungi or viruses, in a short time and with a low cost. As it is well known, only a small percentage of microorganisms can be cultured limiting the knowledge about the community present in a sample. However, during the analysis of the metagenomic-data it is essential to use high-quality database of the barcode, to avoid unclassified or misidentified *operational taxonomic unit* (*OTUs*). The most critical points are the not user-friendly bioinformatics pipelines, which require trained people with advanced informatics skills to facilitate the rapid and precise analysis and interpretation of the results. However, despite these drawbacks, HTS has been applied in the last years to multiple projects such as “The 1000 Fungal Genomes” project (http://1000.fungalgenomes.org/) managed by the Department of Energy of the USA to obtain the genome of 1000 fungal species from over 500 families. The interest of this project is to improve the knowledge of the genes involved in pathogenicity or virulence by using comparative genomics. The new available genomes could be used to obtain sequences specific for a genus/species/*forma specialis*/race. Specific primers for *F. oxysporum* f. sp. *conglutinans* on *Brassica oleracea* have been designed after comparative genomics among different *formae speciales* (Ling et al. 2016; van Dam et al. 2016) and arrays have been developed for *Alternaria longipes* and *A. alternata* after comparative genomics (Hou et al. 2016). Within the *Alternaria* genus, the species identification is controversial: often the results of traditional methods conflict with DNA-based taxonomy performed using informative nuclear and mitochondrial loci, such as ITS, BTUB, EF-1α, glyceraldehyde-3-phosphate dehydrogenase, actin, plasma membrane ATPase and calmodulin. The HTS approaches could overcome this taxonomic troubles, and substitute the MLSA approach (Woudenberg et al. 2015; Lawrence et al. 2016). Genomic data have been also useful to design real time LAMP assays for *Pseudoperonospora cubensis* (Rahman et al. 2017). Furthermore, HTS data have been used to design E-probes from different phytopathogens (bacteria, virus, fungi, and oomycetes) for E-probe Diagnostic Nuclei Acid Analysis (EDNA) (Stobbe et al. 2013; 2014).

Powerful advances in HTS technologies have been specially applied in virology (Adams et al. 2009; Boonham et al. 2014; Al Rwahnih et al. 2015; Roossinck et al.

2015). The most common methods for virus detection in plants are based on serological tests or DNA-based methods, such as PCR, however the low viral load in some samples makes difficult virus detection and identification. On the opposite, HTS technologies have improved the ability for WGS analysis and metagenomics removing the necessity of routine analysis, and therefore they have boosted the discovery of novel virus species (Adams et al. 2013a) or the complete genome sequencing of viruses (Adams et al. 2013b).

8.3 Detection and Identification of Insects and Mites

All arthropods have multiple genomes, mostly included in one of the following three categories: nuclear, mitochondrial and symbiont-associated DNA. Each genome has a different type of transmission, phylogenetic origin and variation rate that will determine which one should be selected as source for molecular markers.

Genetic information contained in the nuclear genome can be divided into different categories depending on their function and location in the chromosomes. These categories are non-repetitive (single-copy genes), middle-repetitive (ribosomal RNA, transfer RNA, histones, or transposable elements, among others) and highly repetitive DNA (satellite DNA). Moreover, DNA fragments between genes, the intergenic spacers (non-coding sequences), can be used as markers depending on the mutation rate and the purpose of the study.

Mitochondria and their haploid genome are inherited cytoplasmically and are transmitted primarily through maternal gametes. This genome is organized in a single circular chromosome where genes can be found in both DNA strands, sometimes with overlapping coding sequences. Because of its bacterial origin, the mitochondrial genome is made of a single continuous coding region being this a substantial difference compared with eukaryotic nuclear genes. The nature (bacterial origin) and transmission mode (maternal without recombination; evolution bottlenecks) of the mitochondrial genome affect its mutation rate. These characteristics make it especially valuable for phylogenetic studies. In addition, the actual gene composition and synteny (order of genes) are conserved enough to be used to compare between taxa. The main disadvantage of using mitochondrial DNA in arthropods is its maternal inheritance, which makes male dispersal patterns to be lost in those species where these patterns differ from females. Thus, for monitoring such populations, the use of nuclear DNA-based markers would be more convenient.

Arthropods keep intimate intra- and extracellular relationships with a diverse group of microorganisms (viruses, bacteria, rickettsias and yeasts), and often these relationships are obligate as none of the parts can live without the other one. These microorganisms have their own genome, which have been recently related to speciation and evolution of some insect Orders. This symbiont DNA is mainly transmitted by maternal lineage, as mitochondrial DNA, with the same restrictions (generational bottlenecks, single chromosome, gene structure and high mutation rate). However, as the relationship between arthropods and their symbiont is not as old as that of mitochondria, the mutation rate of symbiont DNA is related to the evolution of the relationship. Therefore, it is possible to track symbiosis establishment and host speciation by studying the co-evolution of both genomes.

8.3.1 Arthropod Molecular Markers

In recent years, many molecular markers have been used not only to differentiate arthropod populations and species, but also to increase our understanding of their genetics (Behura 2006). These techniques have also shed light on the origin of invasive species and their distribution into new habitats (Xie et al. 2006). They have also facilitated the study of natural enemies commonly used in classical, inundative or conservation biological control (Symondson et al. 2002; Greenstone 2006). A large number of molecular markers have been developed and used in crop protection studies. Isozymes were the first molecular markers used, but they are now virtually obsolete. They are defined as variants of a single enzyme, performing the same or a similar biochemical function. The variants are due to differences in the enzyme amino acid sequence, which originates differences in their electrical charge and molecular weight. Isozymes have been used to analyse the diets of some predatory arthropods (Murray and Solomon 1978; Solomon et al. 1996).

The number of available molecular markers greatly increased after 1983, when KB Mullis conceived the Polymerase Chain Reaction (PCR) (Loxdale and Lushai 1998). These markers are differentiated according to the technique used, being the most common RFLPs (Restriction Fragment Length Polymorphism), RAPDs (Random Amplified Polymorphic DNA), AFLPs (Amplified Fragment Length Polymorphism), SCARs (Sequence-Characterized Amplified Region), SSRs (Simple Sequence Repeats) or microsatellites and SNPs (Single Nucleotide Polymorphisms). Microsatellites might have been the DNA molecular markers most used in ecology and population genetics (Guichoux et al. 2011). The availability of an increasing number of genomes in the databases has increased the generation of inexpensive microsatellite markers (Ge et al. 2013).

It has been traditionally considered that two individuals belong to the same species if they are able to mate and produce fully fertile offspring. However, nowadays this definition of species is being questioned. About 20 concepts based on genetic observations, biology, ecology, evolution and phylogenetics are considered to determine speciation, and only half of them recognize the processes of reproduction and competition as factors that contribute to the process of species evolution (Behura 2006). The speciation concept has benefited from the development of molecular techniques as isozymes and DNA markers, like RAPD and RFLP (Landry et al. 1993; Antolin et al. 1996; Silva et al. 1999; Unruh and Woolley 1999; Zhu and Greenstone 1999; Zhu et al. 2000). RAPD, RFLP and AFLP markers, as well as microsatellites, have also been proven to be effective for species differentiation and population genetic studies. The integrative taxonomy, which takes into account classical taxonomy and the amplification of DNA fragments, has proved to be very useful in the differentiation of arthropod species (Ros and Breeuwer 2007; Matsuda et al. 2012; Castañé et al. 2013; Tyagi et al. 2015). These techniques are also becoming generalized in taxonomic studies of the entomofauna that lives in agricultural ecosystems (Gomez-Polo et al. 2013, 2014). However, in some cases, they are not informative enough to establish the real phylogenetic relationships among groups. Sequencing has arisen as the definitive technique for this purpose. The sequence analyses of nuclear ribosomal DNA (nrDNA) and mitochondrial DNA (mtDNA) have been used in these studies. The information they provide can contribute to answer relevant taxonomic questions for the biological control of pests, where cryptic and genetically close species are common (Hurtado et al. 2008a). There are no fixed rules to establish the amount of genetic variation associated with speciation. As in the case of taxonomic information, the boundaries between species should be the sum of the evidence obtained from several sources, including geographical, morphological, behavioural and genetic data.

8.3.2 Molecular Markers for Phylogeny and Phylogeography

Nuclear, ribosomal and mitochondrial DNA sequences are often used as molecular markers in phylogenetic studies of insects and mites (Yang et al. 2011). The nuclear ribosomal DNA and, in particular, the Internal Transcribed Spacer 2 (ITS2) is one of the most important markers in molecular systematics and evolution (Yli-Mattila et al. 2000; Ben-David et al. 2007; Hurtado et al. 2008a). For phylogenies at low taxonomic levels, the ITS2 region is usually recommended, as well as the 18S, 28S and the mitochondrial cytochrome oxidase I gene (COI). Compared with the ITS regions, the COI shows a low variability that limits the resolution of phylogenetic relationships to intraspecific and interspecific level (Yang et al. 2011). In general, the mitochondrial genome is highly conserved at the level of family and genus (Yuan et al. 2010). Mitochondrial sequences are greatly appreciated in taxon differentiation with a relatively recent divergence not exceeding several million years (Dabert 2006). These sequences are widely used as phylogenetic markers and their use to clarify the phylogeny in mites has increased during the last years (Gu et al. 2014). For example, several phylogenetic studies use the COI gene as a molecular marker in tetranyquids (Navajas and Boursot 2003; Ros and Breeuwer 2007) and other mite families, such as phytoseiids (Jeyaprakash and Hoy 2009; Tixier et al. 2011) or astigmatids (Yang et al. 2011). Pérez-Sayas et al. (2015) have established species boundaries, species barcodes and phylogenetic relationship among several clades of those groups. Sequence identity with a 10% of divergence has been established as species delimitation character, allowing to establish a barcode dataset for Acari identification (Pérez-Sayas 2016).

Phylogeographic studies within and among species are a very effective way to study the origins and impact of the colonization process. It is not easy to determine how colonization of invasive species has taken place. It is difficult to know if a pest has arrived due to human intervention or it has appeared as an explosion of an already existing species, which was in a very low population density. If new habitats are colonized by individuals that come from an initial introduction event and their subsequent expansion, there will be a bottleneck. Over time, the settler population will continue to diverge genetically from the initial population, with a loss of alleles. This process corresponds to a genetic drift, which represents one of the engines that drives evolution. With a sufficient number of generations after isolation, the alleles found in the invading population will become monophyletic. That means that they share an ancestral allele, which can be used to trace back the population of origin. The degree of monophyly depends on two parameters: the effective population size and the number of generations since the invasive species was separated from the initial population (Roderick and Navajas 2003). Molecular markers can provide information about the origin and spread of a pest or a natural enemy. One of the reasons why mtDNA has been successfully used in phylogenetic studies is because it is very informative when it is used with restriction enzymes. The mtDNA is also much more sensitive than other markers for the detection of bottlenecks, since the effective size of mtDNA is one fourth of the chromosomal genes, thereby genetic structure changes of the population are better detected (Roehrdanz et al. 2002). The mitochondrial COI gene has been used in populations with founder effects and bottlenecks, such as those resulting from invasion processes (Gillespie and Roderick 2002). In the case of phytophagous pest mites, several studies have used molecular markers to determine genetic diversity, as well as population or species differentiation and invasion history (Navajas et al. 2002; Bailly et al. 2004; Carbonnelle et al. 2007; Hurtado et al. 2008b; Uesugi et al. 2009; Boubou et al. 2012). Microsatellites have become one of the most popular molecular markers used for population differentiation (Guichoux et al. 2011). They are common in eukaryotic organisms and have a very high polymorphism. Several microsatellite loci have been isolated for the two-spotted spider mite, *Tetranychus urticae* and other related mite species (Nishimura et al. 2003; Uesugi and Osakabe 2007; Sabater-Muñoz et al. 2012) and they have already been used for mite population genetic studies (Bailly et al. 2004; Li et al. 2009; Aguilar-Fenollosa et al. 2012, 2016; Pascual-Ruiz et al. 2014).

8.3.3 Molecular Markers for Biological Control

Biotechnology and genomics have become an indispensable tool also in studies related to crop protection and biological control. New insights into the ecology, population structure and biological control of pest species have benefited from the application of these molecular techniques, which have increased the speed, sensitivity and accuracy of pest detection, diagnosis and management.

In classical biological control, natural enemies are usually searched where the pest is indigenous. Species that have a worldwide distribution are expected to have high levels of genetic variability, however, when considering introduced control agents, its genetic diversity can drop by means of character fixation and heterozygotes loss. With the use of DNA-based markers, natural enemies can be studied like the pest, to determine the population structure, which allows selecting the appropriate races or biotypes of the control agent adapted to the local race of the target pest. The phylogenetic relationships can determine changes or adaptations of the biological control agent to the host. It can also identify patterns of establishment and expansion of the introduced biological control agent. Moreover, to maximize the success of introduction it is necessary to mass-produce and release natural enemy populations with a high genetic variability. In addition, a population introduced into a new habitat has to compete with a wide range of organisms that may not be present at their place of origin. In general, an appropriate estimate of genetic variability can help in determining the survival potential, adaptation to mass-breeding process, and release in the field. Thus, predators, parasitoids or entomopathogens may have a greater chance to adapt to new habitat, respond to new environmental conditions and control the pest properly. However, mass breeding is a limiting process that could induce an increase of consanguinity and a decrease of genetic variability by genetic drift. In such process, some of the natural enemy traits (as insecticide resistance, host-detection ability, etc.) can be lost and the biological control program could be compromised. Molecular markers can provide information on whether these traits are going to remain unchanged during rearing (quality control system) and also become powerful tools for monitoring releases (Roderick and Navajas 2003).

Sequence determination is the ultimate polymorphism detection system, as it allows to clearly identify a single individual. In the last decade, HTS is having an enormous impact on biological sciences allowing the determination of genome variation within a species or a population. Comparative genome analysis of the forthcoming genome sequences will allow the identification of highly conserved gene families, conserved regulatory elements, repeated elements, ingested prey, symbionts, etc., on which new markers will be designed (Kaufman et al. 2002; Belosludtsev et al. 2004). Furthermore, new targets for pest control based on interference RNA (RNAi) on species-specific genes, symbionts suppression through plant biotechnology or by new generation pesticides will become available in the near future (Wang et al. 2011).

8.3.4 Arthropod Trophic Interactions

Monoculture systems, where a plant species is grown in a wide area, could be perceived as a simplification of a natural ecosystem. In these systems, the concept of trophic chain has been traditionally assumed as the relationship between a phytophagous pest and a single biological control agent. However, the concept of trophic relationships in biological control had been changing towards the existence of multiple ecological interactions that form complex networks (González-Chang et al. 2016). The methodology traditionally used for establishing relationships between plants, pests and natural enemies were tedious and provided limited information. In some cases, it also depended on the nature of the natural enemy (predator or parasitoid) and feeding regime (chewing or sucking). In the past, the effect caused by predators was usually determined by direct observation in the field, being sometimes replaced, in the case of chewing predators, by dissection and the subsequent morphological identification of the solid residues present in their gut (Sunderland et al. 1987; Breene et al. 1990). In sucking predators, which suck the liquid content of the prey, as many polyphagous predators do (i.e. bugs, spiders, etc.), predation can be evaluated by the presence of the remaining exoskeletons of the predated preys in the field, although in some cases it is difficult or impossible. Therefore, the analysis, identification and quantification of these multitrophic relationships using traditional methods based on direct observation or dissection followed by visual identification of stomach contents was complicated. However, studies that use molecular methods to analyse prey DNA within predators, allow shedding light on the understanding of these multitrophic dynamics and their application to improve biological control (Furlong 2015; González-Chang et al. 2016; Gurr and You 2016). The molecular techniques used can be classified into two main groups, those used for protein detection and those for DNA detection. The first are based either on detection of isozymes, as mentioned above or on the development of specific polyclonal or monoclonal antibodies followed by a subsequent analysis by serological techniques based on antigen-antibody reaction, like ELISA (*Enzyme-Linked Immunosorbent Assay*) (Greenstone 1996; Agustí et al. 1999a). These serological techniques allow a fast analysis of a large number of predators, although the development of the antibodies is very expensive and laborious (Symondson et al. 1999). They are also specific to only one developmental stage (egg, larva or adult) of the pest, underestimating the total predatory activity on a particular prey. In general, the most common antibodies have been developed for the detection of the eggs vitelline (main egg protein), allowing the detection of only eggs and gravid females, and excluding nymphs and adult males. For this reasons, the use DNA-based methodologies to analyse predator gut contents began to gain ground. Although serial analysis of PCR-based markers can be a bit more laborious, the development of molecular markers is much faster, cheaper and simpler than monoclonal antibodies. These techniques allow knowing the real prey spectrum of a polyphagous predator and/or to determine the range of predators that can feed on a particular pest species.

Once a target gene sequence of each agent involved in the food chain is identified, it is necessary to design species-specific primers for the detection of prey within the predator. It is important that the primers are specific to each prey in order to avoid the amplification of other non-target species. Prey DNA detection is possible if the amplified fragment is present in multiple copies and if the amplified sequences are short, as they are degraded during digestion and can be detected for a longer time after ingestion (Agustí et al. 1999b; Zaidi et al. 1999). Therefore, multicopy regions, such as the COI and COII mitochondrial genes, have been used (Agustí et al. 2003a, b; Chen et al. 2000).

The first studies using DNA-based techniques related with biological control studies in agroecosystems were those of Agustí et al. (1999b, 2000), in which two specific molecular markers were developed to study predation by Miridae bugs on two pest species of tomato crops in the Mediterranean area, the lepidopteran *Helicoverpa armigera* (Hübner) and the whitefly *Trialeurodes vaporariorum*

Westwood. After that, these techniques have been used in numerous studies to evaluate predation of a large number of pest species and to identify potential biological control agents (King et al. 2008; Moreno-Ripoll et al. 2012; Romeu-Dalmau et al. 2012). For example, the generalist predators *Pardosa cribata* Simon (Araneae: Lycosidae) and *Pseudophonus rufipes* (DeGeer) (Coleoptera: Carabidae) present in citrus orchards were identified as main predators of the soil stages (L3, pupae and newly emerged adult) of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Monzó et al. 2010, 2011).

Commonly, in the study of trophic relationships related to biological control, a great variety of predatory and prey species are involved, which requires the design of several species-specific pairs of primers to detect the potential ingested prey. This may increase the number of necessary PCR reactions, the time and the material resources needed. For this reason, the use multiplex PCR to simultaneously detect multiple preys within a predator, started to be used (Harper et al. 2005). This technique is capable of using several pairs of primers in a single amplification reaction for the simultaneous detection of several prey species (King et al. 2011; Pompanon et al. 2012; Sint et al. 2012; Kamenova et al. 2017). It has been recently used to study the trophic relationships between *T. urticae* and *P. citri* and their natural enemies, particularly phytoseid mites (Pérez-Sayas et al. 2015), as well as to study predation by the five most common phytoseid species (*Euseius stipulatus* (Athias-Henriot), *Phytoseiulus persimilis* Athias-Henriot, *Neoseiulus californicus* (McGregor), *Neoseiulus barkeri* Hughes, *Typhlodromus phialatus* Athias-Henriot) on tetranychids and trips (Gómez-Martínez et al. 2019).

Nevertheless, PCR multiplex may be limited to detect other food sources not considered in the multiplex PCR design. In this case, the use of HTS technologies, which is based on the massive amplification of DNA fragments using universal primers, can be very useful, because of being able to amplify all prey DNA and provide a much more detailed information about the trophic networks. This methodology may show a higher complexity of the ecosystems, particularly about the importance of alternative food sources or intragremial predation (Wirta et al. 2014; Gómez-Polo et al. 2015). This method is particularly suited to agricultural studies where the focus is often on the predation of one pest species by several potential predator species (Boyer et al. 2016). For example, a food web comprising seven species over two trophic levels in a Mediterranean lettuce crop has been reconstructed using HTS (Gomez-Polo et al. 2016). However, HTS could also have some limitations. Although these methods allow detecting the DNA of all ingested prey species, it is necessary to have a complete sequence database with the DNA sequences of the whole spectrum of potential prey species in order to detect and identify them. When a DNA sequence of a particular species is not available, this prey cannot be detected and identified. Fortunately, sequence databases, such as GenBank, contain a large number of arthropod sequences and increase day by day. In addition, it has been described that these techniques can produce biases when quantifying the number of prey that the predator has actually consumed (Deagle et al. 2013). Therefore, most of these studies provide only qualitative results, as it happens with conventional PCR. Nevertheless, these new molecular methods are very powerful tools in order to evaluate existing trophic networks in agricultural ecosystems and their impact on biological control.

8.4 Conclusions

New molecular techniques have been developed, optimized and validated in the last years with different applications to pest and pathogen detection and identification. The combination of traditional and molecular techniques permits to characterize, detect, identify and quantify different pests and pathogens. The limit of detection of pathogens, by comparing the molecular techniques, can reach nanograms of DNA for PCR, picograms of DNA for biosensors, and femtograms of DNA for qPCR and digital PCR. HTS technologies are having an enormous impact on biological sciences, allowing the determination of genome variation within a species or a population. Comparative analysis of the genome sequences allows the identification of highly conserved gene families, conserved regulatory elements, repeated elements, uncultured pathogens, new species, symbionts, etc., on which new markers could be designed. On the other side, the use of field techniques, such as LAMP and portable platforms, is a promising tool to early and quickly detect pests and a useful decision support system for appropriate pest and disease management.

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Chapter 9
Host Plant Resistance to Pests and Pathogens, the Genetic Leverage in Integrated Pest and Disease Management

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Abstract The development of genetic resistance is a kingpin of Integrated Pest and Disease Management, by allowing plant resistance to a large range of pests and pathogens. Genetic resistance has mainly been reported in Crop Wild Relatives and selected during plant domestication and subsequent plant breeding. In this chapter, we describe how genetic resistance can be evaluated and genetically characterized. The main molecular mechanisms underlying host plant resistance are described, namely the dominant resistance mediated by R genes, and the recessive resistance based on loss-of-susceptibility, targeting S genes. Finally, we address a major issue of developing genetic resistance in crops, *i.e.*, the durability of resistance, and how the resistance gene repertoire must be preserved to insure its sustainability in plant breeding. A framework showing how genetic resistance fits into the Integrated Pest Management is presented.

Keywords Genetic resistance · Crop wild relatives · Plant breeding · Quantitative resistance · QTL · NLR · Susceptibility factors · Resistance breaking · Durability

9.1 Introduction

Humans have always observed unusual symptoms on the plants they cultivated, without necessarily knowing what caused them. Theophrastus, a Greek philosopher (371–288 BC), reported the existence of diseases on various plants. The Romans implored the god of cultures Robigus to exempt the future harvest from diseases.

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Several biblical verses refer to the blasting or blight of crops, and to several plagues such as caterpillars and locusts. During the medieval period and the Renaissance, crop diseases caused famines. The late blight epidemics on potatoes in Ireland in 1845 raised awareness of the serious demographic and geopolitical consequences of plant diseases. In 1905, Sir Rowland Biffen provided evidence that a wheat resistance to yellow rust was controlled by Mendel's laws of inheritance. It is from this date that breeders realized the importance of plant genetic strategies for controlling plant diseases.

In Nature, plants share the environment with many potentially pathogenic microbes and pests, but survive to most of them because they succeed to prevent the process of infection or because they cannot host the parasite, a resistance qualified as non-host. Beside those frequent incompatible interactions, a few interactions are compatible; thus the pest or pathogen is able to multiply, spread in or on the plant and lead to plant disease. Compatibility depends on environmental conditions that may influence plant susceptibility as well as pest and pathogen development. Epidemics can spread quickly in intensifying production systems, where monocultures permit to extent disease-friendly zones to a large area and crop shelters mimic climatic conditions favorable for pest and pathogen proliferation. Fungi, oomycetes, viruses and insects are frequently reported into covered crops (greenhouse, plastic tunnel…) and some are specific to them. Controlling diseases under shelters requires a combination of good sanitation (monitoring humidity and temperature, avoiding watering by gravity that spread soil pathogens, avoiding introduction of pests and pathogens by humans, wind and vectors, etc.) and cultivation of genetic resistant cultivars.

Plant pests and pathogens affect global crop production in many different ways, including a reduction of crop yield, shelf life, organoleptic properties or appearance of products. They can also impact the nutritional value of food as a result of mycotoxin accumulation. There is an overall consensus to consider that the increasing emergence of plant diseases is not only associated with the appearance of "new" pathogens, but rather to the recently amplified pathogen dissemination resulting mainly from trade and human transports. Accelerated evolution of plant pests and pathogens is also associated with selection pressures generated by pesticides, monocultures or specific resistance genes. Yield losses due to pests and pathogens have been estimated to amount to about 30%, from a set of major food crops (Oerke 2006). Clearly, plant pests and pathogens, as diverse as fungi, oomycetes, bacteria, viruses, viroids, phytoplasmas, arachnids, insects, nematodes, pose a threat to agricultural monocultures. By directly tackling resistance to those pests and pathogens, plant genetics may reduce modern agriculture's dependence on pesticides, which poses a potential threat to human and environment health.

In this review, we address how breeding programs for disease resistance is a major key in Integrated Pest and Disease Management (IPM). We discuss how the knowledge on resistance genetics, plant-parasite interaction, associated molecular mechanisms, and durability of resistance improve the disease management. A list of specific terms used concerning host plant, pests and pathogens, plant-parasite interactions and genetics/genomics is presented in Fig. 9.1.

Cultivar: a plant variety that was obtained from a breeding process; a cultivar is usually registered in an official catalog for its juridical protection.

Plant disease susceptibility: heritable capacity of a plant to be infected by a parasite and to exhibit a disease. In that case, the parasite is virulent or aggressive.

Plant disease resistance: heritable capacity of a plant to hinder establishment or growth of a parasite formerly effective on it and to survive infection.

Host resistance: ability of a plant to hinder the growth and/or the development of the parasite, thus to reduce the parasite load on/in the plant. In that case, the parasite is avirulent or unaggressive.

Non-host resistance: resistance of all members of a given plant species against a parasite: non-penetration, non-colonization by the parasite, no apparent effect on the plant.

Host tolerance: relative capacity of a plant to grow normally when infected by a parasite, and more specifically to reduce parasite-induced damage for a given parasite load.

Complete resistance: resistance, that does not allow growth of the pathogen. There are no sign of disease or of the presence of the parasite.

Incomplete or partial resistance: any resistance that is not complete; there is some growth of the parasite; majority of quantitative resistance and some qualitative resistance can be seen as forms of incomplete resistance.

Plant defenses: plant defenses include constitutive preformed barriers, inducible defenses, toxic chemicals and enzymes that degrade the parasite when plant cells detect an invading parasite.

Qualitative resistance: resistance determined by a single *R* gene that reduces the amount of initial inoculum by removing or strongly decreasing the pressure of the parasite.

Quantitative resistance: resistance determined by several *R* QTLs that reduces the epidemic rate by altering infection efficiency, parasite multiplication rate, etc.

Disease: an abnormal behavior of a living organism (e.g. plant) that interferes with its normal functioning and can usually be recognized by symptoms.

Compatible plant-parasite interaction: infection, multiplication, migration of the parasite, appearance of symptoms on the plant, development of disease; in that case, the parasite is virulent or aggressive.

Incompatible plant-parasite interaction: failed invasion of the plant by a parasite and normal plant growth, because the plant possesses or sets up resistance barriers to the parasite or recognizes the parasite and induces plant defenses; in that last case, the parasite is said avirulent.

Hypersensitive response (HR): the process of localized plant cell death that occurs immediately after entry of a parasite in a plant cell and its recognition by the plant; such a reaction acts as a host resistance mechanism since the cell death often prevents further growth of the parasite.

Resistance durability: efficiency period of a host resistance deployed at a large geographically scale in an environment favorable to the targeted parasite.

Resistance sustainability: deployment of resistant cultivars and use of host resistance in breeding programs without exhausting genetic resources of the species.

Parasite: an organism that lives on or in a host plant, from which it obtains nutriments: pest, pathogen, weed.

Pest: an insect or other small animal (e.g. nematode) that harms or destroys plants.

Pathogen: any disease-causative agent, especially a microorganism.

Variant: a form varying slightly from the standard form of a parasite; variants exhibit the biological diversity in a species; according to parasites, they are called races, pathotypes, strains, isolates…

Pathogenicity: capacity of a parasite to infect a plant and to produce disease.

Aggressiveness: a quantitative component of pathogenicity, non-specifically relative to a susceptible host plant genotype. The more aggressive a parasite variant is, the more of the host tissue it can invade in a given time.

Virulence: a qualitative component of pathogenicity, ability of a parasite to overcome plant defenses or a specific host plant resistance, and to cause disease.

Avirulence: lack of virulence, absence of pathogenicity, when the parasite variant carrying the avirulence gene comes into contact with a host plant genotype that produces a race-specific resistance protein recognizing the avirulence protein.

Genome: all chromosomes and genes of a species or of an individual.

Gene: a DNA segment that provides the coded instructions for synthesis of RNA, which, when translated into protein, leads to the expression of a hereditary trait.

Locus (plural, loci): the chromosomal position of DNA segment (including genes) or nucleotide, as determined by its linear order relative to other loci on that chromosome.

QTL (Quantitative Trait Locus, plural, Loci): chromosomal portion for which variation correlates with a part of the phenotypic variation.

Resistance gene (*R* gene): a plant gene involved in the process of resistance to a parasite by recognizing one of its effector and hindering its development.

Susceptibility gene (*S* gene): a plant gene that facilitates the parasite development by supplying functions unavailable in the parasite.

***R* QTL:** a Quantitative Trait Locus (plural, Loci) involved in the resistance to a parasite.

Allele: any of several forms of a DNA nucleotide or segment (including genes), usually arising through mutation, which are responsible of hereditary variation.

Coupling: the property of two or more alleles that are located on the same molecule of DNA (from the same chromosome).

Repulsion: the property of two or more alleles that are on different DNA molecules from the homologous chromosomes.

Heritability: the proportion of observed variation in a trait (such as plant resistance) that can be attributed to inherited genetic factors in contrast to the variation due to environmental conditions.

Fig. 9.1 Glossary concerning the host plant (in the green box), pests and pathogens (in the grey box), plant-parasite interactions (in the pink box) and genetics/genomics (in the blue box)

9.2 From Natural Plant Resistance in Genetic Resources to Commercial Resistant Cultivars

Breeding programs for disease resistance are based on the assessment of landraces, wild progenitors, and crop wild relatives to identify valuable genetic sources for resistance to pests and pathogens. Those heritage genetic resources, that typically possess a high level of diversity, preserve many traits resulting from the evolutionary adaption of the crop to biotic and abiotic stresses (Warschefsky et al. 2014). Actually, the genes involved in plant disease resistance on one side and pathogen pathogenicity on the other side are among the most polymorphic in the respective genomes (Karasov et al. 2014). It reflects the ability of both the plants and the parasites to quickly adapt or co-evolve in the wild context. Crop wild relatives have been extremely valuable for breeding new cultivars for some crops such as tomato and lettuce, when for other crops such as melon and cucumber, landraces (from the domesticated genepool) have been the major resources of genetic resistance to pests and pathogens (Dempewolf et al. 2017). In both cases, this highlights the importance of conserving the crop genetic resources. Several initiatives are presently bringing together the major international repositories hosting plant germplasms, and aim to harmonize passport, genotypic and phenotypic information on each germplasm resource. Based on this information, core-collections representing a large portion of the worldwide variation have been established and phenotyped for many biotic stresses at multiple locations. Collected data are then used for Genome-Wide Association Studies (GWAS) to identify loci determining host plant resistance (Brachi et al. 2011). Such enterprises, currently underway for three important greenhouse-grown Solanaceous crops (tomato, pepper and eggplant, http://www.g2p-sol.eu/), should help to exploit natural host plant resistance and significantly enhance the utility of germplasm resources to foster crop improvement. Indeed, genetic variation available in genetic resources is assumed to be still largely unexplored, since it has been estimated that less than 0.1% of the biodiversity in resistance loci controlling pests and pathogens is being used in cultivars (Goverse et al. 2009). To this day, to our knowledge, only resistance originating from natural biodiversity is deployed in greenhouse crops and no genetically modified vegetables are currently grown.

In most countries, crop cultivars have to be registered before seeds can be commercialized. Registered cultivars are presented in national catalogs with their characteristics. Up to now, 75 countries are members of the International Union for the Protection of New Varieties of Plants (UPOV, http://upov.int/members/en/). More than 8000 cultivated species are now considered for registration by UPOV. Cultivars of greenhouse crops have been registered for a long time: as early as 1952, lettuce cultivars were registered in France (https://www.geves.fr/catalogue), pepper and eggplant in 1956, tomato in 1965, melon in 1973… This reflects the dynamic breeding for horticultural. In Japan, three flower species are at the top of the number of applications for cultivar registration (MAAF data, http://www.hinsyu.maff.go.jp/en/about/outline.html). In Europe, about 30% of all registered cultivars are vegetables; they represent more than 20% of the yearly registration turnover of the European catalog. Specialized companies breed for the different markets worldwide, making available for producers, cultivars with specific characteristics, including resistance to pests and pathogens.

In the late 1950s, public and private research began to improve cultivars by introducing genetic resistance to pests and pathogens. Starting with resistance to fungi, it was extended to viruses and bacteria, and since 1990 to insects. Nowadays, nearly 40 crops are bred for resistance to 150 pests and pathogens in Europe. In France, GEVES (Groupe d'Etude et de contrôle des Variétés Et des Semences, https://www.geves.fr/variety-seed-expertise/vegetable/resistance-of-vegetable-species-to-disease-and-pests), in charge of registration and juridical protection of new cultivars, characterizes greenhouse crops for their resistance to numerous pests or pathogens: 20 for lettuce, 19 for tomato, 12 for melon, 10 for pepper, 7 for cucumber… GEVES offers opportunity to growers to choose cultivars that are resistant to several pests and pathogens and therefore to reduce pesticide sprays in greenhouses. In addition to the environmental and human health gains associated with such a strategy, reducing pesticide sprays may also allow growers to have more time to access greenhouses.

9.3 Assessment of Resistance Parameters

It is of high importance to critically assess the effect of pest and pathogen resistance to carry on efficient breeding. Resistance to pests and pathogens can be assessed according to three criteria: (i) the efficacy of resistance, which is characterized by the extent to which the development of disease is hindered (complete vs. partial resistance); (ii) the spectrum of resistance, which expresses the range of the controlled variants of the considered parasite species (narrow vs. broad spectrum); and (iii) the durability of resistance, which indicates how a host resistance remains effective in time and space after it has been widely deployed in environments conducive to disease development. The assessment of resistance to pests and pathogens requires to investigate the diversity of parasites that could infect a crop species, and for each parasite, its different infectious forms (e.g. sexual vs. asexual spores) and its own genetic variability. Beside the host plant diversity, the onset and severity of a disease may vary according to the infected organ and the development stage (e.g. plantlets vs. adults). At last, the plant response to a pest or a pathogen may vary according to environmental conditions (e.g. climatic parameters, additional biotic or abiotic stresses). Assessing resistance in the field allow to consider the parasite variant(s) actually present in crop conditions. However, observations of plant responses in natural conditions is only indicative because the inoculum pressure can be erratic or patchy in a field, and sporadic or absent over the years. Therefore, pathologists and breeders generally prefer simple biological assays in artificial conditions. Biological assays consist of inoculating a set of plants, all cultivated in homogeneous conditions, at a specific stage of their development with a specific amount of inoculum of a well characterized variant of the parasite. Inoculated plants are then grown in controlled hydric and climatic conditions. Breeders perform assays on plants as young as possible, and when possible on detached organs to allow the evaluation of other agronomic traits on the same plant. At last, evaluating the correlation of the plant response in both artificial and natural conditions could help to forecast how the biological assay could be a proxy of the plant resistance in field or greenhouses, as evaluated for resistance of melon to the worm *Diaphania hyalinata* (Lepidopteran) (Guillaume and Boissot 2001).

Generally, we distinguish two ways for describing the issue of a plant-pathogen interaction. Biological assays help to compare the *per se* value of host genotypes to endure a biotic-stressed condition (plant-related traits) or to slow down the pathogen development (pathogen-related traits). Plant-related traits measure the impact of disease on plant, such as the intensity of symptoms (e.g. size of necrosis due to fungal inoculation, number of local lesions induced by viral inoculation, silvering induced by whiteflies…). They express the ability of the plant to endure the presence of parasites. Pathogen-related traits measure life history traits or dynamics of the pest and pathogen, such as ELISA evaluation of the viral load, DNA or RNA amplification of the pathogen, and mortality, fecundity, etc. for pests. They express the ability of the plant to affect the pest or pathogen dynamics. Qualitative, or better quantitative, measures can be made at several dates after inoculation to derive plant or pathogen response parameters. They must be well-reproducible and sufficiently discriminating to distinguish susceptible and resistant plants. The heritability value of the measured parameters gives an indication of the reliability of such assays. Biological assays are all the more informative since they permit to distinguish the elementary components that affect the different steps of the plant-parasite interaction (e.g. *Phytophthora* on pepper, Thabuis et al. 2003; Mallard et al. 2013). For pests, the daily fecundity and generation time from adult to adult are considered in whiteflies and in aphids (Hemipteran) on melon (Sauvion et al. 2005; Thomas et al. 2012). Additionally, the pest behavior can be affected by the plant resistance, as for instance aphids escape from the resistant melons (Thomas et al. 2012). Video tracking can be used to assess behavioral traits of insects related to plant resistance (Kloth et al. 2015).

Biological assays may be difficult to develop due to the challenge posed by the inoculum maintenance and production, and by the manipulation of exotic parasites that require a quarantine period or costly devices to prevent their release in the environment. Pathologists usually maintain collections of variants, representative of the known natural diversity of a parasite and often based on collected variants in fields. Developing those types of collections always raises the question of their representativeness compare to the real diversity of the parasite, and therefore of relevance of such collections. Moreover, the maintenance of such collections is particularly challenging for parasites that are obligate biotrophs. Unfortunately, such collections are usually private, while they should be widely described and shared. Parasite collections are very useful for assessing host-parasite interactions under gene-for-gene relationship, where efficiency of different resistance genes may be checked by a set of differential variants that differ for a set of avirulence genes and that clearly discriminate resistant and susceptible host plants for each resistance gene (see Sect. 9.4).

These variant-specific biological assays are rather well-reproducible and the efficacy of the resistance is well-predictive of the host response in the field as long as the parasite population does not evolve. But for pests and pathogens that quickly evolve, variant-specific artificial tests could not correctly predict the host response in field conditions. Inversely, biological assays are rather good predictors for variant-non-specific resistance; in that case, parasite collections gather variants with different levels of aggressiveness. Resistance effective on all variants, *i.e.* non-specific, is supposed to be more durable.

Recently, the use of pathogen effectors was proposed as a tool for identifying resistance genes (Vleeshouwers and Oliver 2014). Effectors are proteins secreted by pests and pathogens to manipulate the host's cellular functions. They may have a positive or negative effect on the outcome of the interaction: they can either suppress the plant defense or act as an avirulence factor when they are recognized by a resistance protein. The effector-based strategy consists of, first, identifying candidate pathogen-secreted factors, and second, transiently expressing them in a set of plant accessions. The accessions exhibiting hypersensitive response (HR) are supposed to possess a cognate plant resistance protein that recognizes the tested effector and triggers resistance. By evaluating diversity of the avirulence genes in the pathogen population, it is possible to search for the most conserved effectors, considered as being under evolutionary constraints and essential for the pathogen. Developing a set of conserved effectors is then a powerful alternative to the sometimes difficult and always time-consuming use of pathogen infection with many variants to screen for disease resistance.

9.4 Genetic Determinism of Plant Resistance

Plant resistance to pests and pathogens is currently described as being qualitative or quantitative, depending in its segregation in a progeny as a bimodal or as a Gaussian-continuous trait, respectively. These two types of segregation correspond to contrasted genetic determinisms.

Qualitative or simple resistance (sometimes also referred to as "vertical") unambiguously distinguishes resistant and susceptible plants in a progeny. This Mendelian trait is determined by a single gene, named *R* gene or *S* gene (see definition in Fig. 9.1), generally playing a major effect on the observed trait, i.e. sufficient to drive the complete or near-complete resistance phenotype in crop plants. Plant resistance proteins encoded by *R* genes are involved in pathogen recognition and trigger plant immunity. Corresponding resistance alleles are generally dominant. Recessive resistance alleles, due to loss-of-function or absence of susceptibility, correspond in fact to dominant susceptibility genes, *S* genes being necessary for the pathogen's development in the plant (see Sect. 9.5). *R* genes can be introgressed rather easily in a few years into elite cultivars through successive backcrosses. Therefore, for a long time, breeders have developed simple resistance controlled by *R* genes (see below). Those resistance genes have been found in genetic resources, including crop wild relatives, where they are associated with high level of resistance. Since the end of the 1990s, many *R* genes have been characterized in numerous crops including greenhouse-grown plants, by a combination of approaches, such as mapping in bi-parental populations, fine mapping, positional cloning, and screening by transposon-tagging or by TILLING in mutagenized populations that permit to genetically map and straightforwardly identify the responsible genes. Most *R* genes have been shown to be organized in clusters on plant genomes. In tomato, two genomic regions on chromosomes T6 and T10 are hot spots of *R* genes. The organization of *R* genes are even often clustered in tandem arrays such as the tomato genes *Cf-2/Cf-5, Ol-4/Ol-6, Mi-1/Mi-9* and *Ty-1/Ty-3* or the melon genes *Fom-1/Prv* conferring resistance to several unrelated pathogens (Peters et al. 2009; Brotman et al. 2013). *R* gene clusters facilitate the introgression of multiple disease resistance when resistance alleles are linked in coupling, as illustrated by the association between resistance to PVX and cyst nematodes in a number of potato cultivars that results from the introgression of a common evolutionary chromosomal segment from a unique wild relative (van der Voort et al. 1999). On the contrary, clustered resistance alleles in repulsion, as *Me1* and *Me3* genes in pepper (Djian-Caporalino et al. 2014), could hinder association of multiple disease resistance within a same plant.

A quantitative or complex resistance (sometimes also referred to as “horizontal”) trait is characterized by a continuum of responses to infection between the most resistant and the most susceptible plants of a progeny. It results from the simultaneous but independent allelic variation of multiple independent loci, called quantitative trait loci (named later *R* QTLs, meaning any QTL related to resistance), and from the effect of the environment. Those *R* QTLs are distributed over the whole plant genome, each exhibiting commonly a minor effect on the observed trait. Quantitative resistance is usually an incomplete or partial resistance; however, it may prove sufficient in the field as long as the inoculum pressure is moderate. *R* QTLs may have additive and/or epistatic effects (Lefebvre and Palloix 1996; Boissot et al. 2010, for example in pepper and melon). When their effects are weak or when they are not yet mapped, *R* QTLs may be embedded in the effect of the genetic background often responsible for modulating *R* gene expression (Gallois et al. 2018). Many *R* QTLs were identified through linkage analyses, first in bi-parental progenies, then in multi-parental progenies such as multi-parent advanced generation inter-cross (MAGIC) and nested association mapping (NAM) populations (Poland et al. 2011; Bossa-Castro et al. 2018). An increasing number of publications have reported the mapping of *R* QTLs in plants since the 1980s. Databases, when they exist, enable quick comparison of QTL mapping results from independent experiments. Otherwise, QTL meta-analyses help to decipher the genetic architecture of resistance with the distribution of the involved loci along the genome and the allelic diversity at *R* QTLs across the different mapping progenies (Danan et al. 2011). Concomitantly, GWAS has been developed for QTL identification (Zhu et al. 2008) and extended to *R* QTLs (Bartoli and Roux 2017). It maximizes the genetic diversity investigated within a crop species. The use of GWAS is still in infancy for resistance traits in horticultural crops. *R* QTLs identified by linkage analysis can encompass hundreds of genes, making difficult the identification of the causal gene, while GWAS may provide much higher resolution, especially in plant species where the linkage disequilibrium rapidly decays along the chromosome. Because of its genetic complexity, quantitative resistance is rather difficult to integrate in a breeding process (Thabuis et al. 2004a, b) and therefore less exploited than *R* genes. However, *R* QTL mapping figures out genomic hot-spot regions affecting quantitative resistance, as well as it is described for qualitative resistance, that facilitate introgression of multiple disease resistance into elite plant material (Wiesner-Hanks and Nelson 2016).

Cataloguing resistance into two types (monogenic, qualitative, complete, variant-specific, vertical resistance vs. polygenic, quantitative, partial, broad-spectrum, horizontal resistance) is convenient but appears outdated. Mixed segregations are frequent, such as multimodal continuous segregations, corresponding to combinations of genes with major effect (such as *R* genes, but also major *R* QTLs) and minor effect genes (minor *R* QTLs) within a unique genome (Caromel et al. 2005). Moreover, in field conditions, a simple resistance could be either fully efficient (complete) in a geographical area or partially efficient in another one (Thomas et al. 2016). Conversely, complex resistance, frequently qualified as partial, may also behave as complete in field conditions (Caranta et al. 1997).

9.5 Molecular Mechanisms of the Plant-Pest and Pathogen Interaction

Understanding the molecular mechanisms underlying resistance to pests and pathogens is not a prerequisite to breeding resistant crops. Genetic resistance has been introduced and selected in elite crops well before being characterized, and its characterization has often never been carried out even after deployment. However, understanding the genetic basis of resistance and the underlying mechanisms can be useful to transfer those resistance mechanisms in other crops, as well as to increase their durability.

Most resistance traits described in plants are controlled by dominant genes and rely on the recognition of pests and pathogens by plants, activating signalization pathways and ultimately resulting in resistance. These resistance traits are said to be conferred by *R* genes and had initially been interpreted by the "gene for gene" model, based on the genetic analysis of the flax/*Melampsora lini* pathosystem (Flor 1971; Flor 1955). According to this model, each *R* gene, encoded by the plant, matches an avirulence factor (*Avr*), encoded by the pathogen. The resistance is triggered by the presence of both the avirulence and the *R* gene factors. Conversely, in the absence or modification of any of these factors, the plant is susceptible to the pest or pathogen. The "elicitor/receptor" model further explained this mechanism by suggesting a direct interaction between the proteins encoded by *R* genes and *Avr* factors (Keen 1990).

In contradiction with this model, direct *R*/*Avr* interactions were seldom characterized and the "guard model" was proposed, based on the analysis of the Tomato/*Pseudomonas* pathosystem and the resistance events mediated by the host factors Pto and Prf (Xiao et al. 2003; Salmeron et al. 1996; Ntoukakis et al. 2014). According to this model, the pathogen avirulence factor AvrPto interacts with, and targets, a plant host factor, the Pto protein kinase, resulting in a modified form of this molecule. The Pto modification is then recognized by the *R* gene *Prf* that triggers the resistance events. In this model, the avirulence factor is called an effector, and is a protein secreted by the pathogen to manipulate the host's cellular functions (here inactivating the Pto kinase). The Pto kinase is the guarded protein, whose modification will trigger the resistance, and the Prf protein is the guardee, encoding a R protein, which will detect the modification of the complex Pto/Prf (be it conformational modification, degradation or dissociation) and trigger the resistance. In this model, the guarded protein, targeted by the elicitor, is essential to the pathogen's virulence (Jones and Dangl 2006; Dangl and Jones 2001). Several evolutions of the "guard model" have been put forward in the last 10 years to refine it. The reader can find details in the literature on the "decoy model", which explains how the effector's target can be driven to duplicate in order to conciliate contradicting evolutionary pressures, or on the "integrating decoy model" (van der Hoorn and Kamoun 2008; Cesari et al. 2014). The succession of models probably shows that a unifying theory on how the plant recognizes the pathogens may not exist but rather highlights the dynamic evolution of the plant/pathogen arms race, a point that will be further discussed in Sect. 9.6. Despite this plasticity of simple resistance mechanisms and the high variability of pathogen effectors, breeders can benefit from the highly conserved unicity of plant *R* genes involved in genetic resistance. For example, they exploited a unique allele of *Mi* in tomato, that confers resistance to nematodes and hemipterans (Kaloshian and Walling 2005), and a unique allele of *Cf2* in tomato, conferring resistance to fungi and nematodes (Lozano-Torres et al. 2012), or even two alleles of the same gene, such as *Vat/Pmw* in melon, conferring resistance to aphids, viruses and powdery mildew (Dogimont et al. 2007). These examples of *R* genes well characterized in plant species cultivated in greenhouses highlight that common dominant *R* genes may confer multiple disease resistance to taxonomically unrelated pathogens.

The largest family of *R* genes encodes so-called NB-LRR (Nucleotide Binding–Leucine Rich Repeat) proteins. The central NB domain is considered to be involved in nucleotide exchange-based conformational changes, following activation, whereas the C-terminal LRR domain is constituted by motif repeats usually involved in protein-protein interactions. Two main families of NB-LRR are characterized at the N-terminal part of the protein by the presence of a TIR (Toll/interleukin-1 receptor) or CC (coiled-coil) domain. Interestingly, NB-LRR proteins are homologous to mammal NOD-LRR (Nucleotide-binding Oligomerization Domain-Leucine Rich Repeat) proteins, which are involved in inflammatory and immune response, suggesting conserved basal mechanisms in mammals and plants. In plants, NB-LRR proteins are encoded by large gene families, with for example 326 NB-LRR genes identified in tomato or 81 in melon (Nicaise 2014; Grube et al. 2000; Garcia-Mas et al. 2012; Andolfo et al. 2014), mostly organized in clusters in the genome. Those families of genes became obviously good candidates for identifying genes underlying disease resistance loci, often characterized only by genetic mapping (Pflieger et al. 1999, 2001a). In lettuce, the majority of the 385 NB-LRR predicted proteins are encoded by genes located in five major resistance clusters (Christopoulou et al. 2015). In melon, 45% of the 81 putative NB-LRR genes are grouped within nine clusters (Garcia-Mas et al. 2012). These clusters can be associated with resistance to several different pathogens. In melon, the sub-telomeric region of chromosome V, containing a cluster of 28 NB-LRR, is associated with resistance to *Podosphaera xanthii*, ClYVV, some isolates of ZYMV, and with partial resistance to *Fusarium oxysporum* f. sp. *melonis* (Boissot et al. 2016a). The result of this organization is ambivalent: on the positive side these gene clusters associate resistance to multiple diseases, that can be introgressed as one single locus from crop wild relatives to crops, but on the other hand, it makes it often difficult to precisely identify the NB-LRR gene directly underlying the resistance to a given pathogen among the cluster. Finally, the organization of NB-LRR in cluster contributes to *R* gene evolution through intra- and inter-genic recombination and sequence exchanges, therefore providing new potential resistance genes.

Following direct or indirect recognition of the pest or pathogen by the R protein, a downstream signaling cascade is activated in the plant cell, resulting in resistance. These signaling pathways involve many different proteins, resulting in specific transcription factor activation and hormone signaling. The eventual outcome of this cascade is the expression of Pathogenesis-Related (PR) proteins allowing resistance towards biotroph parasites. The resistance reaction can result in a Hypersensitive Response (HR), visually recognizable by localized necroses located at the site of pathogen penetration in the plant. This rapid cell death can stop the propagation of the pathogen in the host. In some cases, cell death is much more localized and results in Extreme Resistance (ER), in which case the site of necrosis is not visible. These mechanisms can also be associated with the activation of Systemic Acquired resistance (SAR), a set of long-distance resistance mechanisms that protect the plant against subsequent pathogen infections (Spoel and Dong 2012; Hammond-Kosack and Parker 2003).

Overall, NB-LRR dominant resistance genes constitute the largest repertoire of *R* genes deployed in crops. Although largely associated with qualitative or complete resistance, their use needs to be properly addressed as they can be overcome by pests and pathogens (see sect. 6). Dominant resistance is not limited to NB-LRR genes. Other genetic resistance relying on more specific mechanisms is available too. For example the tomato *Ty1/Ty3*-based dominant resistance to the begomovirus TYLC encodes a RNA-dependent RNA polymerase (Verlaan et al. 2013).

Conversely to dominant resistance genes, resistance can arise from the loss of a factor conferring susceptibility to the pathogen. As a result, those resistance traits are mainly recessive. Susceptibility (*S*) genes are defined as “any plant gene that facilitates the infection process or support compatibility with a pathogen” (van Schie and Takken 2014). This definition encompasses repressors of resistance pathways (as described above), that have often been characterized by genetic approaches.

However, because of the cost associated with de-repressed resistance mechanisms, this special class of genes may not be used in breeding processes. However, the *MLO* (mildew resistance locus *O*) gene, identified in barley and encoding a transmembrane protein, was characterized as a negative regulator (repressor) of cell death and associated with a reduced yield penalty, although a role as a docking molecule allowing the pathogen's entrance in plant cells is also considered. The *mlo* recessive resistance alleles are associated with a very broad spectrum resistance with a high durability potential in the field (Boyd et al. 2013). Interestingly, *MLO*-based resistance was identified in other plant species and crops, including tomato (Bai et al. 2008), and can be translated as well to other crops.

The second class of characterized *S* genes is the one sustaining compatibility between the pathogen and the host. This is particularly true for viruses, which harbor very small genomes encoding only few proteins and need to hijack host factors to complete their infectious cycle in the plant (van Schie and Takken 2014; Pavan et al. 2010). The loss or modification of a susceptibility factor is associated with resistance. Again, the resistance is then mostly recessive (hence the susceptibility is dominant). The best-characterized resistance by loss-of-susceptibility is the one relying on the translation initiation factors eIF4E. Resistance towards single strand positive RNA viruses, including the large group of potyviruses such as PVY, TEV, LMV, is associated with non-synonymous mutations: amino acid changes within the eIF4E protein have been selected in most vegetables (including lettuce, pepper, melon) and are extensively used in breeding (Robaglia and Caranta 2006). The *eIF4E* genes also constitute ideal targets to design *de novo* resistance in crops devoid of natural resistance (Bastet et al. 2017). Indeed, one major drawback of resistance achieved through loss-of-susceptibility is that genes hijacked by pathogens are often essential for the plant development and hence their mutation can be incompatible with the aim of plant production and plant breeding (Hückelhoven et al. 2013; Bastet et al. 2017). The concept of resistance by loss-of-susceptibility can be extended to any other pathogen (van Schie and Takken 2014; Pavan et al. 2010; de Almeida Engler et al. 2005). Recessive resistance also acts towards insects and nematodes, such as resistance to beetles or to *Meloidogyne javanica* in cucumber (Walters et al. 1997; Dogimont et al. 2010). Nevertheless, as far as we know, none such genes have been characterized.

Molecular mechanisms underlying quantitative resistance and responsible gene(s) underlying *R* QTLs are far less known than qualitative resistance and *R* genes. However, a small number of them has been identified, including genes involved in basal plant defense, e.g. the lignin biosynthesis, transmembrane receptors that detect pathogen-associated molecules, transporters such as receptor-like kinases or cell-wall-associated kinases, and transcription factors (reviewed in Nelson et al. (2018). Candidate genes underlying *R* QTLs are frequently organized as operon-like gene clusters consisting of functionally-related genes involved in defense process, sometimes even clustered with NB-LRR genes involved in plant-pathogen recognition such as in pepper (Pflieger et al. 2001b).

9.6 Sustainability of Crop Resistance

Genetic resources are a collective property shared by the whole humanity. In plants, this resource is constituted by germplasm collections, comprising many plant accessions related to the cultivated species that are maintained and characterized by international organisms, national institutes, private seed companies, farmers and amateur associations. Within these collections, resistance or susceptibility alleles conferring high level of resistance are rare: collection screenings for high level resistance to a given pathogen delivered resistance genes in less than 1% of accessions, showing that such resources are finite (Sage-Palloix et al. 2007; Dogimont et al. 2010). Once the resistance conferred by a resistance gene is broken down, finding a new efficient gene is often difficult. Consequently, several cases of "orphan" plant diseases, for which no new resistance gene has been discovered, greatly limit crop production. To ensure sustainability of crop resistance, we have to be careful not to exhaust such resources. *R* QTLs are expected more frequent and should be considered in breeding programs to ensure a longer durability to resistance genes beside solutions that New Breeding Technologies (NBT) might offer.

Resistance genes present in germplasm collections result from reciprocal selection between plants and pests or pathogens at the evolutionary scale. Adaptation of pest and pathogen populations to introgressed resistance into cultivars can occur either quickly – as early as in the 1st year – or over more than 10 years after its deployment. The possible breakdown of the resistance therefore constantly forces breeders to search for new resistance sources in genetic resources and to reiterate the selection process which is costly. Indeed, introducing a new genetic resistance necessitates to re-start the whole breeding process as the introgression of new genetic material in a cultivar is associated with a partial loss of quality and productivity. At the same time, this reiteration promotes a harmful evolution of plant pests and pathogens. For example, plethoric resistance genes to *Bremia lactucae* have been described in lettuce (Parra et al. 2016), most of them rapidly broken down after deployment in cultivars. In pepper, evolution of TSWV populations broke down the unique *R* gene available (Moury and Verdin 2012).

The risk of breaking down resistance to pathogens was analyzed according to population genetic concepts. McDonald and Linde (2002) built a model based on two concepts: (i) the evolutionary potential of a pathogen population is reflected by the amount and distribution of genetic variation within and among populations, and (ii) the level of "risk" for breaking down resistance is reflected by the evolutionary potential of the pathogen. According to this model, pathogens exhibiting the greatest evolutionary potential have a mixed reproduction system (sexual and asexual), a high potential for gene flow, large effective population sizes, and high mutation rates. Pathogens with the lowest evolutionary potential have strict asexual reproduction, a low potential for gene flow, small effective population sizes, and low mutation rates. Mc Donald and Linde (2002) compared the expected evolutionary potential and the observed resistance durability to many pathogens including several occurring in greenhouses. *Bremia lactucae* and *Phytophthora infestans*, both having a mixed reproduction system and a large effective population size, were expected to have a high evolutionary potential, but a medium durability of resistance was observed. *Cladosporium fulvum* and *Xanthomonas campestris pv vesicatoria*, both having an asexual reproduction system and a large effective population size, were expected to have a medium to high evolutionary potential but durability of resistance to both has been observed medium. Three soil pests and pathogens were analyzed, *Meloidogyne incognita*, *Fusarium oxysporum f.sp. melonis* and *F. oxysporum f.sp. lycopersici*, all reproducing asexually and exhibiting a medium expected evolutionary potential. According to the expected risk, durability of resistance to *Meloidogyne incognita* was observed medium, while for both *F. oxysporum f.sp.*, the durability of resistance was high. For all these examples, the evolutionary potential underestimated the resistance durability.

The concept of evolutionary potential as a predictor of the durability of resistance was extended to viruses (Garcia-Arenal and McDonald 2003), a crucial issue because host resistance is a key control method against viruses. Resistance was often found to be durable, as is the case for resistance to MNSV in melon or resistance to LMV and TuMV in lettuce. On the contrary, the tomato resistance to TYLCV was partially broken down few years after deployment, as well as the pepper resistance to TSWV. The selective constraints applied on amino acid substitutions in virus avirulence genes correlate with the observed durability of the corresponding resistance genes (Janzac et al. 2009). Moreover, some mutations in viral genome affected both plant resistance durability and spectrum (Moury et al. 2014).

Large studies of risk of breaking down resistance are not available for insects. Resistance to the aphid *Nasonovia ribisnigri* is conferred by the *R* gene *Nr* in lettuce, and breakdown of this resistance occurred 10 years after its wide deployment. The *Vat* resistance against the aphid *Aphis gossypii* in melon was jeopardized 15 years after its large deployment in France (Thomas et al. 2016). Beside resistance to aphids, *Vat* also confers resistance to viruses when transmitted by *A. gossypii*. Three virus species have failed to overcome *Vat* resistance in experimental evolution assays (Boissot et al. 2016b). Moreover, *Vat* resistance does not affect the structure of virus populations in melon fields (Schoeny et al. 2017). Accordingly, the *Vat* resistance to viruses is predicted durable.

The evolutionary potential of a given pest or pathogen species cannot explain why different plant resistance genes, alleles or genetic backgrounds exhibit different levels of durability. Other factors have to be considered to increase our ability to predict resistance durability. Researchers questioned the durability of different resistance genes, combination of resistance genes, resistance genes in different genetic backgrounds and the strategies of resistance deployment.

Overall, it was observed that resistance was durable or quickly overcome, regardless of their recessive or dominant status. Furthermore, very different durability levels were described towards different alleles of the same resistance gene. This was the case for example for the *R* gene controlling the TMV resistance in tomato where the alleles *Tm-2* and *Tm-2*^{2} differ by only 4 amino acids (Lanfermeijer et al. 2005; Harrison 2002), or the pepper *pvr2* resistance gene controlling the potyvirus resistance (Ayme et al. 2007). Actually, the numerous pathosystems described in the Sect. 9.5, highlight the dynamic evolution of plant/pathogens relationships and no general rule drives the probability that a pest or pathogen variant becomes virulent. Different mechanisms can be involved in the transition from avirulent to virulent status (number and type of mutations, recombination, pseudo-recombination, acquisition of extra-genomic components…); this transition may induce fitness penalty as a pleiotropic effect (Montarry et al. 2012), as for example in the PVY/pepper interaction. Fitness penalty is a key parameter to the reduction in frequency of a virulent strain in the pathogen population. The fitness penalty is highly variable, even among highly similar avirulence gene family members (Leach et al. 2001); again, no general rule appears to drive fitness penalty due to transition from avirulent to virulent status.

Most ongoing strategies to ensure a longer durability of host plant resistance are related to combinations of resistance genes, either at the genome level (usually called pyramiding strategies) or at the field or landscape scale (usually called deployment strategies). In both cases, the aim is to hinder the evolution of the pest and pathogen populations. Both strategies are rather difficult to experiment in fields or greenhouses but several experiments in controlled conditions or mathematical modelling approaches have contributed to this issue.

At the genome level, breeding cultivars with complex resistance is still challenging but genomic selection should quickly offer new opportunities in horticultural crops (Poland and Rutkoski 2016). The key point remains to determine which alleles/genes/loci should be combined. Viruses have been favorite pathogens to study that point because experimental evolution can be easily implemented. The pepper/PVY pathosystem offers the most complete studies. Depending on the pepper landraces, the breakdown frequency by PVY of the resistance allele *pvr2*^{3} varied from 0% to 52.5%, attesting the availability and diversity of genetic backgrounds favorable to resistance durability in the plant germplasm (Quenouille et al. 2015). Some QTLs increasing the *pvr2*^{3} durability overlap with QTLs controlling symptom intensity, suggesting a pleiotropic effect of the latter QTLs on the durability of a resistance gene (Quenouille et al. 2014). Again in pepper, durability of resistance to root-knot nematodes controlled by *Me1* and *Me3* genes was clearly enhanced when pyramiding both genes within a hybrid rather than deploying them simultaneously or in a rotation schedule (Djian-Caporalino et al. 2014). Therefore, according to results collected up to now, combining either different resistance genes together or a resistance gene with *R* QTLs appear better than not.

At the field or landscape scale, three main deployment strategies have been proposed: (i) a single resistance gene is deployed until the resistance is overcome (ii) different resistance genes are deployed year after year (i.e. alternating cultivars carrying different resistance genes), and (iii) mixtures of resistance genes, i.e. mixture of cultivars carrying different resistance genes, are deployed simultaneously. For horticultural crops cultivated in greenhouses, deployment strategies for resistance to nematodes were investigated for peppers grown under plastic tunnels. The most relevant cultural system appeared to be alternating resistance genes (ii) rather than using a mixture of resistance genes (iii) and the sequential use of different resistance genes (i) (Djian-Caporalino et al. 2014). Difficulties to test deployment strategies in fields and greenhouses have prompted the use of modelling approaches. A model was developed to investigate the deployment of resistance to viruses (Fabre et al. 2015). It considers the resistance characteristics, the prevalence of the disease in the agricultural area and the main sources of inoculum (from the field, from neighboring fields containing the same crop or from the wild compartment) called landscape connectivity. Simulations can be implemented according to the ecology of the virus and observed incidence to look for an optimal deployment strategy from ‘mixture’ (where susceptible and resistant cultivars coexist in a field) to ‘pure’ strategies (with only resistant cultivar in a field). Interestingly, the model suggests that for a disease having a medium incidence in an agricultural area, the resistance is predicted durable whatever the ‘landscape connectivity’ and the importance of the resistance deployment.

Most resistance breakdowns have resulted from the use of resistance genes combined with practices that fostered the adaptation of the targeted pest or pathogen, such as the use of a highly susceptible background, a large scale deployment of a single cultivar (monoculture) in an agricultural area highly propitious to the pest or the pathogen. Available knowledge suggests that whatever the type of resistance gene used, it should be combined with other loci involved in either the resistance or its durability to build new cultivars. In a context of medium incidence of the targeted pest or pathogen, large deployment can be considered; however in any context highly favorable to the disease, relevant cultural system should be established by experimental approaches.

9.7 Prospects

The combination of phenotyping, plant genetics/genomics and molecular characterization of resistance loci has led to the introduction, by breeding, of genetic host plant resistance to major pests and pathogens in crops. In this process, the understanding of the underlying mechanisms has resulted in the emergence of very common features that can boost translational studies between crops. This knowledge has expanded in all directions, ranging from detailed understanding of resistance mechanisms to the large scale field assessment of resistance durability (Fig. 9.2). As the progression unravels, the focus can change from a few resistance genes, that can be broken down, to more efficient solutions by taking into consideration the potential stabilization of resistance genes by *R* QTLs embedded into the genetic background or in contrast by discarding alleles of resistance genes with a poor durability potential. Recent studies show how additional surveys on plant genetic background can help to build iteratively more efficient cultivars. Additional quantitative resistance, often relying on multiple *R* QTLs, could reinforce resistance efficiency and durability, an approach fully compatible with the recent developments of both phenotyping platforms and the rise of genomic selection (Poland and Rutkoski 2016; Desta and Ortiz 2014). Moreover, the molecular characterization can be used as a basis for

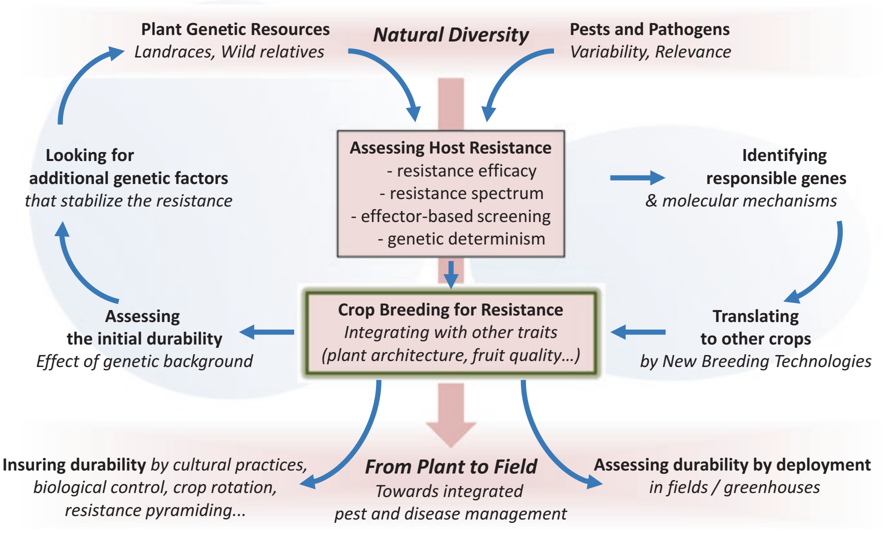

Fig. 9.2 A dynamic framework allowing the efficient development of genetic host plant resistance in crops

combining in the same crop different resistance mechanisms: it is noteworthy that combining both effector-triggered resistance (*R* genes) and resistance by loss-of-susceptibility (*S* gene such as *eIF4E*-based resistance) can (i) allow more stable resistance with higher durability as the pathogen would have to overcome two different mechanisms, and (ii) suppress the HR-derived necrosis on the vegetable that can alter its commercial value. This is the case of resistance to the potyvirus BCMV in common bean (Meziadi et al. 2016). Finally, current trends of research are moving beyond the identification of full resistance to the characterization of tolerance, i.e. "the host's ability to reduce the effect of infection on its fitness regardless of the level of pathogen multiplication" (Pagan and Garcia-Arenal 2018).

As seen above, breeding for genetic resistance to pests and pathogens is built on the analysis of the natural diversity of both crops -including the crop wild relatives- and pest and pathogen populations. Phenotyping host diversity can lead to the characterization of new factors, through the development of GWAS, while the characterization of the pests and pathogens allows focusing on the more constrained effectors of the pests and pathogens as a source to look for relevant plant targets for resistance. Interestingly, although mining through natural collection have allowed to uncover the co-evolution processes between plants and pathogens (Charron et al. 2008), it also makes sense to try to assemble resistance *R* QTLs from very different genetic backgrounds, even from different crop wild relatives, in order to ensure the lack of pre-existing adaptation in the pathogen's variability.

Although genetic resistance exploited so far in agriculture mostly originates from the plant natural diversity, gene modification may also be induced by different means. Random mutagenesis (using chemical agent such as Ethyl Methyl Sulfonate), insertion of DNA in the genome (genetic transformation, resulting in resistant Genetic Modified Plants) or new genome editing techniques such as CRISPR/Cas9 (allowing gene inactivation by knock-out, allele replacement or base replacement) could provide new resistance alleles and allow to translate resistance mechanisms from naturally evolved mechanisms to crops in which such resistance is missing. At the very least, these methods have been successfully used by research laboratories to validate the function of genes responsible for resistance, and to point out to the relevant genes that can be subsequently mined for among natural plant germplasm and introgressed in a crop plant of choice. Recent work on the *eIF4E* susceptibility factor to the main group of *Potyviruses* shows how the molecular signatures associated with resistance can be translated in a cross-species manner to provide broad-spectrum resistance at no developmental cost (Bastet et al. 2018). Alternatively, engineering resistance gene could help combining resistance traits to an elite cultivar, including resistance from different genetic backgrounds, a process sometimes made difficult through classical plant breeding because of linkage drag (Lin et al. 2014). For example, the *R* gene $Tm2^a$ controlling *Tobamoviruses* in tomato is associated with a large chromosomal insertion on chromosome T9, that correlates with significant metabolomics changes caused by the “hitch-hiking” of metabolomics genes from wild tomato origin (Zhu et al. 2018).

Using crop resistance is probably the simplest tool to implement by growers in an IPM strategy. To enlarge the host plant resistance weight in the IPM approach, breeders should propose cultivars with resistance to multiple pests and pathogens. In germplasm of a plant species, it is frequent to identify a host genotype exhibiting resistance to several pests and pathogens, such as the landraces ‘Criollo de Morelos’ in pepper or ‘90635’ in melon (Boissot et al. 2000; Barchi et al. 2007). This multiple disease resistance is controlled by resistance genes, *R* QTLs and/or clusters (that evolve under diversifying selection) dispersed in the plant genome (Wiesner-Hanks and Nelson 2016). Several resistance genes (including *R* genes) and/or *R* QTLs can localize on a same chromosome. Unfortunately, breeders generally “broke” this multi-resistance by introgressing only resistance to a specific parasite in an improved cultivar that at the end is not resistant to the other parasites. Otherwise, multiple disease resistance might be controlled by tightly linked resistance genes and/or *R* QTLs or even to pleiotropic effect of a resistant gene or an *R* QTL. In that case, multiple disease resistance is easily introgressed from the relevant accession to elite cultivars. Finally, breeders should also propose cultivars with durable resistance. An innovative approach consists in looking for QTLs inducing genetic drift in the pathogen population, a key parameter for resistance durability (Tamisier et al. 2017).

Combination of crop resistance with other IPM packages is expected fair, smart and efficient for sustainable agriculture but we miss data to evaluate or predict the gain of each package and their combinations. Recent studies turn to analyzing the effect of abiotic stresses such as drought, soil water saturation, salinity or excessive temperatures on efficiency of plant host resistance (Moury et al. 2014; Lefebvre and Palloix 1996; Abro et al. 2014), and shall be considered when deploying resistant crops in greenhouses (Pandey et al. 2017). The combination of partial resistance with other IPM packages might be effective enough for growers. Introgression of partial resistance in cultivars should be encouraged by cultivar-registering entities such as UPOV and taken over by breeding companies. In addition, IPM might enhance durability of packages related to biotic manipulation. For example, does biological control enhance genetic drift in pest or pathogen populations- and then participate to host plant resistance durability? Reciprocally, host resistance might improve the durability of biological control. We should decipher in the future if the pest and pathogen adaptation to host resistance could induce a trade-off for their adaptation to other IPM packages.

Moving from new genetic cultivars to agronomic innovation through an interdisciplinary and participatory approach holds promise for scientists seeking new integrated pest and disease management approaches to increase the sustainability of agriculture. As an encouraging example, recent studies propose to use a pepper line resistant to root-knot nematodes as a trap crop. Cropping resistant pepper dramatically reduced the nematode population in the soil. This allows cultivation of susceptible crops in crop rotation. Twenty-one to thirty-six percent of farmers in South-East of France found the cropping system completely or partially acceptable (Navarrete et al. 2016).

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Chapter 10
Cultural Methods for Greenhouse Pest and Disease Management

H. Marjolein Kruidhof and Wade H. Elmer

Abstract Cultural control measures can be broadly divided into (a) general agricultural practices that can affect pest and disease incidence (e.g. greenhouse climate control, fertilization, irrigation as well as crop density, training and pruning practices) (b) practices that are solely or mainly used for pest and disease control (e.g. sanitation and insect screens), and (c) practices used for both agricultural and crop protection purposes (e.g. choice of crop cultivar and growing medium, grafting, crop rotation and composting). In this book chapter we describe the ways in which cultural control measures can influence pests and their natural enemies, diseases and their antagonists, and (induced) crop resistance. We discuss how this knowledge can be used to optimize integrated pest and disease management, with special reference to current developments, such as the shift from curative towards preventative pest and disease management, as well as developments in greenhouse energy saving practices and technologies used for sensing, monitoring and decision making.

Keywords Cultural control · Systems approach · Sanitation · Crop resistance · Monitoring and scouting · Insect screens · Greenhouse climate · Artificial light technologies · Fertilization

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10.1 Introduction

Greenhouses can offer a large advantage over field conditions. The main asset of greenhouses is to protect the crop from adverse climatic conditions. This allows for the production of high quality crops in regions with sub-optimal climatic conditions. Moreover, greenhouse structures can reduce the influx of pest organisms, especially when insect screening is used in ventilation openings in combination with other sanitation measures. Depending on the type of greenhouse and its technology level, the abiotic crop environment can be manipulated to a relatively high extent. This offers excellent opportunities for cultural control of pests and diseases. We define cultural control as *changes in crop production methods that affect pests and/or diseases directly, or indirectly through an effect on their natural enemies/antagonists and/or an effect on (induced) crop resistance'.* Cultural control can be broadly divided into three categories: (1) practices that are usually applied for agricultural purposes not related to crop protection but that can have a direct or indirect, positive or negative, effect on pest and disease incidence, such as greenhouse climate control, fertilization, irrigation as well as crop density, training and pruning practices, (2) practices that are used solely or mainly for pest and disease control, such as sanitation practices and implementation of insect screens, and (3) practices that are used for both agricultural as well as pests and disease control, such as the choice of crop cultivar and growing medium, grafting, crop rotation and composting (after Katan 1996). Certain cultural control practices for managing pests and diseases in greenhouse-grown crops have been known and applied for decades already. However, over the past two decades crop protection approaches have largely shifted from curative practices towards preventative practices that enhance the resilience of the cropping system. Among others, this requires a more profound consideration of possible trade-offs between sanitation practices and cropping system resilience. Moreover, recent developments in energy saving practices of greenhouse operations, as well as artificial light technology, have further increased the need for expanding our knowledge on the effects of climate factors on crop health and taking this knowledge into account when making climate- and crop management decisions. Finally, quick developments in technology and tools used for sensing, monitoring and decision making has the potential to profoundly change the way in which cultural control measures will be implemented.

In this book chapter we describe the ways in which cultural control measures can influence (i) pests and their natural enemies, (ii) diseases and their antagonists, and (iii) (induced) crop resistance. Moreover, we discuss how this knowledge can be used to optimize integrated pest and disease management. We start with giving a brief overview of the main changes in pest and disease control practices and in greenhouse climate control of the last two decades. We then sketch the position of cultural methods within the broader context of a systems approach for pest and disease management. Typically, crop health is not the main factor that drives management decisions concerning the crop and the greenhouse environment. Likewise, there is not one set of climatic conditions that supports (biological) control of all pests and diseases, as each organism has its own appropriate and adverse microclimates. Therefore, after discussing the separate effects of the greenhouse (micro) climate and crop management practices on induced crop resistance, pests, diseases and their biological control agents, we finish this chapter with discussing possibilities for approaching the seemingly impossible task of integrating this information into practices that favour both overall crop health as well as crop productivity and quality.

10.2 Recent Changes in Pest, Disease and Climate Control Practices

10.2.1 From Curative Towards Preventative Pest and Disease Control

The possibilities for chemical control continue to become more and more limited. Relatively simple decision support systems, which predict when intervention (being biological or chemical) is required based on pest and disease monitoring in combination with action thresholds, will no longer suffice. Instead, preventative measures should be implemented right from the start of the cropping cycle. It is important to bear in mind that preventative measures have a broader scope than just sanitation practices. Even thus sanitation is still important, the emphasis is nowadays shifted more and more towards measures that enhance the resilience of the cropping system, including the preservation, early introduction and stimulation of natural enemies and beneficial microbes (Messelink et al. 2014). Over the last two decades, the use of generalist predators has won a lot of terrain over the use of specialist natural enemies. The reason is that populations of generalists can be build up and preserved in the absence of the pest, through the use of alternative food (Symondson et al. 2002). Maintenance of the ‘standing army’ approach requires knowledge of their food choices and habitat requirements. Likewise, beneficial microbes are applied as early as possible, so they have a better chance of colonizing the rhizosphere, phyllosphere and/or plant tissues, thus establishing a beneficial microbiome early in the plant production cycle.

10.2.2 Limiting Energy Consumption in Greenhouses

In greenhouse crop production energy is mainly used for temperature control (heating and cooling), humidity control (mainly dehumidification) and artificial lighting in high-tech greenhouses. Only minor amounts of energy are used for greenhouse operation of other equipment (e.g. motors for ventilation, screens, pumps for irrigation). Limiting the energy consumption in greenhouses has received considerable attention in the last decades, especially in climates where a large amount of fossil energy is used, due to sustainability or climate change discussions. Decreasing energy use can be achieved both through changes in the greenhouse and its equipment, or through changes in the management of the greenhouse microclimate and the crop. An example on how changes in equipment can help to save a substantial amount of energy is the use of one or more screens inside the greenhouse, a practice that is spreading among growers in countries like The Netherlands (Hemming et al. 2017). But also permanently insulating covering materials are under development (Hemming et al. 2012; Kempkes et al. 2014). However, higher insulation results in higher humidity values, thus growers may choose to use mechanical dehumidification (Hemming et al. 2017). Another principle of energy is making use of natural sunlight. Increased light transmission, especially during the winter period, can result in increased plant production while reducing energy consumption. Quantitative crop models are used to calculate the consequences of different climate regimes on energy savings and crop production (Elings et al. 2006; De Gelder and Dieleman 2012). Especially reducing the temperature set points and/or allowing temperatures to fluctuate over time ('temperature integration', indicating fluctuations in average temperature exceeding 1 day, and 'DIF', indicating the difference between average daytime and nighttime temperature) can, depending on the bandwidth applied, conserve considerable amounts of energy without adverse consequences for the crop. Moreover, increasing the relative humidity set points and reducing plant transpiration by removing leaves can result in additional energy savings without reductions in plant growth (De Gelder and Dieleman 2012). Filtering out near-infrared can also benefit plant production and reduce water and energy use for cooling in warm climates, but has a negative impact on greenhouse temperatures during the winter period when all sun energy is welcome in the greenhouse (Stanghellini et al. 2011; Abdel-Ghany et al. 2012). The crop models used here typically 'weigh' the consequences for energy savings against the consequences for crop production. However, it is of utmost importance to also take into account the consequences of energy saving measures on crop health.

10.2.3 Artificial Light Technologies

Moreover, artificial lights are used to secure year-round production and improve product quality in greenhouses in the northern regions. The developments in artificial lighting techniques continue to advance, and the currently predominating high-pressure sodium lamps (HPS) will gradually be replaced by light-emitting diodes (LEDs) in the next decades. LEDs have the advantage that the efficiency with which they convert electricity into light is high, that the heat emission is low, and that the spectral composition of the light can be adjusted to the demands of the crop (Morrow 2008). Light quality and quantity does not only affect plant growth (Hogewoning et al. 2010; Johkan et al. 2012), but also affects pests and diseases directly and indirectly through an effect on plant defensive mechanisms (Roberts and Paul 2006;

Vanninen et al. 2010; Johansen et al. 2011). Moreover, increased knowledge of light quality and quantity on crop production will lead to altered lighting practices, which may also directly affect the biology of pests, diseases and natural enemies.

10.3 Systems Approach to Pest and Disease Management

10.3.1 Pest and Disease Tetrahedron

As no single preventative measure is effective by itself, different control measures need to be integrated into a systems approach. This is illustrated by the pest and disease tetrahedron that is depicted in Fig. 10.1. This pest and disease tetrahedron can be seen as an extended version of the disease triangle, where we now explicitly distinguish between the crop environment and beneficial organisms, including (a) natural enemies of arthropod pests, such as predators, parasitoids, and entomopathogens, (b) microbial antagonists of bacterial and fungal pathogens, and (c) microbial elicitors of crop resistance. Moreover, we broadened the scope of the crop environment from its mere abiotic components that directly relate to crop growth to also include the 'ecological structure' (i.e. the availability of (alternative) food, shelter and oviposition sites for beneficial organisms, pests and pathogens not offered by the crop itself). From here it can easily be seen how management of the greenhouse climate and crop influences pests and diseases not only directly, but also indirectly through an effect on beneficial organisms and crop growth and defenses.

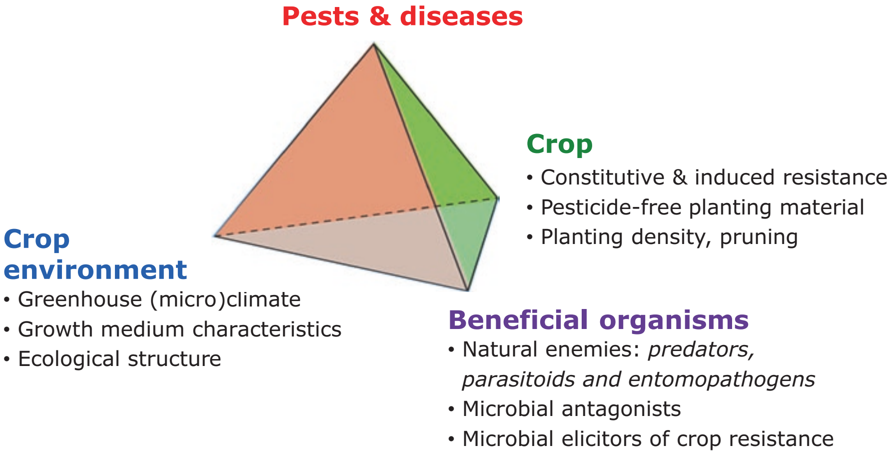

Fig. 10.1 Pest and disease tetrahedron, depicting the 4 main components of a systems approach to pest and disease management, as well as their interactions

10.3.2 Effects of Cultural Methods on Biological Control

For the control of insect- and mite pests in greenhouse-grown crops, in most cases the use of natural enemies will lie at the core of a systems approach. When aiming to combat pests with natural enemies, apart from the effect of cultural methods on the abundance and population growth rate of pests and their natural enemies, also the effect on the natural enemies' attack rate needs consideration. In other words, not only the natural enemies' numerical response to the food sources present in the crop is important, but also its functional response to the target pest. This is especially crucial for specialist natural enemies that spend a large proportion of their energy searching for prey or hosts. Besides climatic conditions, also crop management practices, such as removing plant parts for harvest or pruning purposes, may influence the balance between natural enemy and pests populations when they occupy different microhabitats in the crop. Similarly, the ability of an antagonist to suppress a pathogen, and/or to survive and proliferate in soil or on leaves can become a function of edaphic and environmental factors. Crop production methods affecting abiotic factors such as fertility, soil pH, humidity and temperature, can dramatically alter the interaction among an introduced bacterial antagonist, the pathogen and its host plant.

10.3.3 Crop Resistance and its Linkage to the Greenhouse Environment and Biological Control

Crop resistance is also an essential component of a systems approach to integrated pest and disease management. Crop production methods and greenhouse climate can therefore have a profound effect on the level to which crop resistance is expressed. This, in turn does not only affect pests and diseases, but can also directly and indirectly affect natural enemies and microbial antagonists (e.g. Krips et al. 1999; Gols and Harvey 2009). Crop resistance promotes biological control whenever the negative effect on the growth rate of the pest or pathogen population exceeds the negative effect on the abundance of natural enemies and their attack rate. It is important to note that, apart from potential negative side-effects of plant traits that have evolved as defenses to plant pests and pathogens for natural enemies, plants have also evolved traits to support natural enemies and beneficial microbes (e.g. Bottrell et al. 1998; Cortesero et al. 2000; Bakker et al. 2018).

10.3.4 Monitoring and Scouting

Proper monitoring is key to integrated pest and disease management. Monitoring and scouting has traditionally focused on the incidence of pests and diseases, with direct crop inspection being supplemented with the use of sticky- and pheromone traps. However, when implementing a systems approach for pest management, monitoring the abundance of natural enemies and microbial antagonists should deserve equal attention as monitoring pest and disease occurrence. Only in this way it will be possible to spot any aberrations in the balance of the system at an early enough stage for restoration of this balance being a feasible option. Some commercial apps have been developed that can aid scouting and mapping of pests, diseases, and beneficials in greenhouse crops (e.g. Scarab Precision and Koppert iPM). In recent years important progress has been made in the development of non-invasive detection techniques of crop stress and early stages of disease development. Mahlein (2016) provides a review of the state-of-the-art sensor imaging and data analysis methods for the diagnosis and detection of diseases in crops. Within-crop reliable automated detection of arthropod pests, however, still poses many more challenges (Liu et al. 2017).

Monitoring of the (micro)climate will also be important for proper pest and disease management, as it will help to explain the proliferation of pests and diseases and the efficacy of natural enemies and microbial agents. However, as most plant pathogens and pests, as well as their natural enemies, reside either on the leaf surface or in the soil or substrate, climate data collected by sensors above the canopy cannot be readily related to pest, disease and/or natural enemy population dynamics. Differences between the microclimate on the leaf surface and the ambient air occur due to photosynthesis, transpiration and vapor condensation processes that occur on plant surfaces (Zhang et al. 2002). A variety of electronic sensors are used to measure leaf wetness duration, which is an important determinant of pathogen infections, although there is no established standard sensor type or use (Rowlandson et al. 2015). A recent study has been able to employ tiny hot wire silicon sensors to automatically measure humidity, temperature and wind speed near the plants within the greenhouse, without disturbing the measurements (Makhlouf et al. 2016). However, reliably and directly measuring the microclimate of the leaf boundary layer of the crop with sensors remains technically extremely challenging and its practical implementation is thus far not economically viable. Modeling provides a more viable option to bridge the gap between the climate of the ambient air and the in-canopy microclimate, as for example shown by Zhang et al. (2002), who have developed a dynamic model to estimate the in-canopy and leaf-surface microclimate of greenhouse cucumber crops with respect to humidity and temperature. This model has later been adapted for tomato by Hao et al. (2008).

Although it would be beneficial to monitor the level to which the crop's defenses against pests and diseases are primed or activated, this is difficult to measure in a commercial greenhouse setting due to the complexity of the mechanisms underlying plant priming and induced resistance. Recently, efforts are being made to develop tests for measuring the effect of chemical and microbial elicitors on the plant's defensive state for practical applications (Kruidhof, personal communication). There is also a need for reliable indicators of disease suppressiveness in soils and substrates. Neher et al. (2017) found a good correlation between the microbial ecoenzymes that are active on chitin and cellulose and the disease-suppressiveness of the soil against *Rhizoctonia solani*. At the same time, this study did not show a good correlation between microbial respiration and disease-suppressiveness. The increasing understanding of the composition and functioning of the soil microbiome, and the exciting developments in high-throughput molecular analyses create possibilities for more sophisticated monitoring of the disease-suppressive state of the soil and/or substrate in the future.

10.4 Start of the Cropping Cycle

10.4.1 Sanitation of Greenhouse Structures

Preventative measures can only take effect when the pest and disease pressure is sufficiently low at the beginning of the crop production cycle. This moment presents a very significant opportunity to practice sanitation. Ideally, the cropping cycle should start with a pest- and disease-free greenhouse environment, soil/soilless growth medium and planting material. Close inspection and quarantine of incoming cuttings, plugs, bulbs, corms, and transplants will segregate pests and diseases from the established crop and provide more success in treating them. Fumigating greenhouses with environmentally-safe sterilants will reduce pest densities and minimize environmental damage. The ideal fumigation agent provides maximum dispersal, is non-corrosive to equipment, and quickly degrades, leaving no toxic residue (Wilson et al. 2005; Otter et al. 2007). Disinfesting greenhouse floors, rockwool slabs, bench top surfaces, support strings, trays, pots, and utensils will further reduce common pest reservoirs. Most disinfectants like alcohol, houseful bleach, commercial chlorine products and hydrogen peroxide based materials are adequate for surface disinfecting cutting tools and greenhouse surfaces. Disinfecting hydroponic systems (sumps, plumbing lines, and pipes) requires close attention with respect to the choice of sterilants and costs (Ehret et al. 2001). Standard practices include chlorine dioxide, filtration, hydrogen peroxide/peracetic acid products, ionization of Cu or Ag, and use of bio-surfactants (Hong et al. 2014). Many regions require the treatment and recycling of used irrigation water. In the European Union, for example, regulations for this are arranged in the Water Framework Directive 2000. Growers can choose among many methods to disinfect recycled irrigation water and the choice may depend on availability, cost, ease, and compatibility with other practices. Use of electrolyzed oxidizing water, ozone, UV radiation and nanotechnology have recently emerged as new strategies for sanitizing irrigation water (Elmer et al. 2014).

10.4.2 Disinfestation of the Soil or Substrate

Several chemical and non-chemical practices exist for soil and/or substrate disinfestation prior to planting a new crop. However, in many regions of the world, the use of chemical soil fumigants has become very restricted. Of special relevance to many vegetable and ornamental crops grown in soil, is the prohibition of the use of methyl bromide. As a consequence of the loss of this broad-spectrum soil fumigant, many growers have shifted to growing crops in soilless cultures, allowing for an easy replacement of used substrates. Others have resorted to alternative measures for soil disinfestation, triggering a renewed interest in non-chemical alternatives including steam disinfestation, solarization and anaerobic (or biological) soil disinfestation. Crop rotation is another well-known measure that can aid growers in breaking cycles of crop-specific pests and diseases, but is not commonly practiced by conventional greenhouse growers. Steam disinfestation, on the other hand, has already been applied since the nineteenth century. The general recommendation for steaming is to reach a soil temperature of at least 70 °C during a time period of 30 min, which is sufficient to kill most important plant pathogenic fungi, nematodes and weeds, but not certain plant viruses, such TMV (Newhall 1955; Bollen 1969; Porter and Merriman 1983; Runia 1983). Sublethal temperatures, however, may also be effective as these can damage fungal pathogens, reducing germinability and aggressiveness of their propagules, and increasing vulnerability to other biotic or abiotic agents, such as the action of thermo-tolerant biocontrol micro-organisms (Lifshitz et al. 1983; Freeman and Katan 1988; DeVay and Katan 1991). Among the currently available steam disinfestation methods, the so-called 'negative-pressure steaming' method still ranks best for application in greenhouse horticulture in terms of efficacy and energy- and labour-efficiency (Runia 2000). According to this method, steam is blown under a steaming sheet and pulled into the soil by a negative pressure. This negative pressure is created by a fan, which sucks air out of the soil through buried perforated polypropene tubes (Runia 2000). On clay soils, so-called 'sheet steaming', for which no soil tubing system is required, is also applied. This method, however, is not effective when used in other soil types, and requires almost twice as much energy compared to negative-pressure steaming (Runia 2000). For all steaming methods, deep soil cultivation, as well as an initially relatively dry soil, are required for optimal results. Effective methods for the disinfestation of rockwool have also been developed, whereas peat is very difficult to disinfest with steam because of its high water retaining capacity (Runia 2000). Fixed-point steam disinfestation is mostly applied in temperate regions with heated greenhouses, as the heating system can be used as well for the generation of steam. To increase the possibilities for the application of effective soil steaming in non-heated greenhouses without fixed-point systems, Italian researchers have worked on the development of a mobile, self-propelled, steam injector that is able to operate in tunnels and greenhouses (Gelsomino et al. 2010). Whereas steam injection has generally been found to be less effective as negative pressure steaming, the combination of steam injection with the incorporation of exothermically-reacting compounds such as potassium hydroxide (KOH) or calcium oxide (CaO) can increase the efficacy through a further increase the soil temperature without any negative side-effects caused by toxic residues or harmful fumes (Gelsomino et al. 2010). Solarization, on the other hand, has traditionally been practiced in warmer climates between cropping cycles during the summer season, when the hot weather does not allow for greenhouse cultivation. With this method, solar radiation is trapped under a plastic mulch on moist soil during a period of approximately 4–6 weeks of high ambient temperature. This causes a temperature increase in the upper soil layers to levels that are lethal or sublethal to soilborne pathogens, plant-parasitic nematodes and weeds (D'Addabbo et al. 2010). The efficacy of the solarization process is determined by several factors, including soil temperature, moisture content, and the type of plastic film. Combining solarization with the addition of an easily-degradable carbon source can enhance the effectiveness of solarization, as well as shorten the solarization period or reduce the soil temperature that is needed to reach effective control of pathogens, weeds and plant-pathogenic nematodes (Butler et al. 2012; Morra et al. 2018). The practice of adding an easily-degradable carbon source into wet soil, which is covered by a polyethylene mulch is also coined biological (or anaerobic) soil disinfestation. This process stimulates rapid growth of aerobic microorganisms, leading to the depletion of available oxygen in the soil and consequently causing a shift of the soil microbial community towards facultative and obligate anaerobes (Blok et al. 2000; Goud et al. 2004). Soilborne plant pathogens and plant-parasitic nematodes are consequently controlled by mechanisms that are not entirely clear, but most likely relate to the toxic by-products of anaerobic decomposition (e.g. short chain fatty acids), volatile compounds, biocontrol by anaerobic soil microorganisms and/or oxygen deficiency (Momma 2008, 2015). Although in temperate regions, anaerobic soil disinfection in combination with solarization could also work when applied during spring and summer, it is thus far not often implemented in greenhouse horticulture.

Aiming for sterility, however, may not always be the best management strategy. Depending on the pest or pathogen and the degree of resilience in the crop and growing medium, eradication may have a deleterious effect over the long term by reducing beneficial predators and antagonistic microorganisms. With regard to soil disinfestation methods, the danger of creating a 'biological vacuum' was already recognized early on (Baker 1962). Excessive soil heating, with temperatures exceeding 70 °C, and particularly approaching 100 °C, becomes detrimental to most soil biota, including most beneficial microorganisms, such as microbial antagonists, rhizobia and mycorrhizae. This may result in the rapid re-infestation of excessively heated soil by contaminating inoculum, ultimately leading to disease incidence that is even higher than that of the non-treated soil or substrate. An example of this is provided by Postma et al. (2000), who found that batches without Pythium problems in the preceding cucumber crop had 52–100% lower numbers of diseased plants in nonautoclaved than in autoclaved, previously used, rockwool. Therefore, an important aspect to take care about when applying heat-based non-chemical soil disinfestation methods, is to avoid temperatures exceeding 70 °C as much as possible, e.g. by taking measures that ensure a more even distribution of temperature in the soil profile (Katan 2000). Fortunately, many species of saprophytic fungi were found to be more heat-tolerant in comparison with pathogenic fungi (Bollen 1969), including *Trichoderma* spp. Moreover, bacteria and actinomycetes are generally less sensitive to heat treatment as fungi (Bollen 1969). *Bacillus* spp., for example, have been reported to be the predominant Gram-positive bacteria surviving soil solarization, and to play a major role in disease suppressiveness of solarized soils (Stapleton and Devay 1984; Katan 1987). Several studies have indeed found that combined application of thermo-tolerant biocontrol micro-organisms in combination with solarization, or directly following steam disinfestation, resulted in better control of soilborne diseases than the application of either method alone (Sivan and Chet 1993; Luvisi et al. 2006; Minuto et al. 2006; Porras et al. 2007; Jayaraj and Radhakrishnan 2008). However, it is important to bear in mind that disease suppression in soils and other growth media is not always based on so-called 'general suppression', which relies on the competitive activities of the overall saprophytic micro- and macroflora. In certain cases disease suppression can be specifically attributed to the enrichment of specific subsets of soil microorganisms (Raaijmakers and Mazzola 2016). Apart from the growth medium itself, plants can also actively help shaping the rhizosphere microbiome. The studies of Mendes et al. (2018) and Berendsen et al. (2018) clearly illustrate mechanisms through which plants can actively shape the soil microbiome, and how disease outbreaks – even of foliar pathogens – can aid the build-up of specific disease-suppressive microbiomes. The many studies that are recently being undertaken to gain a better understanding of the factors that shape the soil- and rhizosphere microbiome, and the (functional groups of) microbes that are responsible for disease suppression, may help to provide more insight into the effects of soil disinfestation methods on the specific disease-suppression of growth media. The advancing knowledge in this field should provide a better basis for context-dependent decision making on soil disinfestation measures in the future.

10.4.3 Clean Seed and Planting Material

Clean seed is paramount to beginning a new crop, and the trade in seeds is subjected to strict phytosanitary regulations. However, procedures for seed disinfection have not been well developed for many greenhouse crops. Many pathogens that can travel on seeds inconspicuously are not observed in routine germination/sanitation assays (Elmer 2002). Molecular based assays that can detect known pathogens at low densities have been developed for many plant diseases, but have not been made readily available or affordable for most seed testing. On-site PCR-based kit assays for seeds are being developed and may soon appear in diagnostic and seed testing clinics (Carneiro et al. 2017; DeShields et al. 2018). Furthermore, the role of nanotechnology will further advance the diagnostic sensitivity of these assays by allowing the nano-sensors to access areas on the seed and in propagative tissues where pathogens and their DNA may be more difficult to access. For a detailed discussion on how nanotechnology can advance diagnostic testing, see Elmer and White

(2018). Disinfectants for seed treatments include $NaHClO_2$, hydrogen peroxide, quaternary ammonia compounds, various alcohols, and organic solvents with fungicides. Many times, a brief exposure with agitation in diluted household bleach can achieve 99% eradication of fungal colonists (Elmer and Stephens 1988; Elmer and McGovern 2013). Nowadays, growers are under increasing pressure to produce chemical-free products for the market. In turn, they are increasing their demands on greenhouse nurseries for the production of chemical-free planting material that allows for the quick establishment of beneficial predators and microbial antagonists. Biopesticides that are compatible with the use of natural enemies, such as mineral oils, insecticides soaps and entomopathogenic fungi and nematodes, may be applied to reduce pest numbers prior to planting (Buitenhuis et al. 2016). Some plants propagated by bulbs, corms, and rhizomes may respond well to hot water treatment. However, close attention to temperature and timing is essential to guarantee eradication of the pathogen and/or insect pest without damage to the plant (Magie 1971). This is also true for Controlled Atmosphere Temperature Treatment (CATT), i.e. the exposure of plant material to a combination of relatively high temperature, high CO_2 and low O_2 levels. With respect to its application on propagation material, research has thus far yielded positive results for the eradication of tarsonemid mites and root knot nematodes on strawberry runners (van Kruistum et al. 2014). However, sterility of the planting material is not the sole criterion for a good start of the cropping cycle. Transfer of natural enemies from the propagation site to the cultivation site increases the resilience of the system and should allow for the presence of some (non-quarantine) pest individuals that can be controlled relatively easily. In our opinion, the common viewpoint that planting material should never contain any arthropods therefore needs revision.

10.4.4 Removal of Non-crop Plants and Crop Residues

Obviously, the removal of weeds, crop residues and algae that serve as reservoirs for pests and pathogens should be carried out as a first line of defense (e.g. Northfield et al. 2008). However, situations exist where maintaining certain plants in and around the greenhouse could provide a benefit by supporting beneficial predators. In some Mediterranean regions, an important part of pest control is carried out by naturally-occurring predators. In these cases, the growth and conservation of plants that can harbour natural enemies in and around the greenhouse is an important component of a conservation biocontrol (CBC) strategy. Perdikis et al. (2011) reviewed the existing literature concerning the identification and implementation of non-crop host plants of predatory Heteroptera (including *Macrolophus* and *Dicyphus* species) in CBC strategies. They indicated that more research is needed to (a) correctly identify the predator species on each candidate non-crop plant species, (b) evaluate the predator dispersal ability that determines the appropriate spatial distribution of non-crop habitats, and (c) optimize CBC practices to guarantee timely crop colonization. Moreover, pruning of plants that contain pests can also remove developing natural enemies. When the parasitoid *Encarsia formosa* is introduced in tomato, and black parasitised whitefly nymphs can be detected on the older leaves, it is advised to keep pruned leaves on the floor for at least 2 weeks to allow for the emergence of new parasitoids. However, this practice may lead to build-up of pathogens that profusely sporulate on decaying plant residues such as *Botrytis cinerea*. Certain non-crop plants, also referred to as 'banker-plants' can aid in the establishment of natural enemies in the crop by providing alternative food and/or shelter (Frank 2010; Huang et al. 2011).

10.5 Exclusion of Insect Pests During the Cropping Cycle

Insect screens are the most commonly used means to exclude insect pests from the greenhouse during the cropping cycle. Multiple studies have shown that insect screens help to reduce pest levels and the incidence of vector-transmitted plant viruses (Berlinger et al. 1991; Bethke and Paine 1991; Bell and Baker 2000; Berlinger et al. 2002). The effectivity of insect screens with different mesh sizes and geometrical characteristics against pests of different sizes has been studied in the presence and absence of an airflow (Bethke and Paine 1991; Bell and Baker 2000). However, the smaller the mesh size, the larger the negative interference of the insect screen with the greenhouse microclimate due to the lowered ventilation capacity (Teitel 2007). Miguel and coauthors have developed an algorithm to calculate the change in air velocity when the air passes through porous screens of different mesh sizes (Miguel et al. 1997; Miguel 1998). Moreover, Bell and Baker (2001), as well as Lopez et al. (2016) have compared different types of insect screens for the reduction in air velocity for air velocities resembling those in commercial greenhouses. A combination of insect screens with positive-pressure force ventilation could improve the prevention of leafminer invasions and slightly improve the prevention of whitefly invasions, but was not at all effective against thrips invasions (Sugiyama et al. 2014). Preventing thrips invasions, and to a lesser extent whitefly and aphid invasions, by fixed use of insect screens does not seem feasible without a strong negative impact on the microclimate. One way to optimize ventilation of protected crops while minimizing invasion by whiteflies and thrips is by covering ventilation openings only when and where the risk of pests' entry is eminent. Information from studies that monitored when and where pests enter greenhouses and growing tunnels can serve to design vents and develop ventilation schemes that will also lower the risk of pest invasion. For example, Ben-Yakir et al. (2008) found that in Israel during most of the year about 85% of the thrips were caught in the morning and 10% at dusk, and flight time was correlated with periods of low wind speed. During the peak of sweet potato whitefly populations in autumn, 97% of the whiteflies entered the greenhouse between 7.00 and 13.00 h. Moreover, both whiteflies and thrips flew upwind, with the leeward side of the greenhouse suffering from greater risk of pest invasion. The use of trap plants around the greenhouse may provide an additional aid in assessing risk for pest invasion, and their use inside the greenhouse can reduce pest settling on the crop (Buitenhuis and Shipp 2006; Buitenhuis et al. 2007; Cook et al. 2007; Moreau and Isman 2011, 2012). Recently, the use of long-lasting insecticide nets (LLINs), which have insecticides incorporated within their fibers, is being explored for preventing pest immigration in protected crops (Dader et al. 2015a; Kuhar et al. 2017). By combining physical attenuation of pests with chemical control, mesh size of the screens can be increased, allowing for more adequate ventilation. However, a major drawback is the loss of pesticide efficacy by exposure to the sun. A completely alternative way to reduce the immigration of pests, including thrips, whiteflies, aphids and leafminers into greenhouses, and their dispersal within greenhouses, is to implement UV-absorbing cladding materials, that has been shown to greatly reduce the invasion of several species of pest insects, including aphids, whiteflies, thrips and leafminers (Antignus et al. 1996, 1998, 2001; Antignus 2000; Costa et al. 2002; Chyzik et al. 2003; Raviv and Antignus 2004; Legarrea et al. 2010; Legarrea et al. 2012). It has to be noted, however, that the implementation of the above-mentioned measures for reducing the immigration of pest-insects into the greenhouse, also creates as barrier for the entrance of naturally-occurring biological control agents, thus rendering conservation biocontrol more difficult.

10.6 Direct and Indirect Influences of the Greenhouse (Micro)climate on Pests and Diseases

10.6.1 Introduction

Traditionally, greenhouse climate has been generally managed with the sole objective of optimizing crop productivity. However, with decreasing options for chemical pest and disease control, the value of integrating knowledge on the interaction between greenhouse climate and pest and disease incidence for the optimization of greenhouse climate management is increasingly acknowledged. Here we will discuss the different ways in which greenhouse climate can directly and indirectly affect pests and diseases.

10.6.2 Crop Microclimate Versus Greenhouse Macroclimate

The quantity and quality of the light, temperature and humidity conditions that is experienced by a pathogen, pest or beneficial organism is not solely determined by the greenhouse macroclimate, but also by the microhabitat in which these organisms reside. Depending on the species or developmental stage, the organism can reside inside or outside of the plant tissue, on the abaxial, or adaxial leaf surface, higher or lower in the crop canopy, hidden away inside flowers, bulbs, leaf axils, in the root zone or elsewhere in the greenhouse. As described in Berlinger et al. (1999), at night the temperature within the boundary layer of the leaf can become 1–3 °C lower than ambient temperature due to energy lost by radiation, thus frequently reaching the dew point. In crops that transpire well, the evaporative cooling can also reduce temperature in the leaf boundary layer, whereas insolated leaves that do not transpire well can become considerably warmer, by as much as 2–8 °C, than ambient temperature (Curtis 1936; Shull 1936). Moreover, the temperature on the surface boundary of fruits will depend to a large part on its colour. Schroeder (1965) has found that green tomato fruits remained 4–8 °C cooler under the same conditions than red tomato fruits. Hence, greenhouse climate may not only influence the overall occurrence of pathogenic or beneficial organisms, but also the plant structures where disease symptoms will appear first, as well as the microhabitat where pests and natural enemies preferentially reside.

10.6.3 Temperature

Temperature is a key factor driving the population dynamics of poikilothermic organisms, including bacteria, fungi and arthropods. With respect to pest management, temperature-driven models are an essential tool in helping to predict population dynamics of pests and their biological control agents, and can assist in the selection of biological control agents that are most suitable for the thermal conditions in the greenhouse. Each arthropod species has its own 'thermal window', i.e. the temperature range under which it can grow and reproduce (Dixon et al. 2009). Near the upper and lower limits of this thermal window, oxygen supply and anaerobic metabolism restrict its performance. Numerous studies have focused on the relationship between temperature and arthropod developmental rates, and both linear and non-linear models have been developed to describe these relationships (Campbell et al. 1974; Kontodimas et al. 2004). Linear models provide a thermal constant for development (expressed in degree-days), and allow for the estimation of the lower developmental threshold. However, they are not valid near the upper and lower limits of the thermal window (Campbell et al. 1974; Davis et al. 2006). Nonlinear models more accurately describe the change in developmental rate over the whole range of temperatures of the thermal window (Stinner et al. 1974; Sharpe and Demichele 1977; Briere et al. 1999).

As temperature does not only affect arthropod developmental rate, but also affects all other arthropod life history traits, an often used measure to characterize the impact of temperature on arthropod performance is the intrinsic rate of increase (r_m). The r_m is defined by Birch (1948) as 'the rate of increase per head under specified physical conditions, in an unlimited environment where the effects of increasing density do not need to be considered'. This measure integrates all the different life history parameters including developmental rate, immature survival, adult fecundity, longevity and sex ratio. Using the r_m to estimate the effect of temperature on arthropod performance is more reliable than any single life history parameter, as different life history parameters are often differentially affected by the microclimate. For example, in insects, temperature usually has an opposite effect on developmental rate and adult size. While low temperature results in a slower growth rate and longer developmental time, it usually results in a larger adult size in insects (Butlin and Day 1985; Colinet et al. 2007). This can have important fitness consequences, as larger females often live longer and attain higher fecundity, and larger males often have enhanced mating success (Butlin and Day 1985; Bonato et al. 2007; Colinet et al. 2007). This was, among others, shown by Bonato et al. (2007) for *Bemisia tabaci* Q-biotype, whose immature development rate became higher with increasing temperature up to an optimum of 32.5 °C, but whose total fecundity was optimal at 21 °C. This resulted in a more modest impact of temperature on the r_m than predicted from immature developmental rate alone.

For plant pathogens, temperature also has differential effects on different life history parameters. Jarvis (1992) has described the effect of temperature and humidity on the epidemics of grey mould (*B. cinerea*), with conidia formation being triggered at a temperature (15 °C) that is lower than the temperatures that are optimal for infection (15–20 °C) and colonization of the host (25–30 °C). The same effect can be observed with microbial biocontrol agents. Some important parameters to be considered with microbial biocontrol agents are how environmental parameters affect cell growth versus parasitism and/or production of antibiotics. Since most *Trichoderma* spp. are mesophilic and do not tolerate dry soils, their efficacy can be compromised when the soil microclimate changes, even though their densities in the soil can remain high (Kredics et al. 2003). The estimation of an antagonists' potential to suppress disease by enumerating their total densities can drastically over- or under-estimate their efficacy. For example, the bacterial antagonist *Pseudomonas fluorescens* suppresses disease through production of the antibiotic phenazine 1-carboxylic acid. Although the bacteria proliferate over a wide range of temperatures up to 34 °C, the antibiotic is produced optimally at 25–27 °C (Slininger and Sheawilbur 1995).

With respect to biological pest control, the r_m does not capture the effect of the temperature on the predator's attack rate. Only for a few natural enemy – prey interactions, the effect of temperature on the natural enemies' functional response (i.e. the relationship between the number of prey available and the number of prey killed) has been assessed using the functional response model of Holling (1959) (e.g. Messenger 1968; Thompson 1978; Gresens et al. 1982; Cave and Gaylor 1989; Flinn 1991; Skirvin and Fenlon 2003; Jalali et al. 2010; Englund et al. 2011; Sentis et al. 2012). It is predicted that, within a certain temperature range, search rate increases and handling time decreases exponentially with increasing temperature. However, while this has been well established for prey handling time, the relationship between temperature and search rate is less secure and has been described as linear, quadratic or hump-shaped (Sentis et al. 2012, and references therein). Moreover, it is important to note that studies on the functional response of predators to prey availability have only focused on the short-range search rate, as these studies are usually performed in small arenas where the ability to disperse and locate new prey patches is not taken into account. Only few studies have assessed the flight capability of parasitoids or predators of greenhouse pests over a range of temperatures (e.g. Zhang and Shipp 1998; Jerbi-Elayed et al. 2015). Especially for specialist natural enemies operating at low pest densities, long-range search rate will have a large influence on the efficacy of biocontrol. As temperatures near the borders of the thermal window usually constrain activity more than growth and development, leaving searching rate and prey handling time out of the equation may overestimate the efficacy of natural enemies when greenhouse temperatures approach these values. This is especially important in greenhouses in warmer regions, where temperatures often exceed the upper temperature limits, and in greenhouses of the Northern regions where energy saving practices result in the reduction of temperatures during winter time. Lowering the temperature set-points in the greenhouse may have adverse effects on pest control, as the activity of natural enemies may be restrained before the development of the pest species comes to a halt. The identification of natural enemies that perform well under cool climatic conditions will become important for improving the sustainability of greenhouse grown crops through the reduction of both energy expenditure and pesticide use.

It is important to note that in the context of energy savings, often not just the greenhouse temperature set-points are lowered, but temperatures are also allowed to fluctuate more with ambient temperatures, resulting in a larger difference in day- and night temperatures (DIF) and/or differences in mean temperatures over the days (temperature integration). The impact of fluctuating temperatures on greenhouse pests and their natural enemies has thus far not received much attention (but see Vangansbeke et al. 2013, 2015a, b; Ullah and Lim 2015; Bayu et al. 2017). In theory, the arthropod developmental rate at alternating temperature as compared to constant temperature should be higher at low mean temperature and lower at high mean temperature (Ratte 1985; Worner 1992), whereas it should be unchanged at intermediate temperature (Tanigoshi et al. 1976; Ratte 1985; Bryant et al. 1999). This is referred to as the 'rate of summation effect' or 'Kaufmann effect', and is due to the typically nonlinear relationship between arthropod developmental rate and temperature (Worner 1992). Although models do not account for the influence of temperature fluctuations on relative humidity values, that in turn can affect the performance of some phytoseiid predators and tetranynchid prey (El-Laithy 1992; Weintraub et al. 2006, in Palevsky et al. 2008), and could also not fully explain the impact of temperature alternations at 4 amplitudes on *P. persimilis* and *N. californicus* found in the study of Vangansbeke et al. (2015a), aberrations from the predictions of these models are expected to be small. A much larger effect of temperature fluctuations can be expected on the search rate and prey handling time of predators and parasitoids, as the impact of fluctuations in night- and daytime temperatures on overall predator and parasitoid efficacy may strongly depend on their diurnal activity pattern.

Also for disease management, it might be profitable to gain a better understanding of the impact of cooler mean temperatures and/or fluctuating temperatures on the development of disease symptoms. The optimal temperature for most pathogens to infect and incite disease is close to the optimal temperature for plant production. Many times, reducing the temperature can delay the onset of symptoms. For example, soil temperatures less than 22 °C can prevent symptoms of Fusarium wilt on chrysanthemum and carnation (Gardiner et al. 1987; Benyephet and Shtienberg 1994). However, symptoms usually come back when plants are returned to warmer temperatures. Moreover, cooler temperature can shift the pathogen species complex to those that favor cool temperature. For example, *Pythium aphanidermatum* can be devastating in warm soil, but is relatively less virulent in cool soil. *Pythium ultimum* and related species, on the other hand, are more damaging at lower temperatures. Becktell and Daughtrey (2005) observed temperatures ranging from 13 to 23 °C were generally conducive to the establishment of Phytophthora on tomatoes and petunia, whereas this pathogen failed to establish above 28 °C. The choice of *Trichoderma* species and strain could also be better tailored to cooler greenhouse temperature. A few strains of *T. aureoviride*, *T. harzianum* and *T. viride* grow well at 5 °C (Kredics et al. 2003). Furthermore, the absence of mycelial growth does not imply that enzymatic activity has been reduced (Kredics et al. 2003).

On the other hand, heat extremes can also promote pathogen damage through favoring the reproductive life cycle of the pathogen and by increasing plant stress. Most foliar pathogens infect their host at temperatures that are optimal to the host plant. Likewise, many biocontrol agents against powdery mildew, such as *Tilletiopsis* spp., will proliferate at the same temperatures as the pathogen, which prevents growers from manipulating biological control with temperature (Urquhart et al. 1994). Moreover, raising greenhouse temperatures can promote some pathogens to sporulate more profusely, thus increasing the inoculum.

Furthermore, temperature can have an indirect effect on diseases or determine which plant parts are affected by disease. For example, providing bottom heat can promote rapid rooting, which in turn helps to dry soils out fast and lessen root rots (Jarvis 1992), and higher temperatures can result in an increased number of infected tomato flowers by *B. cinerea*, but can reduce fungus growth proximally to the main stem where the damage would be far more severe (Eden et al. 1996).

10.6.4 Humidity

Free moisture and relative humidity (RH) play key roles in the incidence of plant diseases, as they affect the infection and sporulation processes, and in some cases also colonization of fungi, oomycetes and bacteria (see e.g. Huber and Gillespie 1992, and references therein). Especially the point when water condenses to form a film of water over the leaf, flower or fruit surface is a crucial factor determining infection rates by many important plant pathogens (see e.g. Huber and Gillespie 1992; Jewett and Jarvis 2001, and references therein). Pathogens differ in the duration of surface wetness they require for completing the infection process. Information on the pathogen-specific surface wetness periods required to complete infection has been summarized in Huber and Gillespie (1992) and Magarey et al. (2005). In this last study, a generic model was developed to estimate infection from an organism's cardinal temperatures and surface wetness duration requirement. The key parameter in this model was the ‘minimum wetness duration requirement’ (*W*min), defined as the minimum value of wetness duration required to exceed the critical disease threshold at any temperature. Approximately 90% of the pathogens had a value of *W*min <20 h, and the average value of *W*min was 9 h. It is important to bear in mind that apart from the pathogen and surface wetness duration, infection also depends on several other factors, such as temperature, the presence of exosmosed nutrients on the cuticle, inoculum age and concentration, age of the underlying host tissue and the commensal micro-organisms (Jewett and Jarvis 2001). Indeed, Magarey et al. (2005) pointed out that some of the differences they found in *W*min between related pathogens may have been due to the difference between infection requirements for fruit and leaf tissue. Moreover, their estimates of W_{min} for *B. cinerea* were also different depending on the host species and type of tissue, and varied from 1 to 8 h. Besides pathogen-specific differences in *W*min, Magarey et al. (2005) also showed pathogen-specific differences in the ability to tolerate interruptions of surface wetness. Most plant pathogens were sensitive to surface wetness interruptions between 4 and 20 h. However, some pathogens (such as *Puccinia* spp.) were more sensitive, with 1–2 h interruptions already causing a dramatic reduction in infection levels. Moreover, the timing of the interruption was critical, with interruptions during the initial period of leaf wetness causing the largest suppression of infection levels. In contrast to most important pathogens, spore germination of many powdery mildew species can be inhibited by surface wetness (Yarwood 1939), although it has since been shown that several powdery mildew species need a minimum wet period for infection (Quinn and Powell 1982; Jarvis 1994; Celio and Hausbeck 1998; Jewett and Jarvis 2001).

Preventing wetness of leaf, flower and fruit surfaces, or at least limiting the duration of the surface wetness period or interrupting it, can thus provide a powerful tool for disease management of many important pathogens. Crop surface wetness results primarily from water that has been intercepted by the canopy during overhead irrigation or fogging, dew that forms on the leaf, flower or fruit surfaces as a result of water vapor condensation, or, in some cases, as a result of guttation (Rowlandson et al. 2015). Condensation of water vapor onto the crop surface is triggered when the temperature of the crop surface drops below the dew point temperature of the surrounding air. This happens primarily during clear-sky nights, when long-wave radiation is lost from the canopy to the atmosphere, resulting in cooling of the canopy (Berlinger et al. 1999). The dew point of the surrounding air is reached when the vapour pressure deficit (VPD) (i.e. the difference between the amount of moisture in the air and the amount of moisture the air can hold when it is saturated) is zero. The onset of dangerous conditions for dew deposition can be prevented by increasing the VPD in the canopy boundary layer. This can be done by either increasing the temperature, lowering the RH of the ambient greenhouse air, increasing the mixing of the ambient air with that of the canopy boundary layers, or a combination thereof. Moreover, at very low VPD, transpiration is greatly reduced or stopped, but root pressure can continue to pump water up the shoot, resulting in guttation and waterlogging of leaf tissues. Waterlogged tissues can invite bacteria to invade plant tissues when transpiration resumes and exuded water is sucked back into the plant (Jewett and Jarvis 2001, and references therein).

Growers have many possibilities to directly or indirectly influence VPD and RH. They have the possibility to limit RH by the choice of irrigation system (drip irrigation leads to less air humidity than overhead irrigation) and to decrease RH by dehumidification measures such as heating and ventilating at the same time or using a dehumidification device. The cheapest way is blowing in outside dry air through ducts under the crop gutter (possible in areas with relatively low outside humidity levels). A more water-saving and also energy-saving way is the combination with heat exchangers (most popular are cold surfaces) in order to regain humidity from the greenhouse (De Zwart 2014). In humid areas, a simple way to create a more uniform RH level inside the greenhouse is to install circulation fans to increase the air speed inside the greenhouse. This will also result in a better mixing of the air of the boundary layers of the plant with the ambient air, thus reducing the difference between the VPD of the macroclimate and the microclimate of the leaf surface boundary. Apart from the use of circulation fans, local air velocities and thus the VPD of the crop microclimate will also be highly influenced by crop density and crop architecture, which in turn depends on use of high-wire versus umbrella systems, the implementation of pruning and the use of growth regulators.

Jewett and Jarvis (2001) have listed several studies that addressed the epidemics of plant pathogens in relation to surface wetness duration and ambient air temperature, including the epidemiology of *B. cinerea* in cucumber (Yunis et al. 1994; Shtienberg and Elad 1997), tomato (Eden et al. 1996; Shtienberg and Elad 1997), roses (Marois et al. 1988; Kerssies 1992), and gerbera (Kerssies 1993), as well as the epidemiology of *Didymella bryoniae* in cucumber (Vansteekelenburg 1985). Körner and Holst (2005) developed and tested a mathematical model for *B. cinerea* that avoided disease by keeping the relative humidity set points low with heating and ventilation. They calculated the energy costs of this practice and calculated the time for leaf surfaces to dry based on the energy balance of latent heat on the leaf surface. Climate control was then optimised for maximum energy saving that provides grey mould prevention. As more research on pest damage/risk analysis advances, algorithms in these models can be refined to provide growers with more informed decision making tools. When keeping VPD levels high is not feasible because of technical constraints, or not desirable because of energy costs (e.g. De Zwart 2014), the use beneficial microbes as antagonists against foliar pathogens (Elad et al. 1996; Jewett and Jarvis 2001) or entomopathogenic fungi against insect pests (Shipp et al. 2003; Wraight et al. 2016) may be a relative successful strategy to implement. In general, the factors promoting biological control by bacteria and fungi, namely low VPD, free water on leaf and fruit surfaces and moderate temperatures, are very similar to those promoting infection by pathogens (Jewett and Jarvis 2001). Wraight et al. (2016) found that frequent applications of three species of entomopathogenic fungi were able to cause 70% control of *F. occidentalis* in *Impatiens walleriana* when an RH of 80% was maintained for a one-day post-spray period. Shipp et al. (2003), who investigated the influence of humidity level on the percentage infection by *Beauveria bassiana* on different greenhouse pests and their commercially available arthropod natural enemies, showed a marked increase in the % *B. bassiana* infection when humidity level was increased from 75–80% to 97.5% in Petri dish trials, while similar increases in RH in a cucumber canopy in the greenhouse caused only a moderate infection increase. The movement, survival and pathogenicity of entomopathogenic nematodes is also strongly correlated to humidity. They need a film of free water for movement, and at low soil moistures they may become dormant. Kung et al. (1991) found the survival and pathogenicity of *Steinernema carpocapsae* and *S. glaseri* to quickly decrease when RH dropped below 100%. Whereas both species survived for 32 days at 100% RH, survival of *S. carpocapsae* had dropped to 2 days, and survival of *S. glaseri* to 4 h at 25% RH. Grant and Villani (2003) examined the effect of soil moisture ranging from below the permanent wilting point of plants to near saturation in a sandy loam soil on the virulence of several species of entomopathogenic nematodes. They found nematode virulence to increase with soil moisture content of all species and isolates tested, but also found that low virulence in low moisture conditions could be restored by rehydrating the soil.

The humidity window within which arthropods pests and their arthropod natural enemies can operate is much wider than that of microbial pathogens and their antagonists. Humidity therefore has a much lower impact on pest control compared to disease control. There are, however, some cases in which pest control is affected by relative humidity. A well-known example is the biological control of the two-spotted spider mite *Tetranynchus urticae*. Whereas *T. urticae* thrives under hot and dry conditions, these conditions can severely hamper the efficacy of its main predator *Phytoseiulus persimilis* (El-Laithy 1992; Weintraub et al. 2006, in Palevsky et al. 2008). Several attempts have been made to select for drought-adapted species and strains of predatory mites (Vandinh et al. 1988; Bakker et al. 1993; Monetti and Croft 1997; Palevsky et al. 2008; Ferrero et al. 2010; Doker et al. 2016). Ferrero et al. (2010), who tested the egg hatching response to a range of air humidities of six species of predatory mites, found VPD and RH values at which 50% of the eggs hatched to vary from 18 kPa and 43% for the most drought-tolerant species to 9 kPa and 70% for the least drought-tolerant species. Shipp and coauthors have used VPD as an explanatory factor for the survival of western flower thrips (*F. occidentalis*) and the survival and predation rate of one of its natural enemies, the predatory mite *Amblyseius cucumeris* (Shipp and Gillespie 1993; Shipp et al. 1996; Shipp and VanHouten 1997). The larval stages of both *F. occidentalis* and *A. cucumeris* were more susceptible to suboptimal VPD values compared to the adult stages, whose survival was only compromised at high temperature and high VPD (Shipp and Gillespie 1993; Shipp and VanHouten 1997). Shipp et al. (1996) found predation rates of the predatory mite *Amblyseius cucumeris* for the western flower thrips (*F. occidentalis*) to decrease with increasing VPD at constant temperature for VPDs <1.24–1.44 kPa. Above these VPDs, the predation rate started to increase again. Sanitation trials demonstrated that a 40 °C temperature and VPD above 4.76 kPa will control *F. occidentalis* at the end of the crop season when the greenhouse is being prepared for the next crop (Shipp and Gillespie 1993). Relative humidity (RH) is also able to influence the pupation site of *F. occidentalis*. When RH of the plant surface exceeded 81%, late-instar larvae would remain on the plant surface rather than drop to the ground (Steiner et al. 2011). This dropping behaviour was also influenced by the developmental stage of the plant, with >90% of thrips pupating in the soil of non-flowering potted chrysanthemums and mini-roses grown at RH 55 ± 10% and 25 °C, whereas only 60% of thrips pupated in the soil when plants contained flowers (Buitenhuis and Shipp 2008). A study of Holmes and Kirk (2007) showed that this dropping behaviour occurs predominantly in the evening hours, and that the time of the peak drop is likely influenced by an environmental cue.

10.6.5 Light

For plants light is a primary resource that is essential for its growth and development. Plants also use light for the interpretation of the environment. Every aspect of light, i.e. its intensity, wavelength distribution, direction and photoperiod, can give a plant specific information about its surroundings. A low red (R) to far red (FR) ratio, for example, is a signal that there is competition for light. This will induce a shade-avoidance response that manifests itself by a strong investment in aboveground growth and (rapid) shoot elongation. This usually goes at the expense of the formation of plant defensive metabolites and structures, thus rendering the plant more susceptible to both pests and diseases (Ballare 1999; McGuire and Agrawal 2005; Izaguirre et al. 2006; Ballare 2009, 2014). Moreover, plants protect themselves from harmful wavelengths and peak intensities by means of secondary metabolites, such as phenols and flavonoids as well as thickened leaves, and/or an increased density of leaf trichomes (Jenkins 2009; Ballare 2014; Le Gall et al. 2015; Robson et al. 2015; Escobar-Bravo et al. 2018). Low to moderate UV-B doses elicit a response from the UV-B photoreceptor UV RESISTANCE LOCUS 8 (UVR8), which regulates the production of these protective compounds (Hectors et al. 2007; Brown and Jenkins 2008; Rizzini et al. 2011). Many field studies have shown that losses to insect pests increase when UV-B is attenuated (Caldwell et al. 2003; Ballare et al. 2011; Kuhlmann and Muller 2011). Moreover, Demkura and Ballare (2012) showed that small, ecologically meaningful doses of UV-B radiation could increase the resistance of Arabidopsis to *B. cinerea*. Most protected crops are not subject to UV-B radiation, as UV-B is filtered out by most greenhouse cover materials. However, certain types of greenhouse cover materials, such as low-iron glass, do permit transmission of part of the UV-B radiation. Moreover, UV-B inside greenhouses can be enhanced by means of LED modules. Escobar-Bravo et al. (2019) showed that 30-min daily exposure of tomato plants cv. 'Moneymaker' to UV-B light from LED modules could increase resistance to thrips. Moreover, both and Escobar-Bravo et al. (2018) found the morphology of tomato glandular trichomes to be altered by increased light intensity. This did not only negatively affect spider mites and thrips, but also caused a more frequent entrapment of the spider mite predator *P. persimilis*.

Apart from plants, other organisms – including pests, pathogens and their natural enemies – also use light to steer important developmental and behavioural processes. They all possess photoreceptors that capture specific parts of the light spectrum. Moreover, adult insects as well as the immature stages of hemimetabolous insects possess compound eyes that apart from allowing them to perceive light colour and intensity also have high spatial resolution. Light perception in arthropods, fungi and have been reviewed respectively by Johansen et al. (2011), Schumacher (2017) and Kraiselburd et al. (2017). Manipulation of the light environment in the greenhouse may help to strengthen the biological control of pests and diseases. Several tactics in the greenhouse can be used to manipulate pests and diseases by changing light conditions. One of these tactics is to create a UV-A deficient greenhouse environment. While most traditional greenhouse cover materials poorly transmit UV-B (280–315 nm), they transmit a large part of UV-A (315–400 nm). However, several poly-ethylene materials are nowadays on the market that block the whole UV spectrum below 360–400 nm. Using these type of UV-absorbing materials to cover (semi-open) tunnel greenhouses caused strong reductions in the immigration of pest insects (including thrips, whiteflies, aphids and leafminers) into the greenhouse, as well as their dispersal within the greenhouse (Antignus et al. 1996, 1998, 2001; Antignus 2000; Costa et al. 2002; Chyzik et al. 2003; Raviv and Antignus 2004; Legarrea et al. 2010, 2012). Moreover, the reduction of whiteflies in tomato and the reduction of aphids in cucumber, through the use of UV-absorbing greenhouse cover materials, also led to a strong decrease in the occurrence of the TYLCV virus and the ZYMV virus, respectively (Antignus et al. 2001). Whether blocking UV-light from the more closed glasshouses in the Northern regions can also result in reduced pest densities and virus infections remains to be investigated. Most studies show that UV-absorbing cladding material has little to no effect on the foraging efficacy of most parasitoid species, including *Encarsia formosa* (Doukas and Payne 2007), *Aphidius ervi* (Legarrea et al. 2014), *Aphidius colemani* (Chiel et al. 2006; Dader et al. 2015b) and *Diglyphus isaea* (Chiel et al. 2006). However, the efficacy of *Eretmocerus mundus* for finding whitefly-infested plants was reduced in a UV-deficient environment (Chiel et al. 2006), and flight initiation of *A. ervi* was stronger under monochromatic UV-light (361 nm) than under different spectra of monochromatic visible light (Cochard et al. 2017). Not much research has been conducted to evaluate the effect of UV-absorbing cladding material on the behaviour predatory arthropods. Legarrea et al. (2012) found the predatory bug *Orius laevigatus* to be less mobile at lower UV-intensity, whereas Dader et al. (2015b) did not find an effect of UV-absorbing cladding material on the flight initiation and –distance of the hoverfly *Sphaerophoria rueppellii*. UV-absorbing cladding material can also help to suppress certain plant-pathogenic diseases, as UV-A light has been found to stimulate the sporulation of several plant-pathogenic fungi. These include *Alternaria solani* (Fourtouni et al. 1998), *B. cinerea* (Honda et al. 1977; Reuveni and Raviv 1992; Nicot et al. 1996), *Stemphylium botryosum* (Sasaki et al. 1985), as well as a series of other *Alternaria* species and *B. cinerea* (Sasaki et al. 1985). Whereas UV-absorbing cladding material can help suppress these diseases, it may also help *Trichoderma harzianum* to establish on above-ground plant parts, as this beneficial fungus was found to be susceptible to UV-A radiation (Paul et al. 2005). Reuveni and Raviv (1992) and Sasaki et al. (1985) found blue light and UV-A light to have contrasting effects, with UV-A being able to at least partly cancel out the suppressive effect of blue light. Blue light alone had a clear inhibitory effect on the sporulation of downy mildew (*Pseudoperonospora cubensis*) on cucumber (Reuveni and Raviv 1997). However, it had a stimulatory effect on the sporulation of powdery mildew (*Podosphaera pannosa*) on rose, when compared to white light (Suthaparan et al. 2010b). All in all, UV-absorbing cladding material can have strong benefits for the control of both pests and diseases, and seems to suppress pests and diseases more than their natural enemies. However, care needs to be taken when pollinators are used, as a UV-deficient environment can have negative effects on pollinators (Dyer and Chittka 2004; Blacquiere et al. 2006). Both Johansen et al. (2011) and Diaz and Fereres (2007) have summarized the effect of specific properties of greenhouse cladding materials on several species of pests insects.

The effect of UV-B (280–315 nm) on the behaviour of pests has been less researched, but Mazza et al. (2002) have shown that *Caliothrips phaseoli* avoids an environment with UV-B light, and at the same time is attracted to UV-A light, which coincides with the results of the UV-absorbing cladding materials. This seems logical, as UV-B can directly harm insect- and mite pests (Onzo et al. 2010; Tanaka et al. 2016; Johansen et al. 2017). Some researchers have already experimented with the application of UV-B treatments to crop plants for the direct control of spider mites. Because pests can actively reduce exposure to UV-B radiation by looking for shelter at the underside of the canopy, Japanese researchers have combined the use of UV-B emitting diodes with UV-reflective flash-spun nonwoven fabric sheets (Sakai and Osakabe 2010; Tanaka et al. 2016). This allowed for a good control of the spider mites in strawberry (Tanaka et al. 2016). Norwegian researchers have also found clear effects of short (3-min) applications of 1.6 W/m^2 application of UV-B light during the night on spider mites (Johansen et al. 2017). Whereas the effect of these UV-B applications on adult spider mite females was negligible, more than 99% of the immature spider mites and 100% of the spider mite eggs were killed. Moreover, several studies have found that UV-reflective plastic sheets can delay the colonization of cucurbit crops by tobacco whiteflies (Summers and Stapleton 2002; Summers et al. 2004), as well as crop damage by plant viruses transmitted by aphids (Stapleton and Summers 2002; Summers et al. 2004). Kring (1972) describes that alate aphids that are ready for landing on the crop, are repelled and/or disoriented by UV-reflective sheets, whereas their flight activity is stimulated in the presence of UV-light. However, the possible detrimental effects of UV-B light on natural enemies has thus far not been thoroughly studied. Reitz et al. (2003) found less *Orius insidiosus* predatory bugs in sweet pepper plots with UV-reflective sheets than in adjacent plots without UV-reflective sheets. Conversely, *Trichogramma* parasitoids were shown to be attracted to an environment with higher UV-B radiation in spite of the lower offspring survival in this environment (Van Atta et al. 2015). Researchers have also experimented with the application of UV-B for the direct suppression of plant pathogens. Several authors found the effect of UV-B on plant pathogens to be dependent on the spectrum of the background light (Fourtouni et al. 1998; Suthaparan et al. 2012). Suthaparan et al. (2012) found that 5–10 min applications of 1 Wm^{-2} UV-B during the night could suppress powdery mildew (*Podosphaera xanthii*) in cucumber plants. Moreover, low dosages of UV-C can also help suppressing certain plant diseases (e.g. Urban et al. 2016). Before strategies that enhance low-wavelength UV-radiation in the crop are applied, the effects on both natural enemies and on crop growth will need thorough evaluation.

Application of light in the visible spectrum can also be an important tool for suppressing plant diseases, and especially the timing of the application can be crucial for its effect. Suthaparan et al. (2012) showed that exposure of *P. xanthii* on cucumber plants to additional red light without UV-B at the beginning and the end of the day suppressed disease intensity, and that a short exposure of powdery mildew *Podosphaera pannosa* on rose plants to red light during the dark period suppressed sporulation. Far-red light, on the other hand, had a stimulating effect on the sporulation of this pathogen.

Not only light spectrum, but also light intensity and daylength can affect pests, pathogens and natural enemies. Apart from other factors, such as a change in light spectrum, temperature and humidity levels, this can help explaining differences in IPM success between the different seasons, and give hints on how to improve this. Zilahi-Balogh et al. (2006) showed that both *E. formosa* and *E. eremicus* parasitized twice as many whiteflies at high light intensity (112–114 W m^{-2}) and long daylength (L:D = 16:8 h) than at low light intensity (12–14 W m^{-2}) and short daylength (L:D = 8:16 h). In another study, Zilahl-Balogh et al. (2007) showed that low light intensity also had a suppressive effect on egg laying of the predatory mite *Neoseiulus cucumeris*. Moreover, Wang et al. (2013) showed that the fertility of *Orius sauteri* decreased, and the nymphal developmental time increased with lower light intensity, whereas egg survival improved. Daylength can also affect the production and germination of spores of *P. pannosa* in rose, with a stronger inhibition with increasing daylength (Suthaparan et al. 2010a). Moreover, the use of colour and/or light traps for monitoring pest populations has a long history. Yet, a completely different way to manipulate the behaviour of pest insects with light has been described by Shimoda and Honda (2013). In their review on insect reactions to light and its application to pest management, they give examples of noctural pest species, such as *Helicoverpa armigera, Spodoptera litura* and *Hellula undalis*, whose activity has been shown to be suppressed when exposed to fluorescent lights during nighttime (Yase et al. 1997; Yabu 1999; Yamada et al. 2006; Hirama et al. 2007; Yoon et al. 2012). This strategy, first developed by Nomura et al. (1965), makes use of the fact that when moths encounter light above a certain brightness at night, their compound eyes become light-adapted as if it were daytime (Walcott 1969; Meyer-Rochow et al. 2002).

10.6.6 Other Climatic Factors

Wind speed created by cooling fans may be another climatic factor to be considered with respect to the control of greenhouse pests and diseases. Cooling fans in a well-designed greenhouse produce wind speeds in the range of 0.9–1.3 ms^{-1}, but in many greenhouse operations this may be higher in practice (Prado et al. 2015). Wind speed and turbulence can affect the liberation and dispersal of plant pathogen inoculum (Aylor 1990). Little research has been conducted to assess the effect of wind speed on the behaviour and performance of pests and natural enemies. However, wind speeds of 2 ms^{-1} have been shown to affect the oviposition and resting behaviour of the parasitoid *Aphidius rosae* (Fink and Volkl 1995). Because wind can interfere with the settling and oviposition behaviour of *A. aphidimyza*, commercial suppliers often recommend turning off the fans for some period during and after the release of *A. aphidimyza* (in Prado et al. 2015).

Another factor that can be of importance to pest control is atmospheric pressure, as this can strongly affect parasitoid behaviour (Steinberg et al. 1992). Steinberg et al. (1992) showed that steadily increasing atmospheric pressure yielded a significantly higher response of the parasitoid *Cotesia glomerata* to a host-infested plant in a behavioural set-up than a steadily decreasing or fluctuating atmospheric pressure. As greenhouses structures are not air-tight, changes of atmospheric pressure from outside the greenhouse cannot be controlled. Whenever possible, however, the release of parasitoids should take place when climatic conditions are favourable.

10.6.7 Context-Dependency of the Effect of Climatic Factors on Pests and Diseases

It is important to note that the intrinsic rate of population increase (r_m) of a species is highly context-dependent, and is besides climatic factors also affected by genetic (i.e. biotype) and biotic factors (e.g. food source; i.e. host plant quality for pests and pathogens and prey/host quality for predators and parasitoids). For example, the different parameters of the Weibull-model describing the temperature-dependent fecundity of whiteflies and temperature-dependent oviposition-frequency of *Encarsia formosa* differed strongly between pepper, cucumber and tomato (Van Roermond 1995). Moreover, the preference of *Macrolophus pygmaeus* to feed during the dark period was higher on pepper plants than on eggplant, and this difference was more prominent at higher temperature (Perdikis et al. 1999).

Some pest species, such as *F. occidentalis*, display thigmotactic behaviour and hide in plant structures that are difficult to reach with (biological) insecticides. Timing the application of these insecticides to an activity peak of these pests may increase the efficacy of these insecticides (Shipp and Zhang 1999). Knowledge of the environmental factors that drive activity are then crucial timing of application and/or manipulation of the microclimate. For *F. occidentalis* it has been shown that activity peaks at a light intensity of 4000–6000 lux, RH of 70% and temperatures around 28 °C. At RH 90% and temperatures below 20 °C and above 36 °C, activity is practically absent (Liang et al. 2010).

Moreover, in some pests and natural enemies diapause is induced at certain combinations of day length, temperature and/or quality and availability of food. Most problematic pests in greenhouses do not undergo diapause under normal cropping conditions, with the spider mite *T. urticae* forming an exception. The sensitivity for diapause induction can differ strongly between populations of the same species, and is highly dependent on the latitude where the population originates from. With a few exceptions (e.g. *Orius majusculus* and *O. insidiosus*), biocontrol companies have selected natural enemy species that have low sensitivity for diapause induction. Moreover, the commercially available gall midges *Aphidoletes aphidimyza* and *Feltiella acarisuga* can undergo diapause under certain combinations of reduced temperature and daylength, and/or in case of *F. acarisuga* when its prey *T. urticae* undergoes diapause (Gilkeson and Hill 1986; Gillespie and Quiring 2002). The induction of diapause in *O. insidiosus* in chrysanthemum can be prevented by extending day length with blue LEDs, without having a negative influence on flower-induction of the crop (Stack and Drummond 1997; Stack et al. 1998).

10.7 Direct and Indirect Influences Crop Management Practices on Pests and Diseases

10.7.1 Growing Medium

The choice of the growing medium will largely determine the diversity and activity of the microbiome developing in the rhizosphere. Moreover, it has long been known that the incorporation of certain types of compost can promote the disease-suppressiveness of the soil, although not all types of compost are equally suitable for the promotion of a disease-suppressive microbiome (see Bonanomi et al. 2007, and references therein). Most growers should also consider the length of time a plant will be in the substrate as many high organic substrates decompose over time which favor soil compaction, low aeration, and poor drainage which, in turn, leads to root disease. Specific micro-organisms that originate from the substrate and/or organic amendments can be directly responsible for the disease suppression (Montagne et al. 2016; Antoniou et al. 2017), but at the same time the 'native' microbiome of the substrate can compete with the establishment of separately-added beneficial microbes. Due to the excretion of root exudates by plants, an active microbiome can develop even in relatively 'inert' substrates with a low available organic carbon content (Koohakan et al. 2004). In addition to the quantity and composition of root exudates by plants, the abiotic characteristics of the substrate, such as the availability of easily degradable carbon (C), micro(nutrients), C/N ratio, pH and EC, will influence the composition and the activity of the microbiome, and how well separately added beneficial microbes can establish. How exactly the abiotic characteristics of the substrate relate to the disease-suppressiveness of the soil is thus far, however, not well understood. A meta-analysis performed by Bonanomi et al. (2010) did not yield many clear predictors of disease suppression, but did indicate that enzymatic and microbiological parameters were overall more informative for disease suppressiveness than chemical ones. Disease-suppressiveness of organic amendments turned out to most-often be pathogen-specific, with amendments effective against one pathogen being ineffective or even conducive to other pathogens (Bonanomi et al. 2010). In 73% of the studies evaluated in Bonanomi et al. (2010), the degree of organic matter decomposition was found to be a crucial factor determining suppressiveness. While for peat substrates the disease-suppressiveness generally decreased during the decomposition process, this was more complex for composts and crop residues. For these organic amendments, the way in which the degree of organic matter decomposition affected suppressiveness was again pathogen-specific, with disease suppression either increasing, decreasing, remaining unchanged, or showing more complex responses, such as ‘hump-shaped’ dynamics. Organic amendments that stimulate the active growth of fungi can also be conducive to the development of sciarid flies (Diptera; Sciaridae) (Olson et al. 2002). These noxious flies use fungi as their main food source (Kennedy 1974), but can also harm plants directly and indirectly through root feeding and as vectors of spores of plant pathogens and pose an important threat to especially young plants.

10.7.2 Fertilisation

The cultural practice of fertilization has long been underappreciated for its influence on pest and disease damage. Slight alternations in the choice of nitrogen (N) form or the accompanying ion for phosphorus (P) or potassium (K) can change the host in ways that increase or decrease pest and disease damage. In general, plants grown at high N rates suffer greater arthropod feeding (Mattson 1980). This notion may be exploited to reduce pest abundance in greenhouse crops, by determining the minimum fertilization level that does not compromise crop productivity and testing the effect on pest abundance. This has been done for several ornamental crops, mostly in relation to damage caused by Western flower thrips *Frankliniella occidentalis*. In cut roses, for example, a 30% reduction in thrips abundance, as well as a 50% reduction in spider mite abundance could be reached by lowering the nitrogen, phosphorous and potassium content of the leaf tissue to respectively 33% and 50% of the recommended fertilization level, without compromising flower production (Chow et al. 2009, 2012). Moreover, thrips populations were found to be reduced at lower soil nitrogen levels in a chrysanthemum crop (Schuch et al. 1998). High phosphorus rates favoured thrips development in Impatiens, but did not lead to increased thrips damage (Chen et al. 2014). Moreover, many insect pests as well as soilborne diseases have been found to be influenced by N-form (e.g. Jones et al. 1989; Bentz et al. 1995; Mollema and Cole 1996). For example, changes in N-form fertilization altered the acceptability of poinsettia to the sweet potato whitefly, *Bemisia tabaci* (biotype B) (Bentz et al. 1995), with higher oviposition on NH_4NO_3 treated plants compared to nonfertilized or $Ca(NO_3)_2$ treated plants. Moreover, Mollema and Cole (1996) found in four important horticultural crops (lettuce, tomato, pepper and cucumber) that cultivars with low concentrations of aromatic amino acids compared to total leaf protein, had reduced Western flower thrips damage. Brodbeck et al. (2001) also showed that Western flower thrips adult female abundance during population peaks most highly correlated to flower concentrations of the aromatic acid phenylalanine in a tomato field crop. Moreover, Arancon et al. (2007) observed that adding nitrate-N though vermicomposts suppressed aphids, mealy bugs, and two spotted spider mites when compared to non-vermicomposted soils. However, the mechanism behind this remains unclear. Diseases caused by *Thielaviopsis,* and *Verticillium* were found to be generally suppressed by NH_4-N, whereas *Fusarium* diseases were almost consistently suppressed under NO_3-N regimes (Jones et al. 1989). Jones et al. (1989) also stated that since NH_4 has more influence on the plant than NO_3, growers should be aware that NH_4NO_3 acts as a NH_4-N form.

Moreover, the role of proper K nutrition is important for pests and diseases (Amtmann et al. 2008), but disease suppression may be more linked to the anion Cl^-, since several studies found that non-Cl sources are less effective (Elmer 2007). The same is true for P, with its role in disease suppression being tightly linked to its companion ions NH_4^+, Ca^{+2} or K^+ (Prahbu et al. 2007). Ca is required by plants in relatively small amounts compared to N or K, but its use in plant health has received much attention as it relates to pH management. Applying Ca (lime) to the root medium to raise pH can also have a marked effect on suppressing *Fusarium* wilts or enhancing damage caused by *Verticillium* wilt and *Thielaviopsis* root rot (Huber 2007). Sufficient Ca nutrition has also been associated with less *B. cinerea* (Volpin and Elad 1991).

Micronutrients are closely associated with pest and disease suppression, both from the standpoint of favoring beneficials and from the standpoint of providing essential nutrients to the crop plant to assist in host defense. The addition of the metals B, Cu, Fe, Mn, and Zn have been identified as having specific roles in host defenses (Datnoff et al. 2007a). Although visual deficiencies are not always observed, many plants are more susceptible when root levels of Cu, Fe, Mn, Fe, and Zn are in suboptimal ranges (Datnoff and Elmer 2018). Both Fe and Zn have been specifically implicated in affecting the pathogen and the beneficial microbes (Duffy 2007; Expert 2007; Fones and Preston 2013). Balancing micronutrient availability with the optimal soil pH can be difficult since most micronutrients become less available as pH approaches neutral. Similarly, adequate Si can reduce both insects and disease damage in many plants (Datnoff et al. 2007b). Studies in cucumbers have shown that Si fertilization reduced root disease (Belanger et al. 1995), powdery mildew (Miyake and Takahashi 1983), and insect feeding (Correa et al. 2005; Reynolds et al. 2009). Given that most soilless media are deficient in Si, many greenhouse crops that can accumulate silicon may gain protection from pest damage if adequate silicon would be added to the root medium. Although Cl is regularly applied as a companion ion to K fertilizers, it is not routinely mentioned in fertility regimes. Crops that are tolerant of, or responsive to, Cl tend to benefit the most from Cl applications (Elmer 2007). Most growers do not consider Cl nutrition in their fertilization regimes, which is partly due to a lack of information on each plant's specific requirements. Similarly, insect damage on chloride tolerant plants may be less when chloride is supplied as KCl, probably due to less exudation of organic acids and sugars and improved osmotic relations in Cl nourished plants (Amtmann et al. 2008). Saline water, however, must be not used to supply Cl due to the high sodicity.

10.7.3 Irrigation

Determining the proper amount of water that promotes plant quality while discouraging an environment that would be conducive for pests can be a daunting challenge. Close attention to timing and the amount of irrigation in the root medium can result in improved quality and can reduce many problems in the greenhouse such as root rot caused by *Pythium* and *Phytophthora* pathogens, as well as fungus gnats. Growers have considerable technology available to them. For example, hydroponics eliminates the problem of over/under watering by allowing large amounts of water made available to the plant. Any excess water can be easily drained away or recirculated, thus eliminating the adverse anoxic conditions that drown root systems in soil. Partial saturation of greenhouse crops on flooded floors can provide multiple benefits. It allows for the production of smaller, more compact, and more horticulturally desirable plants that use less water. Moreover, due to the minimization of leachates, less contaminated run-off is produced. More importantly, by making the soil environment dryer, significantly less root rot disease appears compared to conventionally drained flooded floors (Elmer et al. 2012; Gent et al. 2012). Excessive moisture in greenhouse promotes algal growth, which has proven to be an ideal substrate for the proliferation of shore flies. Sub irrigation also avoids the prolonged leaf wetness that results from overhead irrigation, thus preventing the germination and infectivity of many foliar pathogens. Moreover, by using sub irrigation, the spread and dissemination of many foliar and soilborne pathogens through splash dispersal can be diminished. Paradoxically, water sprays applied at considerable pressure (about 470 kPa) can, at least briefly, control some powdery mildews (Yarwood 1939; Perera and Wheeler 1975; Jarvis et al. 1989). The same is true for plant pests, with several studies showing that pest populations of whiteflies (Castle et al. 1996), thrips (Schuch et al. 1998) and mites (Opit et al. 2006) were reduced in sprinkler irrigated crops. On the other hand, however, many generalist natural enemies used for biological control in greenhouses are nowadays supported by alternative food that is spread into the crop. This food will have to be applied more frequently and in larger quantities when overhead irrigation is used, as this will partly wash the food off the plants and may cause the remaining food to spoil quicker. Finally, the level of plant resistance can be influenced by irrigation, as abiotic stresses can affect plant defenses against pests and pathogens (e.g. Achuo et al. 2006).

10.8 Knowledge Integration and Decision Making

Many knowledge gaps still exist with regard to the interaction between greenhouse climate and the development and activity of pests, diseases and beneficial organisms. Especially the effect of light and temperature conditions on the activity and attack rate of natural enemies merits further investigation, as this may provide ample opportunities for enhancing biocontrol efficacy. Moreover, a better understanding of the functioning of the soil microbiome and the microbes that enhance the disease-suppressiveness of the soil or growth medium, in combination with the development of advanced detection methods, should allow for more informed decision making on sanitation measures.

However, even when we assume that in the future detailed knowledge will be available on the effect of greenhouse (micro)climatic conditions on pests, pathogens and their biological control agents, implementation of this knowledge for the benefit of crop productivity and health will by no means be straightforward. It is already difficult for a single pest-natural enemy or pathogen-antagonist combination to define the climatic conditions that maximize control. When regarding the many complex interactions between the different trophic levels that make up the cropping system, it should be clear that adjusting the greenhouse climate such that crop productivity and quality are optimized, pests and pathogens are repressed, and arthropod natural enemies and microbial antagonists are stimulated will be impossible. Yet, on a more positive note, there are always two sides of the coin with regard to the implementation of knowledge on the interaction of environmental conditions and pest and disease control. Proper knowledge on the abiotic requirements of different biocontrol agents will allow for a more targeted selection of biocontrol agents and biocontrol implementation. When considering the options for control measures of a specific pest or disease, the technical, economic and agro-ecological consequences of adjusting the greenhouse (micro)climate should therefore always be weighed against the level of efficacy of different (biological) control measures within the range of prevailing greenhouse crop (micro)climatic conditions. Moreover, the level of threat posed by different pests and pathogens that can potentially infect the crop should be accurately estimated on the basis of the current and expected (micro)climatic conditions, the level of resilience of the cropping system and the developmental stage of the crop. All this can potentially only be realized with the help of decision-support systems that help integrating many different types of monitoring data, crop growth and pest and disease development models, scientific and expert knowledge and the technical possibilities of the grower.

In the past, several decision support models have been developed for managing greenhouse crops (Fisher et al. 1997a, b; Krug et al. 2007; Korner and Van Straten 2008; Gupta et al. 2010; Habib et al. 2017; Hemming et al. 2017), of which some were specifically targeted at integrated pest and disease management (Clarke et al. 1999; Tantau and Lange 2003; Aiello et al. 2018). It is paramount that the interface of such a decision-support system is user friendly and connects well with the perception and way of reasoning of the grower (van Straten et al. 2000). Quick developments in the generation of smart farming applications and the usage of big data (see e.g. Wolfert et al. (2017) for a review of recent developments) may change the way in which (a) information from the crop environment that relates to crop health is gathered, (b) knowledge on the effect of greenhouse climate control and crop management practices on pest and disease development and cropping system resilience is generated, and (c) different sources of information and knowledge are integrated and translated into decision-making tools for greenhouse growers. This may boost new ways of integrating cultural control methods and crop management for the benefit of overall crop health, productivity and sustainability.

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Chapter 11
Seed and Propagative Material

Gary P. Munkvold and Maria Lodovica Gullino

Abstract The greenhouse environment can be very conducive for the establishment and spread of diseases introduced with planting material. Both seeds and vegetative planting material can be infected or contaminated by damaging pathogens, which often can be transmitted to the growing plant or become established in the greenhouse environment. Transmission from seeds or propagative material can occur with fungi and oomycetes, bacteria, viruses, viroids, and a few nematodes. The most effective way to prevent pathogen introduction is to follow best available pest and disease management practices in the seed production operation. The use of validated pathogen testing methods is critical among these practices. This chapter discusses the biology and management of some of the major diseases that can be introduced on seeds, cuttings, or transplants, in major greenhouse crops including tomato and pepper, cucurbits, leafy vegetables, and ornamentals.

Keywords Bacteria · Disease transmission · Fungi · Oomycetes · Pathogens · Sanitation · Seed testing · Seed treatment · Viroids · Viruses

11.1 Introduction

The greenhouse environment can be very conducive for the establishment and spread of diseases introduced with planting material. Warm temperatures and high humidity can facilitate the transmission of bacteria and fungi from seeds, cuttings, or transplants to the growing plants. Many viruses and viroids also are more easily

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transmitted under warm temperatures, although this varies according to the specific pathogen; viruses are often adapted for seed transmission in the climatic conditions where their host crops occur (Albrechtsen 2006). Because of the often favorable conditions for diseases transmission and spread, it is critically important to use care in the selection of seeds and propagative material for greenhouse cultivation.

Plant pathogens can have different types of association with seeds. Pathogens can infect seeds internally (within the embryo or in other seed tissues), pathogen propagules can externally contaminate the seed surface, or propagules may accompany seeds without direct attachment (in soil, dust, or plant debris, or as galls or sclerotia). Pathogens with any of these associations are considered seedborne. Not all seedborne pathogens can be transmitted to the seedling, so the risk connected with seedborne pathogens is very pathogen-specific. In addition to the possibility of pathogen transmission from seeds to seedlings, seeds may also act as a pathway for the introduction and establishment of pathogens in the planting medium or as a contaminant in the greenhouse environment. However, this aspect of seeds as an introduction pathway is less important in greenhouse production than in field production, assuming that careful sanitation practices are used for planting media, containers, and irrigation water. Direct seed transmission remains a significant risk in greenhouse crops, but in many cases the risk of seed transmission is unclear because of conflicting reports or insufficient data. Studies that demonstrate seed transmission under laboratory conditions often represent a "worst-case" scenario and may not be indicative of the risk that exists in commercial production. A database summarizing evidence for seed as a pathway for many pathogens of greenhouse crops is publicly available (www.worldseed.org/our-work/phytosanitary-matters/pest-lists/#isf-regulated-pest-list-initiative).

The most effective way to prevent pathogen introduction is to follow best available pest and disease management practices in the seed production operation. This includes sampling and monitoring, disease diagnostics, the use of resistant cultivars when available, cultural practices, sanitation, biological and chemical crop protection products, all of which are covered in detail in Part III of this volume. Seeds or propagative material from external sources should ideally be certified and from a reputable source. Using seeds and propagative material that have been tested for the presence of economically important pathogens is an integral part of any greenhouse operation. Accurate, thoroughly validated seed health testing methods are available for many, but not all, important pathogens of greenhouse crops. Testing methods include visual inspection, bioassays, microbiological, immunological, and nucleic-acid based (PCR) methods. The appropriate testing method depends on the specific pathogen. General seed health testing methods are described by Agarwal (2006) and methods specifically for fungi, bacteria, and viruses can be found in other volumes (Mathur and Kongsdal 2003; Fatmi et al. 2017; Albrechtsen 2006). Many national and international organizations are involved with the development and validation of seed health testing methods, including the Seed Health Committee of the International Seed Testing Assoc. (ISTA) (www.seedtest.org/en/tcom-shc.html), the International Seed Health Initiative (ISHI) of the International Seed Federation (www.worldseed.org/our-work/phytosanitary-matters/seed-health/), and the

U.S. National Seed Health System (NSHS) (www.seedhealth.org). Diagnostic method standards also are described by the Int. Plant Protection Convention (IPPC) (www.ippc.int/en/core-activities/standards-setting/ispms/) and the European Plant Protection Organization (EPPO) (www.archives.eppo.int/EPPOStandards/diagnostics.htm), some of which can be applied to seeds. It is important to note that diagnostic protocols developed and validated for vegetative plant tissues may not be accurate when used for seeds; only diagnostic methods specifically validated for seed health testing can be used with confidence when testing seeds.

The advanced stage of development of PCR-based diagnostics has had a major influence on seed health testing, although many "traditional" methods are still in use. An important limitation of PCR-based tests is uncertainty about whether the detected nucleic acid sequences are associated with viable pathogen propagules (Int. Seed Federation 2013). For this reason, a PCR assay is often implemented as a pre-screening step, and seedlots testing positive by PCR are confirmed using bioassay or microbiological, culture-based tests. Alternatively, the identity of suspected pathogenic bacteria or fungi recovered from seedlots can often be confirmed by PCR of pure cultures.

Using healthy seeds and propagative material is a prerequisite in any crop system; in addition, since seeds and vegetative material can be contaminated at low levels, treatment of these materials is an important method for disease prevention. Treating seeds and propagative material with fungicides has been widely practiced due to the availability of a number of effective, low-cost chemicals, and also because of the relative ease of such treatment. Recent restrictions in the registration and use of chemicals have incentivized the use of non chemical methods. Old practices, such the use of hot water are currently being revisited, while new methods are being developed (Gullino and Munkvold 2014).

11.2 Tomato and Pepper

Tomato and pepper crops have several seed-transmitted pathogens in common, although some pathogens that infect both crops may not be seed-transmitted in both crops (Table 11.1).

Clavibacter michiganensis subsp. *michiganensis (Cmm)*, the cause of bacterial canker, is the most economically important seed-transmitted pathogen of tomato, and one of the most important diseases in greenhouse production. The bacterium can infect seeds internally by systemic transmission from the mother plant or contaminate the seed surface via fruit lesions (Tancos et al. 2013). All tomato seeds entering greenhouse production should be tested for *Cmm.* Many methods have been developed to detect *Cmm* in seeds, primarily using semiselective culture media or PCR. Results can be complicated by the presence of non-pathogenic strains of *Clavibacter*, therefore suspect colonies must be confirmed by PCR and/or a pathogenicity test. The Good Seed and Plant Practices (GSPP) program (www.gspp.eu/) has been designed to prevent seed and plant contamination by *Cmm* in seed and

Table 11.1 Seed-transmitted pathogens in tomato and pepper crops (Albrechtsen 2006; Ali and Kobayashi 2010; Jones et al. 2014; Perzezny et al. 2003). Other pathogens may be seed- transmitted but definitive data are lacking

Pathogen type	Pathogen	Main crops	Disease
Bacteria	*Clavibacter michiganensis* subsp. *michiganensis*	Tomato	Bacterial canker
	Xanthomonas spp. [a]	Tomato, pepper	Bacterial spot
	Pseudomonas syringe pv. *tomato*	Tomato	Bacterial speck
Fungus	*Alternaria tomatophila*	Tomato	Early blight
	Colletotrichum spp. [b]	Pepper	Anthracnose
	Didymella lycopersici	Tomato	Didymella stem rot
	Fusarium oxysporuim f.sp. lycopersici	Tomato	Fusarium wilt
	Phoma destructiva var. destructiva	Tomato	Phoma rot
Virus	*Alfalfa mosaic virus*	Pepper	AMV
	Cucumber mosaic virus	Pepper	CMV
	Pepino mosaic virus	Tomato	PepMV
	Pepper mild mottle virus	Pepper	PMMoV
	Tobacco mosaic virus	Tomato, pepper	TMV
	Tomato mosaic virus	Tomato, pepper	ToMV
	Tomato bushy stunt virus	Tomato	TBSV
Viroid	*Potato spindle tuber viroid*	Tomato, pepper	PSTVd

[a] *X. euvesicatoria, X. gardneri, X. vesicatoria*
[b] *C. gloeosporioides, C. coccodes, C. capsicum*

seedling production operations. The program includes a seed health testing method. The method accepted for GSPP currently is ISHI 4.3.1 (http://www.worldseed.org/wp-content/uploads/2017/07/Tomato_Cmm_July2017.pdf), which requires a minimum sample size of 10,000 seeds and confirmation by pathogenicity testing (with an optional PCR pre-screening step for suspect colonies). Treating seeds with dilute HCl, calcium or sodium hypochlorite, heated cupric acid and acetic acid, or hot water can greatly reduce seed contamination (Gleason et al. 2014).

Bacterial spot of tomato and pepper is caused by four closely related species of *Xanthomonas: X. vesicatoria, X. euvesicatoria, X. gardneri,* and *X. perforans.* All four can be internally and externally seedborne and seed-transmitted. Seedlings produced in the greenhouse environment from contaminated seeds can be symptomatic or symptomless carriers of the bacteria (Jones and Miller 2014). Seed health testing methods are available, which are based on culturing seed extracts on semi-selective culture media, followed by confirmation of suspect colonies with pathogenicity testing (www.seedhealth.org). Identity of each of the four species can also be confirmed by PCR. Seed treatment with dilute HCl, sodium hypochlorite, or hot water can greatly reduce seed contamination (Jones and Miller 2014). Seedlings in the greenhouse can be treated with bacteriophage to prevent infection (Flaherty et al. 2000). Proper sanitization and irrigation management are important measures to control this disease in the greenhouse environment.

Fusarium wilt of tomato, caused by *Fusarium oxysporum* f. sp. *lycopersici* can be disseminated by contaminated seeds, tomato stakes and transplants. Long-distance spread occurs via infected seeds and transplants, while local dissemination can occur via transplanted tomato stakes (Correll and Jones 2014; Huang et al. 2012; Jones et al. 2014). Seeds can become infected or infested by systemic transmission from the mother plant or by colonization of the blossoms or young fruit (Menzies and Jarvis 1994). The importance of seed transmission is greatly mitigated by the use of chemical seed extraction or seed disinfestation treatments and the widespread use of seed testing. Tomato seed testing for Fusarium wilt is typically performed using blotter tests or culturing on semiselective media; suspect colonies can be confirmed using pathogenicity testing or PCR. Specific races of *F. oxysporum* f.sp. *lycopersici* can be identified using a combination of PCR primers (Inami et al. 2010). *Fusarium oxysporum* f. sp. *radicis-lycopersici*, causal agent of crown and root rot of tomato can be introduced into new tomato-growing areas by means of infected seeds and transplants (Jarvis 1988; Menzies and Jarvis 1994).

Tomato mosaic virus (ToMV) and *Tobacco mosaic virus* (TMV) are among the important seed-transmitted diseases caused by viruses in tomato and pepper crops. In pepper, Pepper mild mottle virus (PMMoV) is a related seed-transmitted virus. All three are in the *Tobamovirus* genus. In tomato, ToMV is more common, and it can be found in the external mucilage, testa, and endosperm of the seed, but is not believed to occur in the embryo (Zitter 2014). Although seed transmission is not internally systemic, these viruses are easily mechanically transmissible from seeds to seedlings, and can be spread quickly by handling after being introduced with seed or transplants. Seed heath testing is usually done by local lesion bioassays using *Nicotiana tabacum* as an indicator plant (www.seedtest.org/en/tcom-shc.html), although other methods using PCR or ELISA have been developed. A bioassay is considered preferable because it indicates whether the seedborne virus is infectious. Seed treatments using trisodium phosphate (10% for 15–20 min) or dry heat (70 C for 2–4 days) can greatly reduce or eliminate contamination by Tobamoviruses (Zitter 2014).

Tomato and pepper can be infected by several viroids, mostly in the Pospiviroid family. *Potato spindle tuber viroid* is the most common viroid in solanaceous plants, and the only viroid with definitive evidence for seed transmission in tomato and pepper. The importance of seed transmission is controversial; it can be demonstrated experimentally (Matsushita and Tsuda 2017), and several outbreaks have been linked to seeds (Constable et al. 2019; van Brunschot et al. 2014), triggering phytosanitary requirements for viroid testing. However, most outbreaks have not been linked to seeds (ISF 2018). PSTVd has been detected in the embryo and endosperm of tomato seeds (Matsushita and Tsuda 2017), and it can be a surface contaminant. Reported seed transmission rates are variable; they be very high for seeds from inoculated mother plants (Simmons et al. 2015), but very low in seeds from naturally-infected mother plants (ISF 2018). Seed testing for viroids is challenging because of the lack of protein coat and the small RNA genome. The recommended method is reverse-transcription real-time PCR, such as the one recommend by ISF (ISF 2018), using a 3000 or 20,000-seed sample size. Many primers have been reported for various combinations of pospiviroids, but high-quality RNA extraction from seeds is the most difficult aspect.

11.3 Cucurbit Crops

Several bacteria, fungi, and viruses are reported to be seed-transmitted in cucurbit crops (Table 11.2).

Bacterial fruit blotch, caused by *Acidovorax citrulli*, is the most notorious seed-transmitted pathogen in cucurbits. Seed transmission has been reported in watermelon, melon, honeydew, squash and pumpkin; it may also occur in other species (Walcott et al. 2017). The bacterium can survive for decades in stored melon and watermelon seed and still be transmitted to seedlings (Walcott et al. 2017). *Acidovorax citrulli* colonizes the pistil or the ovary pericarp of female flowers; pistil colonization results in infection of embryos while pericarp invasion results in superficial infestation of the testa and other parts of the seed (Dutta et al. 2012), and may lead to symptomatic fruit. Seeds from symptomatic fruit may also be contaminated through contact with decaying flesh of the fruit. The primary seed health testing methods for *A. citrulli* are grow-out and PCR. A variation on the greenhouse grow-out test is the use of translucent plastic boxes with high density planting, placed in a growth chamber ("sweat box") (Parker and Sanjeev 2017). Currently recommended methods under the U.S. NSHS and ISHI programs are 30,000-seed samples subjected to grow-out or PCR followed by grow-out for confirmation (www.seedhealth.org). Seed health testing for other seedborne bacteria on cucurbit seeds, such as *P. syringae* or *X. cucurbitae*, is typically done using culture methods on semiselective media. Seed treatments with acid electrolyzed water, peroxyacetic acid, cupric acetate, HCl, or CaOCl can significantly reduce the risk of *A. citrulli* seed transmission, but typically cannot eliminate the bacterium from seeds and in some cases can be detrimental to germination (Feng et al. 2009).

Gummy stem blight is caused by *Stagonosporiopsis citrulli, S. cucurbitacearum (Didymella bryoniae),* and *S. caricae*. It can be seed transmitted in cucumber, melon, pumpkin, and watermelon (Lee et al. 1984; Sudisha et al. 2006). The fungus is found on and in the seed coat and in the cotyledon tissue. Seedling infection occurs on the radicle, hypocotyl and cotyledons, causing emergence failure or subsequent infection of the true leaves and the stem (Lee et al. 1984). Recommended seed health tests for gummy stem blight pathogens are a blotter test with 1000 seeds or PCR with 10,000–30,000 seeds (www.seedhealth.org). PCR can be used to confirm identity of suspect colonies from blotter tests. However, it is not clear if PCR primers developed for *D. bryoniae* prior to 2015 are effective for all three species of *Stagonosporiopsis*. Recently, a loop-mediated isothermal amplification (LAMP)

Table 11.2 Seed-transmitted pathogens in cucurbit crops (Cohen et al. 2014; Parker and Sanjeev 2017; Simmons et al. 2013)

Pathogen type	Pathogen	Main crops	Disease
Bacteria	*Acidovorax citrulli*	Melon, watermelon, other cucurbits	Bacterial fruit blotch
	Pseudomonas syringae pv. *lachrymans*	Cucumber, pumpkin, squash, zucchini	Angular leaf spot
	Xanthomonas cucurbitae	Cucumber, pumpkin, squash	Xanthomonas leaf spot
Fungus	*Colletotrichum orbiculare*	Cucumber, melon, watermelon	Anthracnose
	Stagonosporopsis spp. (syn. Didymella bryoniae)	Cucumber, melon, watermelon, other cucurbits	Gummy stem blight
	Fusarium oxysporum f.sp. *cucumerinum*	Cucumber	Fusarium wilt
	Fusarium oxysporum f.sp. *lagenariae*	Bottle gourd	Fusarium wilt
	Fusarium oxysporum f.sp. *melonis*	Melon	Fusarium wilt
	Fusarium oxysporum f.sp. *niveum*	Watermelon	Fusarium wilt
	Fusarium solani f.sp. *cucurbitae* race 1	Pumpkins, squash, other cucurbits	Fusarium crown, root, and fruit rot
	Macrophomina phaseolina	Melon, other cucurbits	Charcoal rot
Oomycete	*Pseudoperonospora cubensis*	Cucumber, melon, pumpkin, squash, watermelon	Downy mildew
Virus	*Cucumber green mottle mosaic virus*	Cucumber, melon, watermelon, other cucurbits	CGMMV
	Kyuri green mottle mosaic virus	Cucumber, melon, watermelon, other cucurbits	KGMMV
	Melon necrotic spot virus	Cucumber, melon, other cucurbits	MNSV
	Squash mosaic virus	Squash, melon	SqMV
	Zucchini green mottle mosaic virus	Cucumber, zucchini	ZGMMV
	Zucchini yellow mosaic virus	Melon, pumpkin, squash, watermelon, zucchini	ZYMV

protocol was developed for the gummy stem blight pathogen (Tian et al. 2017). Seed treatment with fungicides or biological control agents has been shown to reduce disease severity in cucumber (Kaewkham et al. 2016); fungicide seed treatment is recommended for all susceptible cucurbits (Keinath 2017).

Seed transmission has been reported for Fusarium wilt in several cucurbit species including cucumber, bottle gourd, melon, and watermelon (Table 11.1; Parker and Sanjeev 2017), although in some cases there is little direct evidence for an important epidemiological role of seeds. In watermelon, *F. oxysporum* f.sp. *niveum* has been shown to internally infect seeds through systemic transmission from the mother plant and these seeds can transmit the disease to seedlings. In cucumber, *F. oxysporum* f.sp. *cucumerinum* can be found in the seed coat of seeds from infected plants (Jenkins and Wehner 1983), but occurrence of seed transmission appears to be very low. In other cucurbits, low levels of contamination or infection occur in seeds from infected plants but the importance of seed transmission is unclear. Seed health testing for wilt-causing *F. oxysporum* pathogens is typically done with a blotter test, followed by pathogenicity or PCR testing of suspect colonies. Primers that distinguish specific formae speciales of *F. oxysporum* are available for some of these pathogens (Haegi et al. 2013), but in many cases, pathogenicity testing is needed for confirmation. Fungicidal or biological seed treatments can be used to reduce the risk associated with seedborne *F. oxysporum*.

Several viruses can be seedborne and seed-transmitted in cucurbits (Table 11.1). In particular, CGMMV can sometimes occur at relatively high frequency in seeds from infected plants. The virus can be found as a surface contaminant and in the endosperm and embryos of seeds of several cucurbit species (Hollings et al. 1975). It has been shown to be seed-transmitted in cucumber, melon, watermelon and bottle gourd, and may also be seed-transmitted in other cucurbits. CGMMV was recently introduced into North America through contaminated seeds (Tian et al. 2014), after a similar occurrence in Australia (Tesoriero et al. 2016). *Melon necrotic spot virus* can be seed-transmitted in melon (Herrera-Vasquez et al. 2009), and possibly other cucurbits. *Squash mosaic virus* can be seed-transmitted in melon and possibly pumpkin and squash. *Zucchini yellow mosaic virus* can be seed-transmitted in squash and zucchini (Simmons et al. 2013), and this occur even in cultivars with transgenic resistance (Simmons et al. 2015). Routine testing for CGMMV, MNSV, and SqMV is typically done by ELISA and a seed health testing method for these viruses has been approved by the International Seed Testing Association (ISTA) (www.seedtest.org/en/tcom-shc.html). The method includes a grow-out confirmation for SqMV but bioassay methods are still needed to confirm positive ELISA or PCR results for CGMMV and MNSV. For ZYMV, PCR testing is recommended (Provvidenti and Gilbertson 2017) and PCR primers also are available for the other viruses. Treatment of seeds by dry heat (Kim et al. 2003) or with trisodium phosphate can reduce contamination by CGMMV and other viruses but may not completely eliminate them from cucurbit seeds.

11.4 Leafy Vegetable Crops

Lettuce, spinach, basil and other leafy vegetables suffer from several seed-transmitted diseases caused by fungi and viruses (Table 11.3).

Table 11.3 Seed-transmitted pathogens in lettuce and spinach crops (Albrechtsen 2006; Gilardi et al. 2018b). Other pathogens may be seed- transmitted but definitive data are lacking

Pathogen type	Pathogen	Main crops	Disease
Fungus	*Alternaria cichorii*	Endive, cichory	Alternaria leaf spot
	Alternaria japonica	Rocket	Alternaria leaf spot
	Botrytis cinerea	Lettuce	Grey mould
	Cladosporium variabile	Spinach	Cladosporium leaf spot
	Colletotrichum dematium f. sp. *spinaceae*	Spinach	Anthracnose
	Fusarium oxysporum f. sp.	Rocket	Fusarium wilt
	Fusarium oxysporum f. sp. basilici	Basil	Fusarium wilt
	Fusarium oxysporum f.sp. *lactucae*	Lettuce	Fusarium wilt
	Fusarium oxysporum f.sp. *spinaciae*	Spinach	Fusarium wilt
	Microdochium panatonnianum	Lettuce, endive,	
	Phoma valerianellae	Cichory	Phoma leaf spot
	Plectosphaerella	Lamb's lettuce	Plectosphaerella leaf spot
		Rocket	
	Septoria lactucae	Lettuce	Septoria leaf spot
	Stemphylium botryosum	Spinach	Stemphylium leaf spot
	Verticillium dahliae	Lettuce, spinach	Verticillium wilt
Oomycete	*Peronospora belbharii*	Basil	Downy mildew
	Peronospora farinosa f. sp. *spinaciae*	Spinach	Downy mildew
Bacteria	*Acidovorax valerianellae*	Lamb's lettuce	
	Pseudomonas cichorii	Lettuce	
	Xanthomonas campestris pv. vitiansi	Lettuce	
Virus	*Cucumber mosaic virus*	Spinach	CMV
	Lettuce mosaic virus	Lettuce	LMV

The leafy vegetable sector is particularly exposed to the risk of the emergence of new diseases as a consequence of its dynamism, the wide range of products, continual innovation in procedures or in products and the use of intensive cultivation techniques that characterize it. The sudden, and almost simultaneous, appearance of new diseases on leafy vegetables grown in different continents is linked to structural aspects of the industry. Propagative material is produced in just a few large nurseries, which in turn supply small nurseries in other regions or countries (Garibaldi and Gullino 2010). To reduce the risk of spreading new diseases, it is necessary to intercept the pathogens in the nodal points of the distribution structure. The crops considered in this chapter are lettuce (*Lactuca sativa* L.), wild (*Diplotaxis* spp.) and cultivated (*Eruca sativa* Mill.) rocket, lamb's lettuce (*Valerianella olitoria* L.), chicory (*Cichorium intybus*), endive (*Cichorium endivia* L), basil (*Ocimum basilicum* L.) and spinach (*Spinacia oleracea* L.).

11.4.1 Fungi

Verticillium wilt, caused by *Verticillium dahliae*, has been observed on lettuce, chicory and spinach (Ciccarese et al. 1987; Correll et al. 1994; Davis et al. 1997; Garibaldi et al. 2007) and it is important in the presence of air and soil temperatures of 20–25 °C, causing more losses during spring and fall. In the case of lettuce, seed transmission of the pathogen plays an important role: Vallad et al. (2005) reported a very high percentage (66–90%) of infected seeds. In the case of spinach, seed contamination has been proved. *V. dahliae* is systemic in spinach and readily seed transmitted (Du Toit et al. 2005). On spinach, the spread of this pathogen throughout infected seeds is at present a major concern in areas where fresh and processed spinach crops are grown in rotation with other crops susceptible to the pathogen (Maruthachalam et al. 2013).

Fusarium wilt, caused by different *formae speciales* of *Fusarium oxysporum* affects leafy vegetables, representing a potential threat to their production in many areas, also due to the exceptional survival and dissemination mechanisms. Seed transmission occurs when propagules are carried as surface or internal contaminants of seeds or are associated with plant debris. Many Fusarium wilts of leafy vegetables, such as those of lettuce, rocket and basil, possess these traits.

The Fusarium wilt caused by *Fusarium oxysporum* f. sp. *lactucae* was first identified in 1955 as the cause of a root rot on lettuce in Japan (Matuo and Motohashi 1967). Some 35 years later, a Fusarium wilt was reported in the 1990s on lettuce in the United States (California) and the causal pathogen was named *Fusarium oxysporum* f. sp. *lactucum* (Hubbard and Gerik 1993). Later research demonstrated that the California isolates and Japanese race 1 belonged to the same compatibility group and were considered to be the same *forma specialis* (Fujinaga et al. 2003). Subsequent recognition of the pathogen on lettuce has been reported in Iran in 1995, Taiwan in 1998, Brazil in 2000, Italy in 2002 and in the state of Arizona in the United States in 2001 (Matheron and Gullino 2012). Race 4 recently developed in the Netherlands (Gilardi et al. 2017), Belgium (Claerbout et al. 2018), the United Kingdom and Ireland (Taylor and Clarkson 2018. Fusarium wilts also have been observed on several salad crops in addition to lettuce, as reviewed by Matheron and Gullino (2012). The appearance of Fusarium wilt on lettuce in geographically distant areas, such as Brazil, Iran, Italy, Taiwan, and the United States, at least 35 years after the initial discovery of this disease in Japan, suggests a long-distance method of dispersal of *F. oxysporum* f. sp. *lactucae*. Seed transmission of the pathogen is a possible dissemination mechanism. Garibaldi et al. (2004a) reported that nine of 27 samples of lettuce seed obtained from commercial seed lots planted in fields, that were subsequently affected by Fusarium wilt in Italy, were contaminated by *F. oxysporum*. Also, *F. oxysporum* f. sp. *conglutinans* and *F. oxysporum* f. sp. *raphani*, causal agents of Fusarium wilt of wild and cultivated rocket, are seed-transmitted (Garibaldi et al. 2004b). Therefore, seed transmission on wild and cultivated rocket seeds contributed to the spread of the disease in Italy. Other means of pathogen dispersal within and between fields would include any farming operation that would move infested soil or plant material, such as seed-bed preparation activities, cultivation, movement of mud-encrusted sprinkler-irrigation pipe, and harvesting crew operations.

F. oxysporum f. sp. *basilici* was first described on basil in the former USSR and later spread to many basil growing areas (Garibaldi et al. 1997), causing severe damages also due to its soil-and airborne behaviour (Gamliel et al. 1996). The pathogen has been isolated from seeds, before and after disinfestation with sodium hypochlorite: Martini and Gullino (1991) found that 0.4% of non-disinfested and 0.2% of disinfested commercial seeds harbored *F. oxysporum* f. sp. *basilici.* It is not known whether *F. oxysporum* f. sp. *basilici* is an external contaminant or infects seeds internally (Martini and Gullino 1991; Vannacci et al. 1999), although diseased plants have been obtained from some seed lots after external disinfection (Vannacci et al. 1999). Epidemiological considerations suggest that rapid local spread of Fusarium wilt and crown rot of basil is caused by airborne inoculum derived mainly from macroconidial masses on stem surfaces (Gamliel et al. 1996), through soil particles, and during harvest, whereas seed-borne inoculum is probably responsible for its long-distance transmission (Martini and Gullino 1991; Elmer et al. 1994; Gamliel et al. 1996; Elmer 2001).

F. oxysporum f. sp. *spinaciae*, causal agent of Fusarium wilt on spinach also is seed-borne (Bassi and Goode 1978).

Phoma valerianellae, the causal agent of a foliar disease of lamb's lettuce, is another seed-borne pathogen (Nathaniels 1985). Its recent resurgence and spread in Italy in areas devoted to ready-to-eat production has been explained by seedborne dissemination (Pellegrino et al. 2010).

The recent outbreak of *Plectosphaerella cucumerina* on wild rocket represents a potential threat to rocket production in Italy as well as elsewhere. The disease has been detected on wild rocket, widely grown for processing. *P. cucumerina*, is frequently seedborne (four seed samples out of eight tested were contaminated), which suggests that seeds may be important in disseminating this pathogen, despite a low level of contamination (about 0.15%) in the tested samples (Gilardi et al. 2013a). The fast spreading of the disease that occurred first in southern Italy in 2012, moving in a few months to northern Italy) can be explained with the capability of the pathogen to contaminate seeds. The pathogen was recently detected also on endive (Gilardi et al. 2018a).

Leaf spot of escarole, chicory and endive, caused by *Alternaria cichorii*, is easily transmitted by infected seeds (Barreto et al. 2008).

A leaf spot of basil, causing extensive necrosis and incited by *Alternaria* spp., appeared recently in several countries. Taba et al. (2009) showed that the black lesion of basil grown in greenhouse in Japan were caused by *Alternaria alternata*. Recently in Israel, a similar black spot caused by *Alternaria* sp. was observed at the harvesting of summer basil (Kenigsbuch et al. 2010). A similar leaf spot was observed during the summer-fall 2010 on sweet basil, grown in soilless systems as well as in soil in northern Italy (Gilardi et al. 2018a). All 18 Italian seed samples tested were contaminated by *Alternaria* spp. The frequency of isolation of *Alternaria* spp. colonies was higher in the case of non-disinfected seeds for all samples tested. For instance, in the case of seeds belonging to experimental lines of basil, the frequency of isolation of *Alternaria* spp. from seeds was 1.18% for not disinfected seeds and 0.43% for disinfected seeds. In the case of seeds belonging to commercial varieties of basil, *Alternaria* spp. was isolated respectively from 7.29% and 2.62% of non-disinfected and disinfected seeds (Gilardi et al. 2013b). *Alternaria japonica* was recently reported as the cause of a new leaf spot on wild and cultivated rocket (Gilardi et al. 2018b).

Cladosporium variabile and *Stemphylium botryosum*, causal agents of two leaf spots of spinach, are booth seed-borne In the case of *S. botryosum*, the presence of the pathogens in seed lots, combined with international movement of spinach seeds, might explain the sudden and almost concomitant appearance of the pathogen in several states of the USA (Hernandez-Perez and du Toit 2006).

11.4.2 Oomycetes

Downy mildew pathogens of lettuce (*Bremia lactucae*) and spinach *(Peronospora farinosa* f. sp. *spinaciae (Pfs)* are economically important seedborne pathogens. While there is ample evidence for seed transmission of *Pfs* (Inaba et al. 1983; Kunjieti et al. 2016), the risk associated with seedborne *B. lactucae* is not clear. As early as 1935, Cook reported that spinach crops grown from heavily infested seeds bearing oospores were severely damaged by downy mildew. Inaba et al. (1983) showed that the percentage of spinach seedlings infected by downy mildew was positively correlated with the degree of oospore infestation of seeds. Downy mildew of basil, incited by *Peronospora belbahrii*, (Belbahri et al. 2005; Thines et al. 2009) was observed in Switzerland in 2002 and in northern Italy in 2003, quickly spreading to other Italian regions in Central and Southern Italy (Garibaldi and Gullino 2010) as well as France. This pathogen was first reported in Uganda, identified as *Peronospora* sp. and much later in Switzerland. After this report in Switzerland, the pathogen spread to many basil growing areas, such as Belgium, the USA, Cuba, Israel, Hungary and more countries (Farr and Rossman, 2018). Its spread probably has been favored by the fact that it is seed-transmitted (Garibaldi et al. 2004c).

11.4.3 Bacteria

In lettuce, *Pseudomonas cichorii and Xanthomonas campestris* pv. *vitiansi* have been reported as seed-transmitted in lettuce or spinach (Table 11.1), but data are conflicting about the role of seeds in dissemination of these pathogens. An outbreak of bacterial leaf spot caused by *X.c.* pv. *vitians* in New Zealand was linked to seeds (Ohata et al. 1982), but this was not definitively demonstrated. Lettuce seeds from inoculated plants were externally, but not internally, contaminated with *X.c.* pv. *vitians* (Barak et al. 2002), but seed transmission was not demonstrated and the bacterium is rarely detected on lettuce seeds. There are no widely used seed health testing methods for these pathogens, although semi-selective media have been developed. Seed treatment with 1% sodium hypochlorite for 5–20 min or 3–5% hydrogen peroxide for 5–15 min was effective at reducing contamination by *X.c.* pv. *vitians* (Koike et al. 2017). Transplants may be contaminated with these or other bacteria and proper sanitation of planting media and containers is needed to prevent spread through transplants. In cornsalad or lamb's lettuce, *Acidovorax valarienella* is recognized as an important bacterial pathogen that can be disseminated with seeds. A seed health testing method has been developed using a grow-out procedure followed by PCR confirmation of symptomatic seedlings (www.seedtest.org/en/tcom-shc.html).

11.4.4 Virus Diseases

Lettuce mosaic virus (LMV) is globally the most important pathogen of lettuce crops, occurring on every continent and in most lettuce-growing areas. The importance of seed as a source of inoculum for this pathogen was recognized early on; seed testing and the use of virus-free seed has been recommended for decades (Grogan 1980). Most seed testing is performed using ELISA (www.seedhealth.org), although bioassays are sometimes used with *Chenopodium quinoa* as an indicator plant. Sample sizes for seed health tests are based on thresholds determined for different lettuce-growing areas that differ in disease risk. Sample sizes as high as 30,000 seeds are used for open-field production in California, but smaller sample sizes are typically used in less disease-conducive environments and for greenhouse production, where seed testing accompanied with rigorous control of insect vectors is very effective.

Cucumber mosaic virus (CMV) is an important pathogen in numerous crops, but seeds are an important source of inoculum for relatively few, including spinach. CMV was detected in seeds (embryo and endosperm) and pollen tissues of infected plants (Yang et al. 1997). Seed transmission of approximately 8–15% was detected in seedlings derived from crosses in which either the male or female parent was infected. Seed health testing can be accomplished using a grow-out procedure followed by ELISA testing of seedlings (www.seedhealth.org).

11.5 Ornamentals

The ornamental industry, due to its international nature, is greatly affected by the introduction of pathogens through infected material and this aspect is also well covered in Chapter xxxxx by Daughtrey and Buitenhuis. Ornamental plants are started from seed or from cuttings. Starting with seed may avoid many diseases, although seed can be a source of pathogens, such as *Xanthomonas* spp. among bacteria and *Rhizoctonia solani, Alternaria* spp. among fungi (Daughtrey and Buitenhuis 2019). Also in the case of bedding plants, which were traditionally grown from seeds, there has recently been a shift towards vegetative propagation, with an increase in use of cuttings. In vegetative propagation, stock plants are grown and encouraged to branch, with cuttings being regularly harvested (Faust et al. 2017). Vegetatively propagated material is shipped to growers directly as unrooted cuttings or, alternatively, is rooted at specialized facilities and sold as rooted cuttings (Daughtrey and Buitenhuis 2019). The health status of such vegetative propagated material depends on the quality of the integrated disease management at the propagator, rooting station or plug production sites.

Starting from cuttings increases the likelihood of introducing inoculum of different pathogens. In the case of many ornamental crops the propagation facilities for unrooted cuttings are more and more often placed in developing countries, with an increased risk for movement of new invasive pathogens from the country of origin to new countries (Gullino and Garibaldi 2006; Daughtrey and Buitenhuis 2019).

In the case of foliage plants, material for plant propagation includes seed, cuttings, cane section and tissue culture. The most popular foliage plants are micropropagated through tissue culture, with a much reduced risk of infection by pathogens (Chen and Henny 2006).

Flowering potted plants can start from seed, vegetative cuttings, tissue culture, plantlets or bulbs. Vegetative cuttings are often used to guarantee the quality of the crop; however they often carry pathogens, such as agents of powdery mildew, root rot or wilts, with symptoms developing later at the production stage (Gullino and Garibaldi 2006; Daughtrey and Buitenhuis 2019).

In order to comply with international phytosanitary measures, stock plants used for producing cuttings are often sprayed with pesticides, which increases the risk of importing pathogens which are already pesticide resistant, thus further complicating their management. Moreover, pesticide residues on cuttings may compromise the adoption of biological control, by negatively affecting the survival of the biocontrol agents (Daughtrey and Buitenhuis 2019).

The most important cut flower crops, such as carnation and chrysanthemum, are started from culture-indexed and virus-indexed stock. Cuttings deriving from indexed stock are certified as free from significant diseases (i-e. Fusarium wilts). Rose and gerbera are most frequently propagated in-house, with the highest quality products obtained from stock maintained free from known viruses (Daughtrey and Buitenhuis 2019). The most important ornamental crops will be considered in the following section.

11.5.1 Fusarium Wilts

Several *formae speciales* of *Fusarium oxysporum* are responsible of wilts on a number of ornamental crops. In most cases infected propagative materials contribute to their spread.

Fusarium wilt, caused by *F. oxysporum* f. sp. *cyclaminis* is one of the most devastating diseases in cyclamen production worldwide. Tompkins and Snyder (1972) attempted to demonstrate seed transmission by testing 6000 seeds from various sources,without finding any evidence of the pathogen. Although they were unable to isolate *Fusarium oxysporum* f. sp. *cyclaminis* from seed coats, they did report isolation of the fungus in 1971, with a very low percentage recovery, from debris mixed with seed in seed packets imported from the Netherlands. Rattink (1982) showed that seeds and seedballs of diseased plants used for seed production were not contaminated with the fungus. Even though seed contamination is not common, long distance transmission on seedling plugs is still a significant problem within the cyclamen industry. Growers cannot be sure that plugs that they purchase do not carry inoculum of the pathogen. Determining the sources of inoculum and developing efficient early detection methods, such as molecular assays applied to container leachates, are needed to help identify infested seed parent plants or seedling plugs (Elmer and Daughtrey 2012).

Fusarium oxysporum f. sp. *dianthi*, the causal agent of Fusarium wilt of carnation, is predominantly disseminated with propagative material. The organism may colonize the vascular system without symptom expression; however, the fungus does not progress very high in the vascular system before symptoms appear (Baker et al. 1985). Even so, a substantial proportion of propagative material derived from infected mother plants may harbour the pathogen. The pathogen persists in soil for long periods and is spread by soil, contaminated tools, and infected cuttings. It can survive under greenhouse benches, in field soils, around buildings and even in the wood used for bench supports. It can be spread by the wind, and by running water, together with the soil, equipment, shoes; it can lie under fingernails and on tools used in taking cuttings. Water can also play a major role in the spread of the pathogen (Rattink 1977). Spores of the pathogen can remain viable and germinate and multiply in water for a very long period.

There is no need for penetration by the pathogen if the propagative material already harbours the pathogen in vascular tissue. Penetration from inoculum in soil is typically through root tips (Baker et al. 1985). It can also penetrate throughout wounds; and points of entry may also be caused by nematodes (Schindler et al. 1961).

Carnations are suscepible during the entire period of their life cycle and loss of plants begins typically at one point in the cultivation. Adjacent plants begin to show symptoms, this spread from initial sources of infection to adjacent healthy plants could be explained by growth of the fungus through root grafts or contact.

F. oxysporum f. sp. *chrysanthemi* has been recognized as the causal agent of the wilts observed on chrysanthemum (Armstrong et al. 1970) as well as on gerbera, Paris daisy and African daisy (Minuto et al. 2007). The pathogen can be transmitted through infected propagation stock and/or can infest soil and substrate. When rooted cuttings are planted in soil or substrate infested with the pathogen, the fungus infects the roots and colonizes the zone of elongation in the area of undifferentiated tissue that will become vascular tissue. The xylem vessels become colonized by the pathogen prior to symptom expression. Cuttings for vegetative propagation taken from such plants at this stage may be symptomless but infected. In the presence of high air and soil temperatures, symptoms appear quickly and plants belonging to susceptible cultivars wilt, collapse, and die. When the plants die, chlamydospores may be produced in pieces of plant debris. When these cuttings are rooted and planted, spores produced on infected tissues can infest the growing medium. Plant tissue that breaks down slowly may contain vegetative mycelium as well as chlamydospores. If the growing medium is not disinfested, this material will infest the substrate, providing inoculum to infect the next susceptible crop planted in the same medium. The fact that the same pathogen, *F. oxysporum* f. sp. *chrysanthemi,* can affect different hosts belonging to the Compositae family, often grown in the same farm, if not in succession in the same greenhouse, is very challenging from an epidemiological point of view. A study carried out on different isolates of *F. oxysporum* f. sp. c*hrysanthemi* obtained from the four hosts revealed on the basis of host response the presence of three physiological races. Sequencing the intergenic spacer (IGS) region of ribosomal DNA (rDNA) and with phylogenic analysis revealed that races, observed in pathogenicity tests, coincide with three phylogenetic groups. Analysis of IGS sequences revealed a high degree of similarity among strains isolated in Italy and Spain from gerbera and other host species, thus confirming that recent outbreaks in these ornamental crops were probably caused by the introduction of infected propagation material from a common origin (Garibaldi and Gullino 2012).

The spread of the pathogen occurs via infected cuttings and infested soil/medium. Symptomless, infected cuttings serve as a main source of inoculum to spread the disease. Infested soil/substrate may be dispersed by cultivating equipment, animals and humans.

Propagation material is very important for the spread of important pathogens in many so called "bulb" crops. The word "bulb" is commonly used for a diverse range of storage organs, including stem tubers, rhizomes, corms, root tubers, and the bulbs themselves (Rees 1992). Flowering bulbous plants are grown almost everywhere in the world, for the production of both flowers and propagation material. For the handful of countries that are major commercial producers, cultivated ornamental bulbous crops represented, particularly in the 1980s and 1990s, an agricultural industry of great economic importance.

All bulb crops, including gladiolus, iris, tulip, lilium, narcissus, ranunculus, crocus, fresia, hyacinthus and cyclamen, have been repeatedly reported as being subject to wilt caused by different *formae speciales* of *Fusarium oxysporum* (Moore 1979). The disease is more severe in areas that are warm and humid during the growing season. It also occurs in cooler areas, but in this case disease development is slower and symptoms are reduced (Linderman 1981). Most studies on Fusarium wilts of bulb crops were carried out from 1970 to 1990, when such crops covered a large acreage around the world. Fusarium wilt still remains a problem, although new tissue-culture technology and propagation systems have changed its relative importance (Castagner and Byther 1985; Magie 1985; Cline et al. 1998; Gullino and Wardlow 1999).

The causal agents of Fusarium wilt have been identified as *F. oxysporum* f. sp. *gladioli* on gladiolus and iris, *F. oxysporum* f. sp. *tulipae* on tulip, *F. oxysporum* f. sp. *lilii* on lilium, *F. oxysporum* f. sp. *narcissi* on narcissus, *F. oxysporum* f. sp. *ranunculi* on ranunculus, *F. oxysporum* f. sp. *croci* on crocus, and *F. oxysporum* f. sp. *hyacinthi* on hyacinthus.

The different *formae speciales* causing wilt of bulb crops share common characteristics. Fusarium wilt agents are carried in practically all stocks of bulbs as latent infections (Magie 1985), which tend to remain dormant until plants are fertilized for maximum flower production. Fusaria are often difficult to recover from gladiolus corms due to growth inhibitors in corm tissues (Magie 1985).

Infections by *F. oxysporum* on most flowering bulb crops probably begin in the field, either in the roots, scales or basal plate. However, most infections eventually involve the basal plate, and may be severe enough to destroy the whole bulb (Gullino 2012). The disease usually progresses rapidly in the presence of high temperature and moisture, hence, the symptoms may occur toward the end of the growing season. In many cases, infections starting in the field do not result in symptoms until after harvest, either in storage or transit, or after replant for forcing into flowers. Dissemination of the pathogen occurs by planting bulbs with latent infections, by movement of infested soil on machinery and via water. In the case of gladiolus, it has been shown that susceptibility of the host is enhanced by root-knot nematodes as well as by viral infections (Magie 1985).

F. oxysporum f. sp. *hebae* is considered responsible for wilt on *Hebe* spp. (Raabe 1957), while *F. oxysporum* f. sp. *eustomae* is the causal agent of *E. grandiflorum* wilt (Raabe 1985a).

F. oxysporum f. sp. *foetens* was first reported in Europe in 2000. In view of its pathogenicity to *Begonia* x *hiemalis*, it has been suggested to be a pathogen of wild begonia species, which are native to tropical South America (Simpson and Ogorzaly 1986). Because there is no record of this pathogen's isolation in Europe prior to 2000, Schroers et al. (2004) suggested that the fungus might have been introduced into Europe accidentally along with wild species breeding material. It might have indirectly reached *Begonia* x *hiemalis* nurseries in the southern hemisphere, from where it was introduced into Europe through trade. Latently infected begonia propagation material appears to pose a serious risk of spreading the pathogen, and may explain why *F. oxysporum* f. sp. *foetens* has been isolated in the Netherlands and detected by quarantine inspectors in England since late 2000 (Schroers et al. 2004). In the case of flannel flower wilt, no pathogen has been recovered from seeds (Bullock et al. 1998). In the case of crops such as bitterroot (*Lewisia cotyledon*), *Protea*, jade plant (*Crassula ovata*) and *Hosta*, *F. oxysporum* has been recognized as the causal agent of the wilt and can be spread through infected propagation material (Hahm 1998; Geiser et al. 2001; Gullino and Garibaldi 2012). In the case of Hebe, Fusarium wilt was first reported in 1957 on *Hebe odora* in a nursery in California and described as caused by *Fusarium oxysporum* f. sp. *hebae* (Raabe 1957). The nursery destroyed all of the stock and the disease disappeared until the early 1980s (Raabe 1985b). In 1999, the disease was observed in northern Italy (Garibaldi et al. 2011), where it probably arrived via infected propagation material from northern Europe (Denmark).

In the case of ornamental crops, disease control relies on the integration of different measures. Pathogen-free propagation programmes are routinely adopted, especially for chrysanthemums. Treatment of the growing medium, usually with steam, assures that the medium is free of the pathogen. Sanitation is used to keep the medium free of the pathogen during the growing period. However, problems may occur from reinfestation during production through the use of contaminated water or soil. It is important to use resistant cultivars.

When present, growers use less susceptible cultivars and, in the case of bulb crops, propagation material is treated (Gullino 2012). For years, bulbs were treated by fungicide dip, mainly benzimidazoles, which were effective not only against *F. oxysporum,* but also against *Penicillium corymbiferum*, the causal agent of another bulb rot. However, resistance to benzimidazole quickly developed (Garibaldi and Gullino 1990). The addition of other fungicides, such as dichloran, chlorothalonil or captan to benzimidazoles reduced the spread of benzimidazole resistance (Magie and Wilfret 1974). Later, prochloraz dips replaced benomyl dips (Garibaldi and Gullino 1990; Migheli and Garibaldi 1994; Gullino and Garibaldi 2012).

Interesting disease control results have also been achieved in the case of gladiolus, iris and tulip with hot water treatments, either alone or in combination with reduced dosages of fungicides (Magie 1985; Garibaldi and Migheli 1988; Migheli and Garibaldi 1990). The temperatures used vary according to the host, reaching 49 °C in the case of gladiolus, up to 52 °C in the case of small gladiolus corms and 55 °C for cormels (Magie 1985). Cohen et al. (1990) achieved eradication of *F. oxysporum* f. sp. *gladioli* propagules by hot water treatment for 30 min at 57 °C. Roebroeck et al. (1991) developed a mathematical model for the hot water treatment of gladiolus, showing 5% and 99% death of corms and *F. oxysporum* f. sp. *gladioli* conidia, respectively. Hot-water formaldehyde treatments were carried out on narcissus (Castagner and Byther 1985). When hot water treatment was combined with low dosages of benzimidazole, a synergistic effect was detected in gladiolus and iris (Garibaldi and Migheli 1988; Migheli and Garibaldi 1990). Recently, UV-C at low doses has emerged as an alternative technology, to avoid the use of fungicides. Sharma and Tripathi (2008) controlled Fusarium rot of gladiolus corms by integrating the use of hot water, low dosages of UV-C and essential oil (2008). Chlorine dioxide proved effective in inhibiting conidia of *F. oxysporum* f. sp. *narcissi* (Copes et al. 2004). Finally, suppressive potting mix has been proven effective against Fusarium wilt of gladiolus (Garibaldi 1987). Currently, very few chemicals are registered for use on crops that are considered “minor”, despite their economic value.

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Chapter 12
Soil and Substrate Health

A. Gamliel

Abstract Intensive crop production in greenhouse is a challenging task from various aspects of maintaining soil health. The lack, or short crop rotation practice, boost a buildup of pathogen populations which can damage the crop and put crop profitability at risk. Hence, the use of effective pest control measures, while trying to withstand soil health and its fertility are needed. When resistant plants or rootstocks are not available, some form of soil disinfestation may be essential to eliminate the majority of root pathogens and pests in the soil. Drastic soil treatments (e.g. soil steaming, and fumigation) can create a "biological vacuum" leading the soil to degradation of soil fumigants: occurrence and be disposed to pathogens and pests re-invasion. In contrast, an approach which incorporate various agricultural practices of crop production and protection enhances the development of natural disease suppressiveness and provides an increased growth response is preferred. A system approach which impacts pest onset and disease suppression consists of manipulation of agricultural practices to reduce pest, integrated application of pest control measures, minimizing negative attributes to the crop, environment and the consumer, and maintain measures to assure food safety at harvest and following storage. Pest management is a complicated set of procedure due to the heterogeneity of the production system, and pest infestation. Thus, assembly of all components within a production system may result in effective management. Examples are shown with specific crops, pests and management strategies.

Keywords Soilborne pathogens · Soil fumigation soil resilience · Soil suppressiveness · Solarization · Organic amendments

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12.1 Introduction

12.1.1 *Impact of Soilborne Pests in Greenhouse Production*

Greenhouse production of edible and floriculture crops is an intensive agricultural industry with the objectives is to maintain a profitable crop, and long-term productivity. This practice is characterized by growth in soil, on raised beds or on benches using various artificial or organic growing substrates, and involves the use of various resources for the production, and for pest and disease management (Wittwer and Castilla 1955). Soilborne pests (pathogens, arthropods and weeds) can interfere with the production objectives and cause heavy losses, affecting both yield and quality. The most common soilborne diseases that occur in greenhouse-produced plants are root rots, wilts, root knot nematodes and nematode-transmitted viruses (Gamliel and van Bruggen 2016). Important fungal pathogens of vegetables and flower crops include Fusarium and Verticillium wilt (Giotis et al. 2009, Gullino et al. 2012), Fusarium crown rot of tomato and cucumbers (Gullino et al. 2012), root rot caused by *Sclerotinia sclerotiorum, Macrophomina phaseolina, and Sclerotium rolfsii* on varoious vegetables (Baysal-Gurel and Miller 2010), Phytophthora on pepper and herbal plants. Soilborne virus and viroid diseases such as Tomato mosaic Virus (TMV), and Cucumber Green Mottle Mosaic virus (CGMMV) can be of high damage significance in greenhouse production (Miller 2011). Examples of important bacterial diseases in greenhouse crops include bacterial canker (*Clavibacter michiganensis* subsp. *Michiganensis*) of tomato, cucurbits leaf and fruit blotch caused by *Acidovorax avenae*. *Ralstonia solanacearum* is of high importance as it cause wilt of many greenhouse crops. In addition, *R. solanacearum* race 3 biovar 2 is a quarantine organism in the USA and Europe and will need to be eradicated if discovered (Messiha et al. 2007).

Soilborne pathogens survive and disseminate by various mechanisms which result in many sources and forms of inoculum, all of which have to be detected and managed in intensive greenhouse production to secure a healthy crop. The primary source of pathogen infestation is the soil inoculum which originates from previous crops. However, many other sources are highly important, including infested propagation material, contaminated water, spreading of infested soil, insects and animals, inoculum adhering to the greenhouse structure, weeds and other hosts. Certain soilborne pathogenic fungi also can produce aerial propagules on the surface of plants and infest the entire greenhouse structure. For example, various formae speciales of *Fusarium oxysporum*, including *radicis-lycopersici* (Rekah et al. 2000), *basilici* (Gamliel et al. 1996; Katan et al. 1997), and *radicis-cucumerinum* produce aerial conidia on the surface of plant stems. The aerial conidia of pathogens may have an important impact in greenhouse production, since aerial conidia can spread in the greenhouse and adds other challenges for their management. Each and every source of inoculum need to be controlled before, at and after planting to effectively reduce disease incidence and severity on the following crop. The inoculum density that is left viable before planting will determine the degree of success or failure of the management actions (Katan 2006).

Many soilborne pathogens are also seed-borne, and can become problematic when transplants are used from a non-reputable source. Vegetable seedlings and transplants are produced at very high densities and the slightest seed contamination can result in epidemic spread due to the use of a fine mist to produce transplants. Unlike foliar pathogens, soilborne pests, establish following introduction into soils or substrates, and rapidly buildup. Pathogen with wide host range, e.g. root knot nematodes, can rapidly boom to unacceptable levels (Klein et al. 2012; van Bruggen and Semenov 2015; van Bruggen et al. 2015b). Also, because crop rotations is usually minimal or short, soilborne diseases can rapidly establish. Once well established, soilborne pathogens will continually develop and destroy susceptible crops, with further dissemination to new locations.

12.1.2 Challenges in Maintaining Soil Health

Soil health, is defined as "the capacity of a living soil to function, within natural or managed ecosystem boundaries, to sustain plant productivity, and promote plant health" (Doran and Parkin 1994; Katan and Vanachter 2010). A healthy agricultural soil is characterized by a great microbial and faunal diversity, with ecological resilience and resistance, to pests and disease (van Bruggen and Semenov 2000, 2015; van Bruggen et al. 2006). Inversely, soil infestation, is a biotic disturbance within the soil ecosystem, threatening soil health. The intrusion of a pathogens from external sources into the living system called soil, changes its capacity to function, as a platform for a productive crop (van Bruggen and Semenov 2000, 2015). A healthy soil can be resilient to pathogen infestation) (Kibblewhite et al. 2008; van Bruggen and Semenov 2000; van Bruggen et al. 2015c). An example for a healthy soil is suppressive soils which keep disease incidence or severity at low level, despite the presence of the pathogen and favorable environmental conditions for disease progress (Cook and Baker 1983). Soil suppressiveness is important for a delay in the buildup of pathogen populations in soil.

Crop production in greenhouses and its reflection on the challenges for maintaining soil health are characterized by specific features and difficulties:

- Specialization in narrow spectrum of high-value crops and a high-cost production system. These dictates monoculture or a narrow rotation of crops which, in turn, can increase the inoculum potential and density certain pathogens in the soil following each crop. Monoculture also triggers rapid build-up of other detrimental factors (biological, chemical and physical) in the soil agents.
- Many crops grown in protected structures are susceptible to many devastating soilborne pests. In addition, the long production season and the short time between crops, further facilitates pathogen establishment. and complicates control of pests and diseases
- The long cropping season leaves only a short time window for executing effective pest control measures between crop seasons

- A considerable mass of plant residues are left at the end of the cropping season. These can harbor pathogen propagules and resting structures, thereby hampering the efficacy of pest control measures. Treating and removing this huge mass is significant in reducing inoculum potential.
- The pathogens can infest various niches in the greenhouse, including the growing containers, the water-recycling system and the greenhouse structure. The result is inoculum in all over the structure, not just in the soil or the growing substrate. Hence effective management should consider all of sources of infestation to achieve a pest-free greenhouse for the next cropping season.
- There is a high input of organic material, especially in growing substrates, which can favor pathogens on the one hand, but also has the potential to improve soil suppressiveness, if properly manipulated.

12.2 Approaches and Strategies to Maintain Soil and Substrate Health in Greenhouses

Management of soilborne pathogens is a challenging task that stems from the following characteristics of soilborne pathogens:

- Soilborne pathogens survive in the form or active or dormant structures in the soil. Although, most of the inoculum is usually located in the cultivated soil layer (at about 20–30 cm depth), a small proportion of active or dormant cells can dwell in deeper layers. The deep inoculum, if not managed, can vertically move and infect the new crop (Katan and Gamliel 2012).
- Soilborne pathogens survive harsh conditions as resting structures (e.g. chlamydospores, sclerotia, oospores). These structure may dwell inside the tissues of root debris at various soil depths, hence providing additional obstruction for effective pest control measures.
- Increasing populations of soilborne pest such as certain fusarium species (Gamliel and Katan 2012) can survive also on various parts of the greenhouse structure. Therefore, sanitation and cleaning the structure from inoculum prior to planting is essential to assure healthy crop (Katan and Gamliel 2014).
- The complex soil matrix, forces use of effective pathogen control measures. Application of management measures is significantly difficult and complicate compared with management of foliar pests. It should consider effective and uniform distribution, in order to reach the propagules at each soil site and depth
- Additionally, the greenhouse structure imposes challenges with regard to optimal application especially around posts and walls (Gamliel 2014).
- The growing practice in greenhouse production provide a short window for application of control measures. Hence, Agents which are harmful to plants need to dissipate by planting time and leave minimal residual attributes on the soil and surrounding environment (Gamliel 2002)

- Drastic soil disinfestation measures (e.g. chemical fumigation or soil steaming) may be harmful to beneficial organisms, e.g. native biocontrol agents, mycorrhizae and rhizobia (van Bruggen and Semenov 2015; van Bruggen et al. 2015a), therefore further disturb the soil health and promote disease conduciveness conditions.

Many methods for the management of soilborne pathogens have been developed since the introduction of soil steaming in 1888 in Germany, and its commercial use in in 1893 in the United States (Lawrence 1956). Most of these measures (chemical, physical, biological and cultural methods) aim at suppressing or eradicating them, or at least reducing the size of the existing population pathogens in the soil (Gamliel and Katan 2009). Many of the soil fumigants have been phased out during the last 50 years, mainly due to negative environmental and human health hazards. These leaves agriculture with minimal arsenal of fumigant and additional restriction on registration and use of new fumigants. Today, effective management tools need to consider environmental, economic, technological and legal issues. In current crop production in greenhouse, an effective method for pathogen control in soil should effectively reduce inoculum density in the soil. Furthermore, it should involve minimal disturbance of the soil's biological, chemical and physical components. The pathogen control tool has to be environmentally acceptable with minimal hazards to non-target living organisms and abiotic components. It should be economically acceptable and technologically feasible, and free of safety problems during application.

12.2.1 The Industrial Conventional Approach

The industrial approach in agriculture views farm as a factory (Levins 1986). Crop production involves high inputs of seed, fertilizer, fuel, water, and pesticides for the goal of increasing profits by maximizing yields. Industrial agriculture, synthetically utilizes fertilizers as the principal source of plant nutrients. These, in turn, disrupt the natural accumulation of organic substrates in the soil and impact their associated microbial communities. Management of soilborne pest in the industrial approach consists upon soil disinfestation before planting using effective, (usually highly toxic) pesticides or combination of pesticides with other potent control measures. The objective of using soil disinfestation is to keep a disease-free and productive crop. It consists of the ability of the pre plant treatment to reduce the pathogen inoculum below the threshold of disease potential and ensure economic benefit. Soil disinfestation is a backbone of the industrial approach and is not necessarily intended to provide soil health, hence, pesticide and fumigant are routinely applications together with the continuous monoculture. These measures may further degrade the integrity of soil ecosystems by intensifying selection for rapidly colonizing soil microorganisms including soilborne pathogens. As a consequence, crop production becomes further dependent upon the extensive use of inputs to keep profitable crop productivity.

Significant global trends during recent decades have changed the face of the industrial approach for soil disinfestation from some important features.

- Important effective soil fumigants were phase-out of during the years including, ethylene dibromide, dibromo-chloropropane, and more recently methyl bromide. In contrast, new fumigants were not introduced, leaving only few fumigants that are currently registered and available (Anon 2010, 2014). These include 1,3-dichloropropene (1,3-D, Telone), metam sodium (MS), Dazomet (Basamid), Chloropicrin (CP), formaldehyde (formalin) and a combination of a few of these chemicals. However, the use of these fumigants is restricted in several countries, due to regulatory stipulations.
- The soil fumigants which are left and still available, have a narrow range of controlled pests and do not always provide the anticipated and satisfactory control of soilborne pests (Anon 2014).
- The failures in pest control following soil fumigation can be also the result of ineffective application technology or non-uniform distribution of the fumigant within the cultivated soil layer. Ineffective performance of the fumigants often results in a more frequent application to assure crop productivity (Lembright 1990; Gamliel 2014)
- Accelerated degradation of soil fumigants is increasingly reported, since the first report by Smelt et al. (1989) on accelerated degradation of methyl isothiocyanate (MITC) and 1,3-D in soil after repeated application of the parent fumigants (Warton et al. 2003; Triky Dotan et al. 2007; Gamliel and Triky Dotan 2009). This phenomenon has significant implication on pathogen control and future use of repeated fumigation in a given field.

Industrial agriculture will certainly sustain as a dominant approach for assuring production of food feed and fibre. However, the above mentioned trends, significantly push towards different approaches for managing pest especially those dwelling in the soil interphase.

12.2.2 Systems-Based Approach

Systems-based approaches to management of soilborne pests evolved from the IPM concept. it changes the objectives from the primary goal of simply killing the pathogen, to its management and regulation within the production system. The emphasis is to recognize the special features of soilborne pathogens with regard to their biology, and ecology within the cropping systems and incorporate pest management procedures within the agricultural practices. Moreover, survival of the pathogens in soil presents not just difficulties but also options for their management within the approach framework. Ultimately, systems-based approach promotes pest and disease suppression through natural biological feedback mechanisms (Lewis et al. 1997).

A systems-based approach consists of the following pillars (Chellemi et al. 2016):

- Management of soilborne pests is done by maximizing the potential of natural pest suppression mechanisms. Examples include the manipulation of biological, chemical, physical, and environmental conditions, to create an agroecosystem that is hostile to pests and pathogens. Additionally, preventing the entrance of pathogens by feasible pathway (e.g. propagation material, manure) are important component of the management practices.
- Incorporate natural disease suppression into the design of cropping systems;
- Restriction and minimization of the impact of disruptive actions (pesticides, biopesticides and other agents) through the use of an integrated approach for pest control which optimizes the use of pesticides, biopesticides and other agents at the relevant crop stages, in order to interfere with the pathogen life cycle at the different stages.
- Proper and effective application technologies are key factor to assure maximum impact of disruptive actions on the target pathogen and to reduce populations to levels where they can again be regulated naturally.
- Minimal negative attributes of pest management intervention activities to the crop, environment and the consumer;
- Use of measures that assure food safety during harvest and post-harvest.

Managing soilborne plant disease within a systems-based approach requires a broad, multidisciplinary perspective. Hence, execution of this approach involves several continuous processes which should be harmonized with the crop production cycle (before, during and after the end of the crop). The important process are listed below.

- *Inoculum detection and quantification in soil*. A practical approach to assess the inoculum potential is a disease survey in the susceptible crops as the cropping season ends. Pathogen detection is simple at this stage, enables predicting the expected disease level at the next crop, and guides for the optimal management measures to be performed. Disease survey at the end of the cropping season, also serve as a decision tool for effective measures such as root destruction with the living pathogen inside. It also directs for activities to prevent redistribution of infective propagules by tillage practices used to incorporate crop residue.
- *Strategies to reducing initial inoculum in soil.* Risk management drives the decision making process as to the tools to use for cost-effective results From a risk perspective, application of broad spectrum biocides including soil fumigants is usually (but not always) the desired tool for the initial step of reducing the population in soil below a threshold level. Using soil fumigants enables a wider spectrum of control, which is much needed more than one pest exist. Combined measures can further improve the results of reducing inoculum level in soil (Gamliel et al. 2000; Jayaraj and Radhakrishnan 2008). Combining control measures is more than merely mixing various methods. For example, sequence of

applications is very important (Eshel et al. 2000). The goal should be to achieve a synergistic effect, although an additive effect is also highly desirable. Also, a long-term effect such as soil suppressiveness (see next section) can also be expected. Such procedure will provide a friendly platform to the crop growth. Risk management also drives the ongoing measure to be taken in order to maintain a health crop, and also improve soil health and fertility.

- *Control of pathogen spread during production season.* Spread of pathogen during the production season can impact both the present crop and also can infest various niches in the greenhouse, including the growing containers, the water-recycling system and the greenhouse structure. Hence measures to reduce potential spread are essential. The use of cultural measures and application of pesticide will minimize the risk for more cycles during the season. Furthermore, it will reduce the inoculum potential for the next season.
- *Disease suppression during crop production.* Soil disinfestation does not achieve full elimination of the inoculum in soil, hence, the surviving inoculum can proliferate and incite a disease in the coming crops. Further steps to suppress the remaining inoculum include improvement of plant tolerance by biopesticides or chemicals. Additionally, improving water quality and fertilization also improve plant tolerance.
- *Reducing pathogen buildup at the end of the crop.* Root destruction at the end of the crop aims at killing the roots and the pathogens colonizing them. This procedure does not provide any benefit to the current crop but only blocks additional inoculum to the soil and for the coming crops. Root destruction combined with removal of the crop debris, outside the greenhouse reduces the potential inoculum and facilitates the efficacy of the soil disinfestation to be taken before the next crop.

Adoption of a system-based approach involves extended time frames and increased costs as this approach is performed. However, the benefits of developing disease suppressive soils, the long-term benefits of minimizing pesticide use, improving soil fertility and reducing environmental impacts outweigh the costs and efforts. It is difficult to assume economic calculations on those savings over long time frames as it also depends on the crop values over time. Hence, adoption of a system-based approach should be considered already during the strategic planning process associated with present future crop production. More attention to quantitative assessments of the financial costs and benefits associated with systems based approaches is needed.

12.2.3 Organic Farming

Organic farming in greenhouses constitutes only a small proportion of total greenhouse production. (Meijer 2009; Dorais and Alsanius 2015). Crops are grown in soil, on raised beds or on benches using organic growing substrates (mix of peat, composts). The farmers follow the same basic principles and rules for organic farming in field production, including maximal use of renewable resources and energy sources, and prevent environmental pollution during production. Organic farming as the conventional one faces the challenges of pest management due to the intensive cropping and short rotation (van Bruggen et al. 2015a). Hence, integration of management methods is needed for successful plant disease control (Hasna et al. 2009; van Bruggen et al. 2015a). Integrated pest management in organic farming can be regarded as a special case of a system-based approach with specific characteristic and additional restriction derived from the basic principles of organic farming. Most management tools in organic farming aim at preventing the introduction or establishment of pathogens in the soil (crop rotation as much as possible), suppressing them, or at least reducing the size of the existing populations (Gamliel and Katan 2009; Katan and Gamliel 2012).

- **Sanitation** is an essential measure to reduce the initial inoculum of a wide array of plant pathogens. Removal of inoculum associated with crop residues is a common practice in organic greenhouse production. The residues can be composted at sufficiently high temperatures of the composting materials to kill residual pathogens (van Bruggen 2015; van Bruggen et al. 2015a). The compost can then be used to contribute to the nutrition of the following crop. Additional sanitation approaches are described in later sections.
- **Application of appropriate soil disinfestation**. Drastic, but effective, physical measures which are detrimental to the crop, e.g. steaming or hot water treatments, can be used before planting. Soil solarization can be also used in organic farming with effective results (Gamliel and Van bruggen 2016)
- **Application of organic amendments** as a tool for soil disinfestation. This may include either anaerobic soil disinfestation, or aerobic disinfestation. The use of organic amendments of various sources (e.g. crop residues, composts and organic wastes) can be further improved by the combination with solarization. (Gamliel and Stapleton 2012)
- **Organic matter management** is important throughout the year, especially in greenhouse crops that utilize a lot of nitrogen, like tomatoes (Gravel et al., 2010; van Bruggen 2015; van Bruggen et al. 2015b). The development of stable soil organic matter ultimately leads to natural suppression of soilborne pathogens (van Bruggen 1995; van Bruggen et al. 2015a, b, c). On the other hand, root diseases may be temporarily enhanced by the application of easily decomposable materials like plant- or animal-derived materials and immature compost (He et al. 2012; Grünwald et al. 2000; Zelenev et al. 2005). The effect of organic amendments on root pathogens depends on the specific material used, its C:N ratio, and the stage of decomposition of the material (van Bruggen and Termorshuizen 2003). Since composts originate from various sources, and various levels of maturity. They may result in great variability and inconsistency of results. Therefore there is a need to develop quality control tools for assuring composts performance, and providing consistent disease control.

Disease suppressiveness is a desired and anticipated outcome in soil management in any farming especially in organic. Baker and cook (1974), defined disease suppressive soils as "soils in which the pathogen does not establish or persist, establishes but causes little or no damage, or establishes and causes disease for a while but thereafter the disease is less important, although the pathogen may persist in the soil". Soil suppressiveness may be either constitutive, or induced by agricultural practices. Conducive or natural suppression of plant pathogens soil allow high disease incidence and severity, shortly after the invasion of the pathogen. Natural suppressiveness is largely attributable to the composition of resident soil microbial communities they interact with (Weller et al. 2002; Mendes et al. 2011; Schlatter et al. 2017). The mechanisms by which resident microbial communities suppress pathogens and nematodes is complexed and most likely results from combinations of specific and general disease suppression mechanisms (Schlatter et al. 2017). Induced suppressions can be induced by application of organic amendments, e.g. composts (Cook and Baker 1983; Hoitink et al. 1997) or other. Beneficial shifts in microbial community composition can occur when organic material is amended and combined with other practices are implemented, such as soil solarization (Gamliel and Stapleton 1993b, 1997). Both soil suppressiveness and conduciveness are connected with microbial biomass, activity and diversity, Therefore, any practice that negatively affects these variables will alter soil health.

12.3 Soil Disinfestation and Reducing Inoculum Potential

Soil disinfestation is the principal way destroying the initial inoculum of harmful pathogens in soil, hence preventing early infection and disease. It is executed before planting by the application of highly potent and non-selective means. However, today it should target to minimal effects on chemical and physical soil properties and also to avoid disturbance of the biological equilibrium. Application of soil disinfestation in its modern form was developed at the end of the nineteenth century, in parallel to the establishment of crop protection sciences. As a principle soil disinfestation is a pre-plant soil treatment and should be applied as the final agricultural procedure before planting, in order to avoid contamination of the disinfested soil by disturbing the soil layers. Soil disinfestation can only control the existing populations of soil pests. It does not protect the soil from contamination from outside sources. Such contamination must therefore be avoided. Soil disinfestation consist of the following features (Katan and Gamliel 2012).

- It is applied to eliminate (or forcefully reduce) populations of a range of soilborne pests. The pests are usually as resting structures in a dormant stage. Therefore, their control requires more potent measures for effective results.
- Soil disinfestation is usually implemented using non-selective chemical or physical measures to accomplish the control of a wide spectrum of harmful organisms in the cultivated soil layers, or even deeper, and all soil niches. Disinfestation of

growth substrates, on the other hand, is applied to treat a shallow layer. Growth substrates, However, tend to accumulate organic matter (mainly residues of root biomass) following repeated cropping, which results in reduced efficacy of fumigants. In contrast, the efficacy of solarization or steaming is not affected by the organic content in the substrates

- The soil fumigant, or its decomposition products, must dissipate before planting with no phytotoxic residues which can injure the subsequent crop. Therefore, it should be applied sufficiently long before planting, so that phytotoxic residues from either the agent or decomposed organic material could dissipate after the termination of the process (Katan and Gamliel 2012)
- Application of soil disinfestation is a complicated process in most cases, hence requires special equipment and training. It is a costly treatment that must be properly executed for optimal results.
- In addition to pathogen control, soil disinfestation can also affect beneficial microflora (van Bruggen and Termorshuizen 2003; van Bruggen and Semenov 2015; van Bruggen et al. 2015a) and change mineral nutrition status of the plant, and release of toxic substances (Chen et al. 1991).
- Soil disinfestation should preferably result in disease suppressiveness to provide protection the soil from future outside infestation. This can be accomplished by amending the soil with organic material just before the disinfestation process or by adding certified composts afterwards, reducing the hazard of re-infestation (Hoitink and Boehm 1999) or biocontrol agents (Elad et al. 1982).

12.3.1 Soil Fumigation

Soil fumigation consists of applying wide-spectrum biocides which act in the vapor and liquid phases. Methyl bromide (MB), the most dominant fumigant in the last decades effectively controlled a wide array of soilborne pests and enabled the production of acceptable commercial yields (Klein 1996, Gullino et al. 2003). With its high vapor, pressure low boiling point and high specific gravity, MB moves easily downward and laterally and fills the porous soil spaces rapidly after application. Additionally, MB volatilizes from the soil after a short period, enabling the planting of a new crop within a short time after the fumigation process. The use of MB has been phased out following its inclusion in the list of chemicals that deplete the ozone layer, leaving a narrow selection options in the soil-fumigant arsenal for effective chemical alternatives to control soilborne pests. The list of currently available fumigants is very limited and includes chemicals with a narrower range of controlled pests (Ajwa et al. 2003, Gullino et al. 2003). The following fumigants are currently available:

- Chloropicrin (trichloronitromethane) – effective against soilborne fungi and some insects and. At rates of 30–40 g/m^2 chloropicrin provided a satisfactory and consistent control of Fusarium wilt on melon, Verticillium wilt on eggplant, *F.*

oxysporum f. sp. *radicis-lycopersici* and Fusarium wilt on tomato, particularly in sandy soils (Gullino et al. 2002) Similar results for Fusarium wilt and Fusarium crown rot of tomatoes were recorded in Florida (Gilreath et al. 1994). Chloropicrin is not effective, however, in controlling *Macrophomina phaseolina* in strawberry production (Anon 2014). It has limited activity against weeds (Ajwa et al. 2003).

- 1,3-Dichloropropene (1,3-D) – effective nematicide and against a wide spectrum of parasitic nematodes. It is also effective in controlling insects and suppresses some weeds. It is not effective in controlling and pathogenic fungi, although some reports on effective fungal control were reported (Noling and Becker 1994; Raski and Goheen 1988).
- Methyl isothiocyanate (MITC) generators (dazomet, metam sodium and metam potassium) – effective at controlling a wide range of arthropods, soilborne fungi, ectoparasite nematodes and weeds. Fusarium (especially Fusarium crown rot of tomatoes) exhibits variable response to MITC (McGovern et al. 1998, 2003). MITC is less effective against bacteria and root-knot nematodes.
- Iodomethane or methyl iodide – liquid chemical which has been recently tested on a wide range of crops and found to be highly effective at controlling a wide range of soilborne pathogenic fungi, nematodes, and weeds (Becker et al. 1998; Zhang et al. 1998). The relative potency values of methyl iodide to methyl bromide are higher for most fungi (2.7 more efficacious than methyl bromide). The potency of methyl iodide to *F oxysporum* is 1.5 higher (Hutchinson et al. 2000). Since 2013, methyl iodide has been registered for commercial use only in Japan (Anon 2014).
- Formaldehyde – effective in controlling broad-spectrum of soilborne pathogens, especially bacteria, oomycetes and ectoparasitic nematodes (Kritzman et al. 1999). It is formulated as formalin (37% in aqueous solution) which is highly soluble in water. Formalin is not effective against *Fusarium oxysporum* at the commercial rates, however, when combined with metam sodium it provides effective disease reduction (Gamliel et al. 2005).
- Dimethyl disulfide (DMDS) – toxic to various nematodes, including *Meloidogyne javanica*. The toxicity of DMDS varies among soil fungi. *F. oxysporum* f. sp. *radicis lycpersici* appears to be sensitive to the fumigant. *Sclerotium rolfsii* and *Macrophomina phaseolina* are highly tolerant to DMDS (Anon 2014)

The above mentioned fumigants are characterized by inferior physical and chemical properties, such as high boiling point, and low vapor pressure and water solubility. All the fumigants, excluding dazomet, are applied to soil in liquid form to the desired depth with various equipment. The chemicals move through the liquid phase, diffuse into the soil and vaporize in the soil. Application can be performed by injection (Ogg 1975; Klein 1996), drip irrigation (Ajwa et al. 2003; Papiernik et al. 2004) or sprinkler irrigation (Gamliel et al. 2005). None of these fumigants offers a satisfactory alternative to MB, when used alone. Furthermore, the inconsistent efficacy of some fumigants is evident, resulting from variable dissipation rates in different soils (Triky-Dotan et al. 2007). Recent reports have also demonstrated enhanced biodegradation of compounds containing MITC after repeated application to soil, causing some concern about the future of these products used alone (Wharton and Matthiessen 2000; Di Primo et al. 2003). Obviously, the future of Soil disinfestation lies in combining fumigants with other methods, in order to obtain acceptable performance. Additional constraints for all fumigants is their rapid permeation through a common low density polyethylene (LDPE) film, (Austerweil et al. 2006). Hence, the use of virtually impermeable film (VIF) which provide barrier against fumigant emission, has demonstrated benefits resulting from the use of VIF tarp: better control, effective control to deeper soil layers, and the ability to apply lower rates of fumigant (Gamliel et al. 1997; Gullino et al. 2003). Shank injection of the fumigants dichloropropene plus chloropicrin under VIF dramatically improved their retention in the soil. Survival of *Fusarium oxysporum* f. sp. *lycopersici* in soil declined significantly when compared with soil fumigation treatments applied under low-density polyethylene (Chellemi and Mirusso 2006). Application of fumigants under a VIF tarp resulted in a higher dosage of fumigant in the soil and in a more uniform distribution at the tested soil depths.

The use of the few fumigants left is strongly regulated in many countries. The dosage of applied fumigants is limited. Additionally, the maximum amount of certain fumigants (e.g. 1,3D) is limited per given area in the USA (Anon 2010). These regulations and restriction of fumigants will probably increase. Hence, the future of fumigants use for soilborne pest control is unclear.

12.3.1.1 Combinations of Fumigants

Mixture or combined application of fumigants is an effective tool to improve soil disinfestation and also extend the spectrum of controlled pests. A mixture of chloropicrin with 1,3-D (under the brand names of Telopic, Telodrip, Inline), is an example of a commercial product widely used to control soil nematodes and fungal diseases (Ajwa et al. 2003). Such mixture effectively controlled *F.oxysporum* f. sp. *lycopersici*, or f. sp. *radicis- lycopersici* in tomato greenhouses in sandy loam soils, (Minuto et al. 2006). Chloropicrin is an important component in fumigant mixtures which has been adopted in most developed countries. Mixture of chloropicrin, with methyl iodide applied jointly were and 2.8 times more efficacious, respectively, against *F oxysporum* than when each of the compounds was applied singly (Hutchinson et al. 2000). A combination of chloropicrin and MITC also results in improved pest control, especially when both are applied under plastic tarp (Porter et al. 1999; Minuto et al. 1999). Mixtures of formalin and metam sodium are also used to provide an extended spectrum of controlled pests (Gamliel et al. 2005), including *F. oxysporum* f. sp. *radicis-lycopersici, Monosporascus cannonballus* and *Rhizoctonia solani*, some of which are hard to control by treatment with a single chemical (Gamliel et al. 2005). Combinations of fumigants often result in synergistic effect in the control of target pests, compared with the use of each fumigant alone effect. In such application one of the components in the mixture pushes the second fumigant to deeper layers as compared with its movement when applied alone. The synergistic effect enables application at reduced rates without compromising pathogen control (Gamliel et al. 2005). Combinations of fumigants can also reduce the risk of developed accelerated degradation phenomenon in soils in which it has been shown to occur Triky-Dotan et al. (2009). Reported that application of formalin-metam sodium mixture resulted in effective control of Verticillium wilt and other diseases in soil, in which accelerated degradation and loss of activity of metam sodium was observed, use of a.

Combinations of certain fumigants may also lead to negative results, especially when fumigants antagonize each other, or their combination produce toxic products in the soil. Combination of metam sodium with certain halogenated fumigants (i.e. 1,3-D, chloropicrin), can lead to generation phytotoxic products that inhibit plant development and production Guo et al. 2005)). Such combinations should therefore be applied sequentially to avoid the risk. Further research is needed to explore additional effective fumigant combinations (Zheng et al. 2004).

12.3.2 Steaming

Soil steaming is performed by applying steam to the soil surface under a suitable soil cover, using "passive". Lower layers are then heated by heat transfer, until the desired temperatures are reached to lethal level at the depth of the cultivated soil layer (Runia 1983). Most plant pathogenic fungi and bacteria are quite sensitive to moderate temperatures (45-65 °C), (Chellemi et al. 2015; Klein et al. 2011a). Hence, pathogens are effectively controlled by steaming. Viruses are inactivated in the range of 55–70 °C, but certain viruses, e.g. tobamo viruses (TMV) can survive even extreme heat. Steaming is limited to a shallow soil layer, especially sandy soil, hence efficacy might be only partial. Achieving effective steaming to deeper layers requires "active steaming" by either the negative pressure system or injected by spikes (Runia 2000). The highly hot temperatures which are non-selective may create a "biological vacuum" in the treated soil, by non-specific reduction of microbial activity. In turn soil soils are vulnerable to infestation by introduced pest. Once destroyed, soil suppressiveness, for example to nematodes and other pathogens, does not easily return (van der Wurff et al. 2010). Alternatively, aerated steaming would be selective heat-treatment by applying air-steam mixtures, at a lower temperature (50–60 °C). Such treatment does eliminate plant pathogens but not the resident soil microorganisms responsible for biological bufferingat lower temperatures leaves part of the saprophytic population uncontrolled (Bollen 1985). All steaming treatments are expensive and complicated, however, can by useful and economical for disinfestation of shallow layers of substrates on various containers. Research has been carried out over the past years in order to reduce energy costs by tuning the duration of steaming according to the type of soil/substrate to be treated and also by designing special equipment for soil steaming. Seventy Years ago, efforts were made to apply a mixture of air and steam mixtures (aerated steam) at lower temperature (50–60 °C). Such treatment eliminates plant pathogens but not the resident soil microorganisms responsible for biological buffering (Baker and Olsen 1960). However, this approach was adopted only for treatment of plant material.

12.3.3 Hot Water

Hot-water treatment consists of applying hot water at 70–95 °C to the soil surface and saturating it in order to raise soil temperatures lethal levels for plant pathogens, pests and weed seeds. This methods was developed in Japan in the late 1970s, and is applied only in protected cultivation. Application consists of a supplying hot water from a boiler through heat resistant irrigation pipes. Hot water is applied under a plastic film in order to reduce heat loss (Nishi et al. 2003). Hot-water treatment was found effective at controlling several fungal and bacterial pathogens, as well as cyst nematodes and non-cyst-forming nematodes, and lethal temperatures could be achieved up to a soil depth of 30 cm. Hot-water treatment also remarkably decreased viruses from the tobamovirus group as well as pathogens causing 'damping-off' in shallow upper layers of the soil (Nishi et al. 2003). Hot-water treatment was effective in controlling *Rosellinia necatrix* in existing Japanese pear trees, when by drip irrigation at 50 °C, (Eguchi et al. 2002). Hot-water treatment at 55 °C for more than 30 min was found to be effective at inactivating tuber pathogens in *Cyperus esculentus*, grown for the production of tiger nut milk (García-Jiménez et al. 2004). Hot-water treatment was improved in Australia and New Zealand for weed control by adding a surfactant (Collins et al. 2002).

12.3.4 Soil Solarization

Soil solarization is applied by covering the soil surface with a clear plastic film to trap solar radiation and accumulate heat. Soil temperatures can be elevated to levels that are lethal to many, but not all plant pathogens. Under the appropriate climatic conditions, solarization can effectively control a wide range of soilborne pests, including fungi, bacteria, weeds, nematodes and insects. The effectiveness of soil solarization in controlling many diseases in a variety of annual crops has been shown under a variety of conditions, soils and agricultural systems in many countries. Numerous solarization studies were reviewed and discussed in Katan (1981), Katan and DeVay (1991), Stapleton (2000), and Gamliel and Katan (2009, 2012) and other. Solarization is usually conducted for 30 days or more, in order to achieve pathogen control down to a depth of 40 cm or more. Temperatures in field soils during solarization are relatively low compared with artificial heating methods such as steaming, although in containerized systems, soil temperature can reach 70 °C. Thus, the effect of soil solarization on living and non-living soil components is more moderate. Indeed, negative side effects, e.g. phytotoxicity and pathogen reinfestation due to the creation of a biological vacuum, have been rarely reported with solarization. In contrast, soil solarization is frequently accompanied with the induced suppressiveness, in which pathogen reestablishment is suppressed after treatment (Gamliel and Katan 1992).

The mode of action of solarization is complex. It affects soilborne pathogens and pests directly through heat inactivation of cellular processes and indirectly by increasing their sensitivity to antagonistic microorganisms and abiotic stresses (Klein et al. 2011b). Solarization also enhances plant growth by increasing the availability of mineral nutrients and improving soil tilth (Chen et al. 1991; DeVay and Katan 1991). The ultimate effectiveness of soil solarization depends on the maximal and minimal temperatures reached and the depth to which the soil is heated, as well as the sensitivity of the targeted pathogens (Chellemi et al. 2015). Root knot and cyst nematodes are sensitive in the upper solarized soil layer, but may survive in deeper soil layers. Most weed seeds, especially annual weeds, are also killed between 50 and 60 °C, but there are some exceptions, for example some perennial grasses and pigweed (Noble et al. 2011).

Soil solarization has also limitations such as the period of 4–6 weeks for the treatment, and a dependence on climate. Moreover, solarization does not control all pathogens. Improved control by solarization is achieved by integration with other physical, chemical, and biological control methods. Such combination can maximize the efficacy and predictability of pathogen control (Gamliel et al. 2005; Shlevin et al. 2018). Additionally, improved plastic films enhance soil heating and improved pathogen control (Gamliel et al. 2005).

12.3.5 Aerobic Soil Disinfestation

Aerobic soil disinfestation (also named “biofumigation”) is based on the generation of toxic volatiles in the soil by certain organic amendments. Some high nitrogen amendments, such as fish meal, blood meal, and feather meal generate ammonia which is toxic to a wide range of pathogens and nematode pests, and can reduce various soil-borne diseases (Bailey and Lazarovits 2003; Lazarovits et al. 2005; Lazarovits and Subbarao 2010). In addition, volatile fatty acids can be emitted by some animal manure. The most common biofumigation method is the cultivation and incorporation into soil of green manure crops that produce precursors of toxic compounds like glucosinolates that are common in members of the Brassicaceae family including rapeseed, broccoli and mustard. Decomposition of glucosinolates results in the release of toxins such as isothiocyanates (Gamliel and Stapleton 1993a). Plant species may produce different glucosinolates. For example, *Brassica napus* primarily has non-ITC releasing glucosinolates while Indian mustard, *B. juncea*, mostly has ITC-releasing glucosinolates (Chellemi et al. 2015). This species has been effective in reducing populations of the wilt bacteria *Ralstonia solanacearum*, various nematodes and fungal pathogens (Matthiessen and Kirkegaard 2006). *Allium* plants are known to release aliphatic disulfides including dimethyl disulfide (Cao and van Bruggen 2001; Chellemi et al. 2015). Besides *Brassica* and

Allium species, plants in many other genera have been reported to have biofumigation properties (Cea Spedes et al. 2006; van Bruggen et al. 2015a). Incorporation of plant materials can also impact disease control through alternative mechanisms besides their production of biotoxic volatile compounds, for example, by microbial activation and changes in microbial community structure and possibly induced resistance.

The effectiveness of biofumigation with green manures is affected by crop species and cultivar, the amount of biomass produced, crop age at the time of incorporation, its moisture content, the size of fragments and the depth and distribution after incorporation into soil. For biofumigation with brassicas, care has to be taken that the plants are incorporated into the soil shortly before flowering when the glucosinolate contents are highest (Stapleton 2004). In addition, factors that favor glucosinolate hydrolysis, namely neutral pH, moderate temperature, and high soil moisture content are important (Chellemi et al. 2015; van Bruggen et al. 2015a).

12.3.6 Anaerobic Soil Disinfestation

Biological soil disinfestation, also called anaerobic soil disinfestation (ASD), involves the incorporation of fresh organic material in moist soil under airtight plastic for 3–6 weeks, depending on the outside temperature (Blok et al. 2000; Runia et al. 2014; Streminska et al. 2014). The carbon source provides a substrate for the proliferation of bacteria, which deplete the available oxygen, so that anaerobic bacteria continue to decompose the carbon source as long as the oxygen remains sufficiently low. Strong to moderate anaerobic conditions, as measured by an oxygen probe (around 1% oxygen in the soil air) or an oxidative reduction potential meter (between −300 and 200 mV), are required during the treatment period (Blok et al. 2000). ASD is effective at controlling a variety of soilborne plant pathogenic fungi, bacteria and nematodes (Blok et al. 2000; Messiha et al. 2007, Butler et al. 2012). The levels of pathogen reduction are similar to those obtained using chemical soil disinfestation against soilborne pathogens and pests. The growth of most weeds is also drastically reduced after anaerobic soil disinfestation. In addition, more nitrogen is available after this treatment. Together, these effects generally result in improved crop growth (van Bruggen et al. 2015a). A disadvantage for organic greenhouse production is the need for plastic sheeting. However, research has been ongoing to replace the usual plastic by films derived from renewable resources (Lamers et al. 2004).

The exact modes of action of anaerobic soil disinfestation are still uncertain (Runia et al. 2014; Streminska et al. 2014). Creation of anaerobic conditions in the soil leads to accumulation of toxic products, including alcohols, aldehydes, organic acids, and other volatile compounds (Huang et al. 2014; Runia et al. 2014), as well as a low pH, which all can impact the survival of soilborne pathogens. In addition to the toxic products produced, biocontrol by anaerobic bacteria such as *Bacillus* and *Clostridium* spp. may contribute to pathogen inactivation (Streminska et al. 2014;

van Bruggen et al. 2015a). A shift in the microbial community composition has been demonstrated (Streminska et al. 2014), while the microbial diversity is unaffected (Messiha et al. 2007). Anaerobic soil disinfestation triggers microbial changes in the soil which are relatively persistent (Messiha et al. 2007). These often result in general disease suppression, which may vary for different pathogens and nematodes (van der Wurff et al. 2011), but that can remain active for a long time (van Bruggen et al. 2015a).

12.3.7 Combining Disinfestation Methods

Integrated management strategy should assemble different methods of control and disease suppression, to overcome the limitations of individual tactics and maximize their potential when combined with other measures. This concept can include the manipulation of biological, chemical, physical, and environmental conditions, to create the optimal platform of disease suppression and incorporate it into the design of cropping systems. The following combination demonstrate the options for added value of combining methods for soil disinfestation while minimizing the impact of disruptive actions for pest control.

12.3.7.1 Combining Solarization with Pesticides

Combining solarization with fumigants, fungicides, bactericides, insecticides or nematicides can enhance the potency, of each component alone. The activity of a pesticide and sensitivity of propagules to the pesticide in soil are increased in heated soil (Gamliel 2012), hence the spectrum of controlled pests can be expanded. The improved pest control may consequently lead to reductions in the pesticide rates and the cost of the treatments. When solarization is combined with volatile pesticide (especially soil fumigants), the volatiles which are captured under the plastic film, can better distribute in the soil for longer exposure. Such combinations can shorten the required period for effective solarization, hence making the disinfestation process more amenable to farmers' practices. Minuto et al. (2000) demonstrated improved control of Fusarium wilt and crown rot of tomato, Verticillium wilt of tomato and Fusarium wilt of sweet basil, all in a situation of high disease incidence, by combination of dazomet at a reduced rate with solarization. The treatment was conducted within a closed greenhouse for a short period of 3 weeks. A similar trend for the combination of solarization with dazomet and metam sodium for the control of Fusarium crown rot of tomato was shown in Israel in both the greenhouse and an open field (Gamliel and Katan 2009). Combining solarization with dazomet was also effective in the control of pink root of onion. In Israel, the combination of solarization with fumigants was applied in areas where solarization alone does not control certain heat-tolerant pathogens such as *M. cannonballus* and *F. oxysporum.* f. sp. *radicis-lycopersici* (Sivan and Chet 1993; Cohen et al. 2000).

Solarization combined with fumigants can also recover soil from accelerated degradation and restore pesticide performance (Gamliel and Triky Dotan 2009). Di Primo et al. (2003) have found that disinfestation of a history soil by steam or solarization eliminated the AD phenomenon. Furthermore, solarization can be combined in order to prevent the development of AD in soils with repeated fumigation. Indeed in the study conducted by Triky-Dotan et al. (2008) AD of MITC did not develop in a soil which is annually solarized combined with MS.

12.3.7.2 Combining Solarization with Organic Amendments

Combination of solarization with the appropriate organic material is based on heating the organic matter in soil together with the biological activities which are involved in its decomposition. As a result the decomposition of certain amendments (e.g. crucifers, aromatic herb plants, chicken manure) results in a generation of toxic volatile compounds (Gamliel and Stapleton 1993b, 1997; Klein et al. 2007; Arriaga et al. 2011).

Possible mechanisms take place during solarization of organic amended soil.

- Increased vapor pressure of compounds present in the liquid soil fraction as the temperature rises, resulting in greater release to the soil atmosphere. The plastic mulch over a solarized soil is important for retaining soil moisture and keeping the volatile compounds in the soil
- changes in the soil's chemical and physical properties, such as pH, which enhance the degradation and release of pH-dependent volatiles such as ammonia (Lazarovits et al. 2005)
- heat-induced breakdown of more complex compounds and heat-induced release of polar molecules from clay particles contained in the solid fraction of soils

The collaborating effect of soil heating, generated toxic compound and shift in microbial activity lead to the enhanced inactivation of a variety of pest propagules (Arriaga et al. 2011; Klein et al. 2011a). The effectiveness of combining solarization and organic amendments can also improve the control of heat-tolerant organisms which are not affected by solarization alone (Gamliel et al. 2000). For example, root-knot nematodes are effectively controlled when solarization was combined with chicken manure in tomato and pepper plants in high temperature areas (Gamliel and Stapleton 1993b; Oka et al. 2007). Disease control by a combination of organic amendments and solarization has been assessed for several decades (Ramirez-Villapudua and Munnecke 1988; Gamliel and Stapleton 1997; Keinath 1996). In recent years, this approach has also been used for organic farming (Oka et al. 2007). Repeated application of organic amendment and solarization over a 2-year period provided good control of both root knot nematodes and annual weeds (Guerrero et al. 2005).

The implementation of solarization combined with the incorporation of organic amendments in greenhouse production should involves adjustments in the cropping system including rotation of the appropriate crops, and development the optimal incorporation method, especially when the crop is grown in substrates packed in containers. Additionally, attention should be paid for the plastic mulching material to hold the volatile compounds which are generated in the soil under the film.

Application of solarization and organic amendments inside the greenhouse conflicts somewhat with common agricultural practices. Since basically only high-cash crops are grown in greenhouses, it is usually not cost-effective to grow a crop which will serve as an organic amendment. Another option is to bring the crop residues from another field. However, with such production systems (e.g. herb farms), crop rotation needs to performed between crops that are susceptible to disease and those serving as organic amendments.

The combination of solarization with organic amendments may result in soil suppressiveness, preventing re-infestation of the soil by introduced pathogens (Klein et al. 2011b). Klein et al. (2012) created soil suppressiveness to root-knot nematodes following herb amendment and soil solarization in greenhouse plots infested with *M. javanica*. This phenomenon may be due to the stimulation of beneficial microbes that affect the pathogens directly or induce resistance in the plants (Klein et al. 2013). As a result of a variety of changes in the soil, the combination of solarization and organic amendments often results in increased crop yield. For example, solarization and chicken compost increased the yield of successive lettuce crops (Gamliel and Stapleton 1993b) and various cole crops (Stevens et al. 1991; Ozores-Hampton et al. 2005). Solarization of cabbage-amended soil significantly increased watermelon yield as a result of gummy stem blight control (Keinath 1996).

12.4 Sanitation and Additional Tools

12.4.1 Disinfestation of Greenhouse Structure

Certain soil borne pathogen (e.g. Fusarium species) generate areal spores, hence can spread inoculum within the components of the greenhouse structure. Additional propagules of the pathogens from previous crops also remain within the walls, poles etc. This inoculum may serve as a source of infestation for the new crop; hence, disinfection of the greenhouse is essential and important complementary tool for assuring a pathogen-free environment for the next crop. Structural disinfestation can be done by spraying a surface active chemical. However, application is not easy and some of the structure components can be sensitive to the chemicals. Solarization of structure by closing the greenhouse for a certain period of time during the appropriate season, is a practical approach. The temperatures inside a closed plastic house during the summer reach 60–70 °C or more, but the relative humidity is very low (Shlevin et al. 2004). Hence, a dry-heating process prevails during structural solarization, which is inferior to wet heating with respect to thermal inactivation of pathogens (Mahrer et al. 1987; Shlevin et al. 2004).

Solarization of the greenhouse structure can be also used for sanitation of other mobile components which are sued for the production, such stakes and pole. These are effectively disinfested from pathogens such as *Didymella lycopersici* (Besri 1983).

12.4.2 Root Destruction at the End of the Crop Season

Soilborne infect plants and produce biomass during crop season. The pathogen biomass within infected plant tissue can reside in the roots function as the primary inoculum for infection of the next crop. Ascospores of *M. cannonballus,* chlamydospores of various Fusarium species, and eggs of root nematodes are produced on infected roots, at the end of the season (Cohen et al. 2000). Therefore, it is essential to reduce propagule formation and minimize population densities of the pathogen in the soil. A practical approach to achieve this goal is to destroy the pathogen in its active form in infected roots and prevent the formation of resting structures. A key for successful root destruction is its execution as soon as crop ends and thereby inhibit their reproduction. The approach of root destruction as a sanitation tool was demonstrated by McIntyre and Horner (1972) for post-crop burning peppermint stems. Later Easton et al. (1975) applied the burning approach in desiccated potato vines to eliminate *V. dahlia*. While these studies were focused on the treating the foliage. Root destruction targets the root in order minimize the deposit of inoculum to the soil. Root destruction is significant especially with pathogens which produce masses of propagules root and even on the foliage such as certain fusarium species (Rekah et al. 2000; Gamliel et al. 1996). Waugh et al. (2003) showed that application of metam sodium and exposure of the roots by cultivation after harvest kills *M. cannonballus* in infected roots, resulting in little or no significant pathogen reproduction relative to untreated controls.

12.5 Concluding Remarks and Future Prospects

Maintaining soil health in intensive greenhouse production is an increasing challenge. Production of crops changes based upon new markets, economics and availability of natural resources. Subsequently, new disease outbreaks emerge, necessitating additional changes to the system and a adjusting ways of mitigation. In a production system with many uncertainties regarding pest emergence and eruption, a systems-based approaches is needed to maintain a healthy and productive crop. Effective management of soilborne plant pathogens responsible for yield and quality reduction is principal. However, the entire pest complex in a given production system will set the priorities and the decision-making which will guide for the order of managing actions. Grower practices can contribute to the increased incidence and severity of soilborne diseases, or for their suppression. These decisions are determined by factors affecting profitability. When disease are of immediate concern their consideration is will take a high priority and guide for the appropriate management strategy. For example, shortening the growing season to apply effective root destruction and minimized inoculum build up can lead to reduced inoculum reservoirs in soil. This procedure, although cutting the immediate profit from shorter harvest season, pays off with lower inoculum for future crops. On the other hand, lack of revenue associated with practices such cover crops, limit the adoption of crop rotations practices and promote the continuation of monocultures.

Browning (1983) describes plant health as the relative freedom of the green plant and its ecosystem from biotic and abiotic stresses that limit its producing to the maximum of its genetic potential over time. Browning also emphasized that plant health is far more than simply the opposite of plant disease, as commonly used by plant pathologists. Soil health management is combines understanding the factors that affect crop health in order to practice and generate the optimal field for crop performance. Such philosophy directs to target all sources of inoculum, during the entire crop production period and the life cycles of the pathogen. This is especially important when targeting the unseen inoculum which can be easily overlooked and neglected. Hence sanitation should be an integrate tool at all stages of crop production. The ultimate goal of sustainable agriculture is adequate supply of quality food feed and fibers without compromising the ability of future generations to maintain life on this planet. Soil disinfestation methods together with other procedure can contribute to the sustainability of the system when fundamentally thought and carefully selected.

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Chapter 13
Biocontrol Agents Against Diseases

Marc Bardin and Massimo Pugliese

Abstract Biological control against plant diseases has been extensively studied in recent decades, leading to the identification and development of a significant number of biocontrol agents with various modes of action. Considerable scientific and industrial investments are needed for the development and the commercialization of these protection tools. One of the main issue for the adoption of biocontrol by farmers is the reliability and stability of its efficacy in field conditions including greenhouses. Efficacy of biocontrol agents (especially that of microbes) is managed by complex factors linked to the changeable environmental conditions encountered in the field (e.g. microclimatic variations) and to farming practices (e.g. compatibility with other control methods, plant fertirrigation). Efficacy is also linked to the biological properties of the biocontrol agent (e.g. ecological competence, quality of the products, mode of application, mechanism of action, persistence of its efficacy) and of the plant pathogen (e.g. type of disease, inoculum pressure, diversity of sensitivity). In this chapter, examples of biocontrol agents used against soil-borne and foliar diseases, their modes of action as well as the factors of their efficacy will be addressed.

Keywords Biocontrol · Mode of action · Efficacy · Durability

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13.1 Introduction

Even though microorganisms have probably always been involved in the protective effect against certain plant diseases, the first documented work concerning the use of a microorganism as a biocontrol agent against a plant pathogen is that of Carl F. von Tubeuf in the 1910s in Germany. It concerns the use of the fungus *Tuberculina maxima* as a hyperparasite of the pine rust fungus *Peridermium strobi* (Maloy and Lang 2003). Further works involving the introduction of microorganisms in the soil against soil-borne pathogens were carried out, with some success, in the 1920s (Cook 1993). Since that time, the biological control against plant pathogens using microorganisms (fungi, oomycetes, bacteria, viruses) has been extensively studied and a large number of microbial agents have been identified.

The development of a new biocontrol agent requires the screening of a large number of candidate strains on multiple criteria. These criteria include the efficacy against the targeted plant pathogen, the ecological competence of the candidate, a method for producing and formulating large amount of the product, a validation of its effect in crop conditions but also economical aspects and safety issues (Kohl et al. 2011).

13.2 Definitions and Strategy of Biocontrol in Greenhouse Crops

The terms 'biological control' and 'biocontrol' are considered as synonymous and we used indifferently the two terms in the rest of the chapter. According to Eilenberg et al. (Eilenberg et al. 2001), biocontrol is "the use of living organisms to suppress the population density or impact of a specific pest organism, making it less abundant or less damaging than it would otherwise be". This definition of biocontrol was simplified by van Lenteren et al. (van Lenteren et al. 2018) as "the use of a population of one organism to reduce the population of another organism". This definition, which limits the extent of biocontrol agents to living organisms, will be used throughout this chapter, with however examples of biocontrol using natural products such as plant extracts.

Three strategies of use of biocontrol agents are generally distinguished: classical biological control, conservation biological control and augmentative (or inundation) biological control (Eilenberg et al. 2001). Biological control of plant diseases relies heavily on this latter strategy which requires, in most countries of the world, the use of registered commercial products. The other two strategies, which relies respectively on the acclimation and the promotion of natural enemies in a given crop or environment, are used primarily for the biological control of invertebrate pests using predators or parasitoids.

13.3 Biocontrol against Plant Diseases

Producers of biocontrol agents are grouped in the International Biocontrol Manufacturer's Association (IBMA, http://www.ibma-global.org/) which brings together more than 250 companies spread over all continents. For a long time, the production of biocontrol agents has concerned small to medium-sized companies but more recently large agrochemical companies are getting involved. According to Gwynn (Gwynn 2014), 44 microorganisms are commercially developed in the word against plant diseases of which 25 are fungi, yeasts or oomycetes, 14 are bacteria or actinomycetes and 5 are viruses. A recent study from (van Lenteren et al. 2018) have identified 91 microbial biocontrol agents (49 fungi or yeast or oomycetes, 37 bacteria or actinomycetes and 5 viruses or phages) registered against plant pathogens in Australia, Brazil, Canada, European Union, Japan, New-Zealand and USA. This number of microbials is probably underestimated due to the lack of data in some countries, in particular in China and India, where the biocontrol industry is very dynamic. Moreover, a similar strain of a given microbe can be commercialized with different names, either because it is formulated differently or because it is distributed by different companies.

13.3.1 Examples of Biocontrol Agents Used Against Soil-Borne Diseases

Fusarium oxysporum, Pythium spp., *Phytophthora* spp., *Rhizoctonia* spp. and *Sclerotinia* spp. are among the main soil-borne problems encountered in greenhouses, particularly on tomato, pepper, cucurbits, leafy vegetables and strawberry (Katan 2017; Gilardi et al. 2018; see Chap. 5, Fungal diseases in this book). Based on a literature survey, we can estimate at about 200 strains that have shown efficacy against soil-borne plant pathogens in the last 80 years. Some of these strains, such as the fungi *Coniothyrium minitans*, *Trichoderma* spp. and the bacteria *Bacillus* spp., *Pseudomonas* spp. have been successfully introduced into the market and used since several years (Gwynn 2014; O'Brien 2017; van Lenteren et al. 2018).

Fertilizers which contain biocontrol agents are also present in the market and are sometime used to control soil-borne pathogens. Although for some strains, like *Trichoderma* spp., the distinction between plant protection products and biofertilizers is difficult because they possess both activities, these biofertilizers may fail to give any efficacy because the viability and concentration of microorganisms is not guaranteed as for plant protection products. This chapter will not consider microorganisms applied as biofertilizers. Examples of commercialized products are given below.

The fungus *Paraphaeosphaeria (Coniothyrium) minitans* is worldwide distributed and it is a highly specialized antifungal agent (strain CON/M/91-08) that targets sclerotia of *Sclerotinia sclerotiorum* and *S. minor* on high value vegetable crops as lettuce, beans, peas, but also in sunflower, oilseed rape (Chitrampalam et al. 2008; Zeng et al. 2012). In nature it occurs also on *S. trifoliorum* and other *Sclerotinia* species. Spore germination, mycelial growth and sclerotial infection take place at temperatures between 5 and 25 °C. It is applied by spraying onto soil and incorporating into upper soil layer before planting and it can survive and spread in the soil for at least 2 years. This product can also be applied to the soil 3–4 months prior to the onset of disease and after harvest, by applying the product on crop residues (Chitrampalam et al. 2008; Zeng et al. 2012).

Gliocladium catenulatum (Clonostachys rosea f.sp. catenulata) strain J1446 is another example of naturally-occurring saprophytic fungus which is widespread in the environment. It is used to control damping-off, seed- root- and stem-rots caused by *Rhizoctonia*, *Pythium, Phytophthora*, and wilt diseases caused by *Fusarium* and *Verticillium*. It is applied at sowing, potting or transplanting and 2–8 weeks later by soil incorporation, soil drench, foliar spray, and also by dipping of cuttings, bulbs, and tubers (Chatterton et al. 2008; Cerkauskas 2017).

Trichoderma strains are applied against a wide spectrum of plant pathogens, including soil-borne pathogens (Samuels and Hebbar 2015). *Trichoderma* is a genus of fungi worldwide distributed, frequently isolated in both temperate and tropical soils and colonizing also wood and plant materials, being soil inhabitants and good colonizers of organic matter. Several species and strains belonging to the genus *Trichoderma* have been identified so far as biocontrol agents of plant diseases, including nematodes, and registered as biocontrol agents: *T. asperellum, T. atroviride, T. harzianum, T. gamsii, T. polysporum*, *T. viride,* etc. Commercially available strains include *T. asperellum* ICC012 (formerly *T. harzianum*), T25 (formerly *T. viride*), TV1 (formerly *T. harzianum*), *T. asperellum* SF 04 (URM) 5911, T211 and T34, *T. atroviridae* SKT-1, IMI 206040 (formerly *T. harzianum*) and T11 (formerly *T. harzianum*), *T. gamsii* ICC080 (formerly *T. viride*), *T. hamatum* TH382, *T. harzianum* KRL-AG2 (syn. T22), ESALQ-1306, IBL F006, ITEM 908 and T-39, *T. virens* G-41 and GL-21 (formerly *Gliocladium virens*). Each strain shows specific characteristics and adaptation to the environment, some of them being very good soil or rhizosphere colonizers, and showed antifungal activity towards a broad spectrum of plant pathogens, i.e. *Colletotrichum, Fusarium, Pythium, Phytophthora, Rhizoctonia* (Vos et al. 2014; Gilardi et al. 2016; Deketelaere et al. 2017). To be effective the *Trichoderma* strains should be carefully chosen according to their adaptation to the specific soil characteristics and to their mechanisms of action. Few weeks after its application the concentration of exogenous *Trichoderma* tends to decrease to the basal level of that specific soil, consequently insufficient concentration in the soil, poor viability of conidia, short time for activity and too high disease pressure may cause a failure in the control of soil-borne pathogens (Vos et al. 2014). In order to improve the efficacy of *Trichoderma* and other soil-colonizing strains of biocontrol agents, the combination with other soil disinfestation practices is suggested, such as inoculation of the biocontrol agent after soil solarization, steaming, anaerobic soil disinfestation or biofumigation (Porras et al. 2007; Galletti et al. 2008).

Nonpathogenic strains of *Fusarium oxysporum* have been shown to control *Fusarium* wilt in many crops, including basil, cucumber, melon, tomato, spinach and watermelon (Hoitink and Locke 2013), and several papers have also reported efficacy against *Pythium ultimum, Phytophthora capsici* and *Verticillium dahliae* (Alabouvette et al. 2009; Deketelaere et al. 2017). Despite the idea of using non-pathogenic strains of *F. oxysporum* to control *Fusarium* diseases is known since the 1970s (Garibaldi et al. 1986), at present only the strain IF23 is sold as fertilizer.

The endophytic fungus *Muscodor albus* (strain QST 20799), recently registered in Europe, produces volatile organic compounds with broad spectrum antimicrobial activity; it is an effective biofumigant against various soil-borne plant pathogens such as *Pythium ultimum, Phytophthora cinnamomi, Rhizoctonia solani, Sclerotinia sclerotiorum* and *Verticillium dahliae* (Strobel 2006; Mercier and Jimènez 2009).

The oomycete *Pythium oligandrum* M1 is a mycoparasite of plant pathogenic fungi which is active in and around seeds and in the rhizosphere of plants, thereby suppressing the growth of several soil-borne plant pathogenic fungi, including *Fusarium, Pythium, Sclerotinia* and *Sclerotium* (Vos et al. 2014). It is applied as seed dressing, pre-plant soak, overhead spray, soil drench, or through irrigation system application and it requires a moist environment and a temperature range of 20–35 °C during the infection period, which can last for 3–4 h (Deketelaere et al. 2017).

Streptomyces spp. and *S. lydicus* are ubiquitous and naturally-occurring bacteria that are commonly found in soil environments. *S. griseoviridis* K61 and *S. lydicus* strains ATCC 554456 and WYEC 108 are used to control *Fusarium, Rhizoctonia, Pythium, Phytophthora, Monosporascus, Armillaria, Sclerotinia, Verticillium, Geotrichum*, and other plant pathogenic fungi (Palaniyandi et al. 2013; Deketelaere et al. 2017). They are applied as a soil mix/drench to potted plants. It can also be applied in nursery. In this case, after successfully colonizing the tip of the roots, it can continuously protect the plant (Palaniyandi et al. 2013).

Rhizobacteria, like those belonging to the genera *Bacillus* and *Pseudomonas,* are well known for their antagonistic effects and their ability to trigger induced systemic resistance in the plants (Benedui et al. 2012). *Bacillus subtilis*, *B. amyloliquefasciens, B. firmus* and *B. pumilus* are among the beneficial bacteria mostly exploited as biopesticides to control plant diseases, including nematodes. Commercially available strains to control soil-borne pathogens include the strains MBI 600, AH2 and D747 of *B. amyloliquefaciens* and *B. subtilis* GB03. They are Gram positive rod-shaped bacteria that can form a protective endospore that can tolerate extreme environmental conditions. *Bacillus* spp. are able to control fungal pathogens by competition at the root surface, direct antibiosis and induced resistance (Eljounaidi et al. 2016; Deketelaere et al. 2017; Shafi et al. 2017). They are used either as soil or as root application before transplanting and the ability of a specific strain to colonize and permanently establish on the roots of a specific crop is crucial and sometime it is cultivar specific (Handelsman and Stabb 1996). Application of *Bacillus* spp. should preferably target the rhizosphere of seedlings, because it should colonize the roots in order to be active and consequently its efficacy may be low in case of high pathogen inoculum in the soil or against very aggressive soil-borne strains (Gilardi et al. 2016). Application in combination with other biocontrol agents targeting the redution of soil-borne population in the soil is a way to improve its efficacy (Xu et al. 2011). Furthermore, *Bacillus* strains have a good efficacy when applied in hydroponic systems and by fertigation (Lee and Lee 2015).

Pseudomonas spp. are aerobic, gram-negative bacteria, ubiquitous in agricultural soils, and are well adapted to growing in the rhizosphere. They are commonly used to treat seeds, tubers, bulbs or roots of plants before planting (Eljounaidi et al. 2016). They grow rapidly, utilize seed and root exudates, colonize and multiply in the rhizosphere and spermosphere environments and may also produce bioactive metabolites. They have also a good compatibility with fungicides, but, compared to *Bacillus*, they are unable to produce resting spores (Salman and Abuamsha 2012; Jayamma et al. 2013). Commercially available strains include *Burkholderia (Pseudomonas) cepacia* M54 and J82, *P. chlororaphis* 63-28 and MA342, *P. fluorescens* G 7090, *Pseudomonas* sp. DSMZ 13134.

13.3.2 Examples of Biocontrol Agents Used Against Foliar Diseases

A bibliographical study conducted in the framework of the European project ENDURE (European Network for Durable Exploitation of Crop Protection Strategies) established that 157 different species of microorganisms have been described for their effectiveness against five of the major airborne plant diseases, all crops combined (*Botrytis*-incited diseases, powdery mildews, rusts, downy mildews including *Phytophthora infestans* and brown rot) between 1973 and 2009 (Nicot et al. 2011), among which are important diseases of greenhouse crops (see Chap. 5, *Fungal diseases* in this book). Among these microorganisms, 29 fungal/oomycetes species and 18 bacterial species have proven to have a significant effect in the field to control at least one of these five major airborne diseases.

Powdery mildew and *Botrytis*-incited diseases are among the main airborne phytosanitary problems encountered in greenhouses, particularly on tomato. Biocontrol has been widely studied since these diseases represent an important economical market and a wide range of microbial, botanicals and minerals have been reported to exhibit inhibitory activity against these fungi (Bélanger and Labbé 2002; Nicot et al. 2016). It has led to the development of commercial products registered in various countries of the word.

Several fungi (e.g. *Ampelomyces quisqualis*, *Pseudozyma flocculosa*), bacteria (e.g. *Bacillus subtilis*, *B. amyloliquefaciens*) or plant extracts (e.g. *Fallopia* (*Reynoutria*) *sacchalinensis*, *Rheum officinale*) are for instance registered to control powdery mildews on various crops, including greenhouse crops (Paulitz and Belanger 2001; Gwynn 2014; van Lenteren et al. 2018; Yang et al. 2008). The fungus *A. quisqualis* AQ10 is one of the first biocontrol agents registered and used at a commercial scale against plant diseases (Hofstein et al. 1996). It has been authorized in the USA in 1994 for controlling powdery mildews on various host plants. It acts as an intracellular mycoparasite of powdery mildews and it develops in the mycelium of the fungus and inhibit mycelial growth, sporulation and conidial germination (Sztejnberg et al. 1989; Kiss et al. 2004). A new strain of *A. quisqualis* (ITA3) was recently found to be more effective against powdery mildew than the commercial one (Angeli et al. 2017). The plant extract from *F. sacchalinensis* has also been widely studied and proved to be effective against several species of powdery mildew on various greenhouse crops (Bardin et al. 2008; Bokshi et al. 2008; Konstantinidou-Doltsinis et al. 2006; Pasini et al. 1997; Petsikos-Panayotarou et al. 2002). This plant extract is also approved against grey mould on tomato or pepper in several countries including USA (Nicot et al. 2016). The mode of action of this plant extract is associated with plant-induced resistance (Daayf et al. 1997, 2000; Fofana et al. 2002; Randoux et al. 2006) but it has also been shown to act directly on the fungi through the inhibition of conidia germination (Randoux et al. 2006; Bardin et al. 2015). Various salts (i.e. silicon, sodium or potassium bicarbonate, calcium chloride, calcium nitrate, potassium phosphate) have also proved a high level of efficacy against this disease on various crops (Fauteux et al. 2005; Ehret et al. 2002; Fallik et al. 1997; Reuveni et al. 1996) and some of them are now registered in several countries. Potassium bicarbonate is for instance available in European Union to control powdery mildews on greenhouse crops such as tomato, pepper, eggplant, cucumber, zucchini or strawberry.

Numerous commercial biocontrol agents, having different mode of action, are also now available to control *Botrytis*-incited diseases. At least 14 microbial-based products and 2 botanical-based products are registered all around the word to control this pathogen (Nicot et al. 2016). This includes various fungi or yeasts (e.g., *Chlonostachys*, *Gliocladium, Trichoderma*, *Ulocladium*, *Aureobasidium*, *Candida*) and various bacteria or actinomycetes (e.g. *Bacillus, Pseudomonas*, *Streptomyces*). However, vigilance is required to ensure the durability of biocontrol against this fungus as it has shown to be able to develop resistance to antibiotic-producing biocontrol agents (Bardin et al. 2015; Ajouz et al. 2010; Fillinger et al. 2012; Li and Leifert 1994).

Few botanical or microbial species have been reported as having successful effect against oomycetes species causing diseases on vegetables (Nicot et al. 2011). Only a small number of biocontrol products (*Bacillus pumilus*, *B. subtilis* and *B. amyloliquefaciens*-based products) are commercialized so far worldwide to control downy mildew (Gwynn 2014). Potassium phosphonate is also registered against downy mildew on various vegetable crops including lettuce, cucumber, melon and tomato.

Various microbials with potential biocontrol effect against *Didymella*-incited diseases have been identified (Utkhede and Bogdanoff 2003; Utkhede and Koch 2002, 2004; Zhao et al. 2012) and biocontrol agents (i.e. *Gliocladium catenulatum* or *Trichoderma* spp. based-product) are registered worldwide against *D. bryoniae* (Gwynn 2014).

Virus-based products have also been developed against aerial plant diseases, such as viral or bacterial diseases. For instance, a weak strain of Zucchini Yellow Mosaic Virus (ZYMV-WK) has been isolated in 1986 in France and is used for cross-protection against ZYMV (Desbiez and Lecoq 1997). This strain is registered to protect melon and cucumber in some European countries, including France. Bacteriophages are registered in USA and Canada to protect tomato and pepper against various bacterial diseases such as *Xanthomonas campestris* pv. v*esicatoria*, *Pseudomonas syringae* pv. *tomato* or *Clavibacter michiganensis* subsp. *michiganensis*. In this case, the protective mechanism is related to lysis of bacterial cells infected with the bacteriophage which is released and can infect other bacterial cells (Alvarez and Biosca 2017).

13.4 Modes of Action of Biocontrol Agents

Various modes of action are involved in the protective effect of biocontrol agents against plant pathogens. Although the number of studies done on this subject is important, knowledge of the precise mode of action of biocontrol agents is still partial. However, it is generally admitted that there are three main ways for a biocontrol agent to control a plant pathogen (Alabouvette et al. 2009): first, by acting directly on the plant pathogen, through antibiosis, competition for nutrient or space, or parasitism; secondly by interfering with the mechanisms of pathogenesis of the plant pathogen, and thirdly by modifying the interaction of the plant pathogen with its plant host for instance through the induction of local or systemic acquired resistance.

These modes of action are not incompatible, they can instead be complementary and a single strain of a biocontrol agent may act with several of these modes of action and the final observed effect on a plant pathogen can be the result of their combination. The most studied case concerns the fungus *Trichoderma*, for which different modes of action have been established for a given strain (Lorito et al. 1993; Elad 2000). Similarly, the strain QST713 of *Bacillus subtilis* acts *via* antibiosis and induced resistance to control different plant pathogens such as *Botrytis cinerea*, *Pythium ultimum*, *Rhizoctonia solani*, *Plasmodiophora brassicae* or causal agents of powdery mildew (Paulitz and Belanger 2001; Lahlali et al. 2013). A given biocontrol agent may therefore operate through several mechanisms possibly expressed successively, simultaneously or synergistically and depending on the environmental conditions encountered. Nevertheless, it is not yet clear if biocontrol agents have a dominant mode of action and under what conditions they switch from a mode of action to another.

13.4.1 Direct Effect on the Plant Pathogen

Antibiosis is probably one of the most studied mode of action for biocontrol agents, possibly because it is easy to demonstrate in laboratory conditions by dual culture method on nutrient agar (Fig. 13.1a, b). In this case, the biocontrol agent produces toxic secondary metabolites for the target plant pathogen. These metabolites

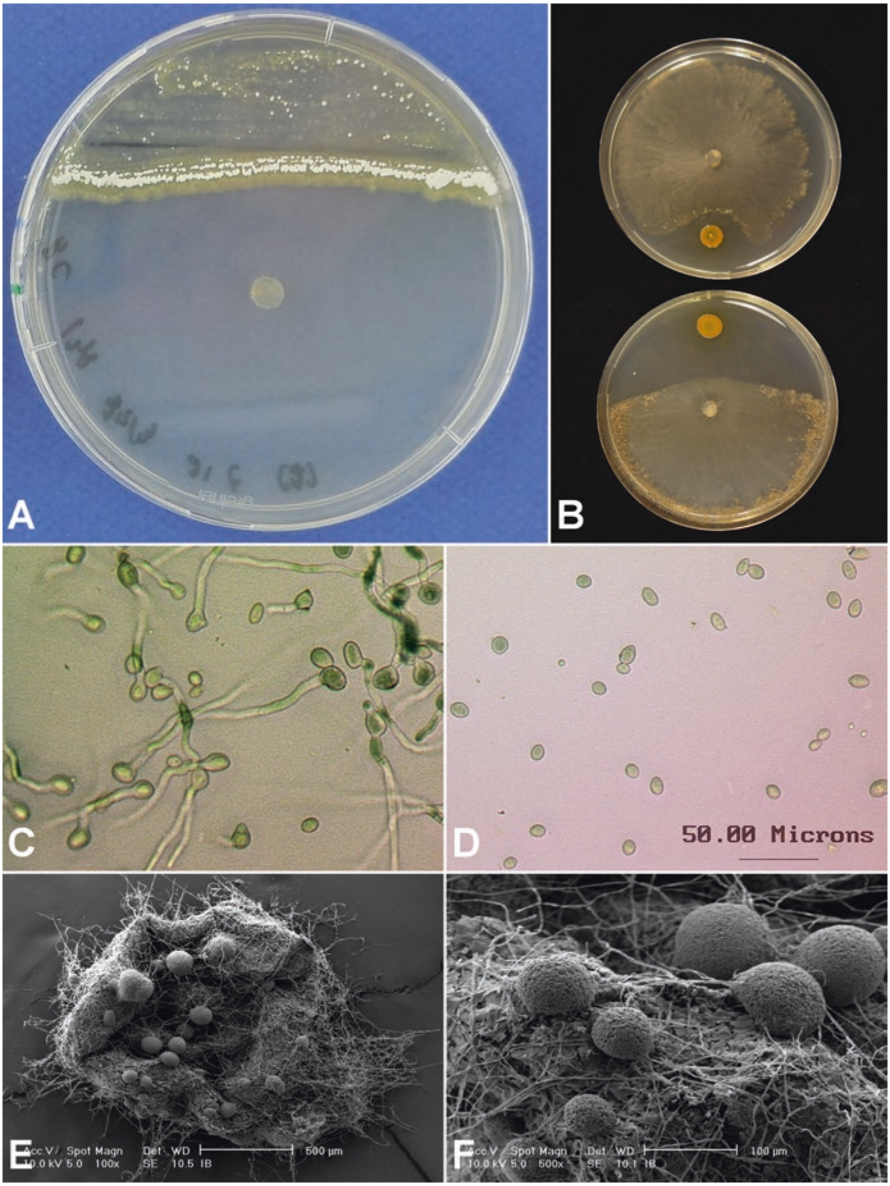

Fig. 13.1 Dual culture on nutrient agar media to reveal the antibiosis properties of various bacterial strains against *Botrytis cinerea* (**a**, **b**), inhibition of germination of spores of *B. cinerea* induced by metabolites produced by biocontrol agents (**c**: control, **d**: with an antibiotic produced by a biocontrol agent), hyperparasitism of sclerotia of *Sclerotinia sclerotiorum* by *Coniothyrium* (*Paraphaeosphaeria*) *minitans* (**e**, **f**)

produced at low concentrations may inhibit germination, mycelial growth and / or sporulation of pathogens (Fig. 13.1c, d). However, the production of antibiotic compounds depends on many environmental factors in which the microorganism is challenged, such as the water potential, the pH, the temperature and the type of nutrient (Whipps 1987). Substances responsible for antibiosis could be characterized in strains belonging to various microbial species and the genes involved in the production of some of these substances have been identified (Duffy et al. 2003; Raaijmakers et al. 2002). There are many examples of bacteria and fungi producing antimicrobial compounds, including the genera *Bacillus*, *Pseudomonas*, *Streptomyces* and *Trichoderma*. This mode of action is quite similar to that of molecules used in chemical control. It can therefore be very effective in inhibiting the development of a plant pathogen, but it may raise issues concerning the safety of the molecules produced (for environment, users and consumers), and also concerning the emergence of resistant strains of the plant pathogen to the biocontrol agent (Ajouz et al. 2010; Li and Leifert 1994).

In the case of hyperparasitism, the antagonist agent is a parasite that specifically recognizes its microbial target, penetrates through the cells and causes its destruction via the colonization of its organs. For example, *Coniothyrium* (*Paraphaeosphaeria*) *minitans* is able to parasite the sclerotia of various species of *Sclerotinia* (Fig. 13.1e, f), of *B. cinerea* and *Sclerotium* (Whipps and Gerlagh 1992; Bennett et al. 2006). This fungus produces enzymes that can degrade cell-wall of the target pathogen. The fungus *Ampelomyces quisqualis* specifically parasitizes the fungi responsible for powdery mildews (Kiss et al. 2011). The use of a hyperparasite in biocontrol generally requires a direct contact with the pathogen and a rapid action to ensure its destruction.

Some microorganisms (bacteria, yeasts, filamentous fungi) can inhibit the germination of plant pathogen conidia through competition in the environment for nutrients such as nitrogen, carbon, or macro- or micronutrients. This mode of action can be particularly effective against fungi whose spores need a source of nutrients to initiate their germination (as for example *B. cinerea*). In this case, the uptake of nutrient in the environment by the biocontrol agent leads to a reduced spore germination of the pathogen and it can also lead to a reduced mycelial growth. Thus the number of infections and the expansion of the lesions can be reduced (Blakeman and Fokkema 1982). Competition for nutrients or space has been established for different yeasts applied to apples in post-harvest treatments against *B. cinerea* such as *Candida oleophila* (Mercier and Wilson 1994). *Trichoderma harzianum* strain T39 is also able to inhibit conidial germination of *B. cinerea* by competing for nutrients at early stages of infection (Zimand et al. 1996). Competition for carbon between pathogenic and nonpathogenic *F. oxysporum* has proved to be one of the main modes of action of non-pathogenic biocontrol strains of *F. oxysporum* (Alabouvette et al. 2009). The study of the protective effect of the non-pathogenic *F. oxysporum* strain MSA 35 has shown that it is related to the interaction with ectosymbiotic bacteria, suggesting that the antagonistic effect of this strain is not a strict fungal trait (Minerdi et al. 2008).

13.4.2 Interference with the Pathogenicity Process

During the first steps of the host-pathogen interaction, synthesis of hydrolytic enzymes (e.g. cutinases, pectinases, cellulases...) by pathogens and in particular by fungi is essential for the success of the infection process (Agrios 2005). Biocontrol agents may interfere with fungal pathogenicity by inhibiting or degrading certain hydrolytic enzymes (Duffy et al. 2003). Interference with the pathogenicity of *B. cinerea* has for example been described with the strain T39 of *T. harzianum* where the activity of some pectinolytic enzymes produced by the pathogen was reduced in the presence of the biocontrol fungus, reducing the penetration of *B. cinerea* into host tissues and consequently the impact of the disease (Kapat et al. 1998). Other biocontrol agents can have an indirect effect on the pathogen, for example by modifying the pH of the medium. Thus the bacteria *B. pumilus* and *P. fluorescens*, by changing the ambient pH at the infection site, result in a reduction of the effectiveness of degrading enzymes plant tissues produced by *B. cinerea* (Swadling and Jeffries 1998). Microorganisms degrading oxalic acid, a molecule produced by *S. sclerotiorum* or *B. cinerea* during their interaction with the plant, have been shown to protect plants against attacks by these pathogens (Schoonbeek et al. 2007).

Some bacteria have the ability to change the surface characteristics of plant leaves by synthesizing surface-active compounds such as surfactins or other lipopeptides (Ongena and Jacques 2008). This can have the effect of hampering the process of attachment and growth of pathogens on the leaves. For example, bacteria of the genus *Bacillus* spp. and *Pseudomonas* spp. are able to modify the wettability of the leaf surface and thereby interfere with the development of certain plant pathogens (Bunster et al. 1989). The enlargement of water drops on the leaves, and consequently their quicker drying, may prevent the appearance of favorable conditions for the development of certain plant pathogens.

13.4.3 Induced Resistance

This mode of action is currently the subject of abundant research and tremendous progress are made in understanding the mechanisms involved. Many microorganisms, plant extracts, natural or synthetic compounds have been shown to induce resistance mechanisms in plants (Lyon 2014; Tayeh et al. 2014; Walters and Bennett 2014). Examples of plant-beneficial microorganisms are bacteria of the genus *Bacillus* or *Pseudomonas* or fungi of the genus *Trichoderma* or mycorrhizal fungi (Beardon et al. 2014). Induced resistance is initiated by the recognition of a signal that will trigger a cascade of events that may lead to systemic resistance of the plant. Intercellular communication is ensured in the plant by signaling networks involving the plant defence hormones, salicylic acid (SA), jasmonic acid (JA) and ethylene (ET). Beneficial microorganisms such as plant growth promoting rhizobacteria (PGPR) or fungi (PGPF) would preferentially activate the JA-dependent pathway and/or ET-dependent pathway in various plant species (Shoresh et al. 2010; Pieterse et al. 2014). However, *Trichoderma* spp. has shown to activate both SA and JA/ET pathways (Hermosa et al. 2012) and the long-term response to *Trichoderma* in tomato involved SA-signaling (Tucci et al. 2011).

Induced resistance can be established in different ways in the plant: thickening of the parietal structures reinforcing their role of physical barrier (e.g. callose deposition), stimulation of secondary metabolic pathways allowing the synthesis of antimicrobial substances (e.g. phytoalexins), accumulation of defense proteins (Pathogenesis Related proteins) (Shoresh et al. 2010; Pieterse et al. 2014). However, the beneficial effect of induced resistance in plant vary with the genetic background of the host plant, either with beneficial microorganisms such as *Trichoderma* (Tucci et al. 2011) or with organic or mineral compounds (Maisonneuve et al. 2013).

13.5 Determinant of Efficacy

One of the main issue for the adoption of biocontrol by farmers is the reliability and stability of its efficacy in the greenhouse. The protective efficacy of biocontrol agents, and particularly microbial, is generally considered variable and inconsistent under field conditions (Nicot et al. 2011). Most studies report good efficacy of biocontrol agents when experiments were conducted under controlled conditions but efficacy of these biocontrol agents in the field is more problematic being less effective or completely ineffective when introduced under commercial conditions (Guetsky et al. 2001) as exemplified with the biocontrol agent *T. harzianum* T39 applied alone in different tomato and cucumber greenhouses to control *B. cinerea* (Shtienberg and Elad 1997). This biocontrol agent was effective in most cases, sometimes as effective as the fungicide of reference, but in a few cases it was completely ineffective. Similarly, although many strains of *Pseudomonas* exhibit good control performance in laboratory studies, they often perform inconsistently in diverse field situations (Mark et al. 2006). However, examples of stable efficacy of biocontrol agents have been described in the field (Calvo-Garrido et al. 2013). Efficacy of biocontrol agents (especially that of microbes) is managed by complex factors linked to the changeable environmental conditions encountered in the field, to the biological properties of the biocontrol agent and of the plant pathogen and to farming practices. The effect of farming practices on the efficacy of biocontrol agents will be treated in the part 6 of this manuscript. Therefore, variability of efficacy is generally attributed to climatic variations, lack of ecological competence of the biocontrol agents, and/or unstable quality of the products (Ruocco et al. 2011; Elad and Stewart 2004). For example in the phyllosphere, nutrient resources are poor and biocontrol agents are subject to water flow, temperature fluctuations, vapor pressure, direct exposure to UV and infrared radiations, and may have to compete with other microorganisms. According to Mark et al. (Mark et al. 2006) the lack of consistency of efficacy of *Pseudomonas* strains used as biocontrol agents in the rhizosphere may be a result of external factors such as soil or climatic conditions, and of intrinsic traits of the antagonistic microbe, such as variable production of required metabolites or poor root colonization under certain conditions. However, reduction of efficacy in the field may also result from the diversity of sensitivity of plant pathogens to biocontrol agents, with the existence of less sensitive isolates in natural populations of plant pathogens (Bardin et al. 2015). Contrary to pests (Siegwart et al. 2015), the durability of efficacy of biological control against plant pathogens has only been slightly studied and there is no publication proving loss of efficacy due to resistance development in practice.

13.5.1 Environmental Conditions

The effect of microclimate on the efficacy of biocontrol agents have been evaluated in controlled conditions by several authors, showing up that both temperature and relative humidity are generally critical factors. Microclimatic conditions may influence survival, establishment and activity of microbial agents on or around the plant (Morandi et al. 2008). In some cases, even small variations in microclimatic conditions can have a significant effect on the efficacy of biocontrol. For example, changes by 4 °C in temperature and by 5% in relative humidity can drastically modify the protective effect of microbial strains against *B. cinerea* on bean (Hannusch and Boland 1996). Water availability can also have a major effect on the efficacy of *C. minitans* to parasitize sclerotia of the plant pathogen *S. sclerotiorum* (Jones et al. 2011). However, in desert ecosystem, a successful control of *S. minor* on lettuce can be achieved by increasing the application rates of the biocontrol agent *C. minitans* (Chitrampalam et al. 2010a). In specific cases, such as the protection of pruning wounds, the impact of the microclimate may be less important because the biocontrol agent is protected within the wound from fluctuations of ambient relative humidity (Nicot et al. 2002).

In addition to microclimatic fluctuations, biocontrol agents are subjected to variations in nutrient availability that may affect their efficacy on the plant. The chemical exudates present at the root level or at the surface of the plants may change, and these qualitative and quantitative modifications in composition may directly affect the introduced microflora. Moreover an introduced biocontrol agent should compete with the natural microbiota that may change overtime, in a generally limiting nutritional context.

13.5.2 Ecological Competence of Microorganisms, Dose Effect, Timing of Applications and Quality of the Preparations

The protective efficacy of a biocontrol agent depends on factors related to the product itself, such as its mode of application, its mechanism of action, the persistence of its efficacy, and especially for microbes, its ecological competence (i.e. tolerance to biotic and abiotic environmental stress). The ability to tolerate water stress could for example be an important factor of efficacy of a biocontrol agent during its interaction with a plant pathogen (Kohl and Molhoek 2001). These factors can affect the persistence of the biocontrol agent on the plant or in the soil after its application.

In the case of microbial, the product must contain a sufficient amount of living cells after production and it should be maintained properly during the whole distribution process in order to have a sufficient number at the time of application by the farmer. Thus, the dose of biocontrol agent used can affect the protective efficacy, as for example in the case of the interaction between strains of *Pseudomonas* sp. and *B. cinerea* (Bouaoud et al. 2018). The amount of living cells depends on the intrinsic survival capacity of the microorganism (ecological competence) and it also depends on its formulation that is designed to increase its shelf life. The protective efficacy of the biocontrol agent also depends on the conditions of transport and storage of the product. Exposure, even temporary, to excessive temperatures, can severely degrade the product.

In addition to the number of living cells, the efficacy of a biocontrol agent depends on its physiological state and on its growth rate once applied. The purity of the product is also an important factor to ensure the stability of its efficacy over time. The accurate distribution of the biocontrol agent on the target (leaves, roots, wounds…), its ability to survive or even to multiply are also essential qualities to ensure a stable efficacy over time. These factors depend on the specific characteristics of the microorganisms but they can be modified and improved by the formulation of the product (Mokiou and Magan 2008; Vemmer and Patel 2013). An important benefit of microbial biocontrol agents is that they can multiply and colonize the surfaces to be protected (leaf surfaces, soil, wounds …) and thus compensate for any lack of precision of the application. But ecological competence of a given microorganism is often only partially known.

An important part of the protective efficacy of a biocontrol agent is related to its mechanism of action. The different modes of action identified above will influence how it is used in practice. Antibiosis can cause a rapid and curative effect against a plant pathogen. In addition, the biocontrol agent can act distantly if it produces antimicrobial volatiles (Boukaew et al. 2017). In this case, a direct contact between the biocontrol agent and cells of the plant pathogen agent would not be required. In comparison, modes of action such as competition for nutrient or space, or induction of plant resistance have essentially a preventive effect. Induction of resistance in the plant requires for instance a delay between the application of the biocontrol agent and the development of a resistance in the plant. Hyperparasitism has a predominantly preventive effect when it targets the survival forms of a plant pathogen, as in the case of *C. minitans* used to destroy the sclerotia of *S. sclerotiorum* in the soil (Whipps and Gerlagh 1992). But when the biocontrol agent acts on the active cells of the plant pathogen, it will exert a curative effect. In this last case, the protective efficacy of the biocontrol agent will depend on the relative growth rate of the pathogen on its host plant and of the biocontrol agent itself (Caffi et al. 2013; Kiss et al. 2004). The efficacy of the protection can also benefit from the combination of biocontrol agents which are, individually, only partially effective (Katan 2017).

By combining them, an additive or even synergistic effect is expected, especially if they have different modes of action.

13.5.3 Targeted Plant Pathogen

The characteristics of the plant pathogen and the type of disease to be controlled have an influence on the protective efficacy of a biocontrol agent. Polycyclic diseases, for which epidemic rate is generally important, are probably more complicated to contain than monocyclic diseases for which the amount of inoculum does not increase significantly during the season. The amount of inoculum of the pathogen is also a factor determining the protective efficacy of a biocontrol agent. Many studies have evaluated the relationship between inoculum density and efficacy of biocontrol. Generally, when the inoculum pressure of the pathogen is high, the effectiveness of the biocontrol agents is reduced. Conversely, a single application of *C. minitans* has shown to reduce the incidence of *S. sclerotiorum* on lettuce, even at high sclerotium densities (Chitrampalam et al. 2010b)

Recent work also shows that there is a diversity in the efficacy of biocontrol tools according to the strains of pathogens (Bardin et al. 2015). Thus, the diversity in the sensitivity of various strains of a pathogen to a biocontrol agent, and its ability to evolve towards resistance, must be taken into account to ensure an effective and durable protection.

13.6 Use of Biocontrol Agents in Integrated Pest Management Strategies

The use of biocontrol agents requires that they can be effectively incorporated into complex integrated pest management (IPM) schemes. Issues related to their compatibility with other control methods is for instance crucial. One aspect concerns the compatibility with chemicals. Data on this point is sometimes available on the product label edited by the company; several scientific studies have also been published. For example, *B. subtilis* strain QST713 and *B. amyloliquefaciens* strain D747 proved fully compatible with synthetic fungicides, including mixtures of these products, and partially compatible with copper-based products (Rotolo et al. 2017). *Trichoderma viride* is inhibited in vitro by hexaconazole, copper oxychloride, and benomyl and was found to be incompatible with seed treatment with mancozeb, captan, and carbendazim (Madhavi et al. 2011). Similarly, *T. harzianum* is affected by fungicides, including hexaconazole, propiconazole, triflumizole, tebuconazole, tridemorph, folpet, mancozeb and zineb, as well as the abamectine insecticide (Sarkar et al. 2010; Gonzalez et al. 2015). Other *Trichoderma* spp. isolates were shown to be compatible with some fungicides (e.g. thiophanate-methyl, mancozeb, metalalaxyl + mancozeb, pencycuron and flutolanil), and incompatible with others (carbendazim and thiram + tolclofos-methyl) (Elshahawy et al. 2016). However, the pesticide compatibility observed in the field may be different from what happen in vitro. For example, *C. minitans* is highly sensitive to iprodione in vitro but this fungicide does not affect its ability to infect sclerotia of *S. sclerotiorum* in tests realised in the soil, suggesting that it can be used in the field when using the fungicide (Budge and Whipps 2001). Plant growth promoting rhizobacteria like *Pseudomonas* were found to survive seed treatments with chemicals like lindane, carboxin, thiram, iprodione and captan (Zablotowicz et al. 1992). Fungicides can also act synergistically with biocontrol agents. For example, the combination of *T. harzianum* and iprodione is able to reduce the disease incidence and severity of grey mould almost entirely and much better than the application of them separately (Elad et al. 1993). The combination of *Trichoderma* spp. with flutolanil, pencycuron and thiophanate-methyl reduces the growth of *Fusarium solani, F. oxysporum*, *Rhizoctonia solani, Macrophomina phaseolina* and *Sclerotinia sclerotiorum* at higher level than the application of the fungicides alone (Elshahawy et al. 2016). In field trials carried out on table grapes in southern Italy, the use of the biocontrol agents *B. subtilis* strain QST713, *B. amyloliquefaciens* strain D747 and *A. pullulans* strains DSM1494 alternately or in mixtures with the succinate dehydrogenase inhibitor fungicide fluopyram showed a high level of efficacy against grey mould, comparable with the chemical reference strategy (Rotolo et al. 2017).

The application of microbial antagonists has proved to be particularly effective against plant pathogens in the soil after steam or chemical disinfestation, or solarisation, because it helps to prevent the "biological vacuum" created in the soil, and it contributes to its biological activity and can also improve plant production (Katan 2015). This protective efficacy has been demonstrated with *T. harzianum* combined with solarisation against *Fusarium oxysporum* f. sp. *radicis lycopersici* (Sivan and Chet 1993) and against *Armillaria* (Otieno et al. 2003), and with *T. virens* against *S. rolfsii* (Ristaino et al. 1991). Additionally, *T. harzianum*, combined with soil fumigants like methyl bromide, resulted in improved control of *S. rolfsii* and *R. solani* by 93% and in increased yield by 160% (Elad et al. 1982; Gamlilel et al. 1993). Finally, according to a recent meta-analysis of 51 publications, soil solarization combined with microbial agents increases the effectiveness of disease control (Shlevin et al. 2018)., For example, a 100% control is obtained against soil-borne pathogens such as *Fusarium*, *Sclerotium cepivorum*, *Verticillium*, *Pyrenochaeta*, *Rhizoctonia*, *Pythium* and root-knot nematodes.

Information on the compatibility of biological control agents themselves are also required to use them in an IPM strategy. For instance, Bardin et al. (2008) have shown that the efficacy of three biological products is not altered when applied together, suggesting that they could be used together to intervene in tomato greenhouses against *Botrytis cinerea*, *Oidium neolycopersici* and *Bemisia tabaci*.

Finally, other cultural practices may affect the protective efficacy of microbial biocontrol agents. For instance, the protective efficacy of a biocontrol agent may vary depending on the cultivar used for a given crop. Thus, the efficacy of tomato protection against *B. cinerea* by *Trichoderma atroviride* and *T. harzianum* depends on the accession of tomato used (Tucci et al. 2011). Plant fertirrigation may also affect the protective efficacy of biocontrol agents. High nitrogen fertilization is for example associated with a better efficacy of the two biocontrol agents *T. atroviride* and *Microdochium dimerum* for the protection of tomato plants against *B. cinerea* (Abro et al. 2014).

13.7 Future Prospects

The current socio-economic and political context is particularly favorable to the development of biocontrol products. The currently available products do not cover all plant diseases and it is therefore necessary to continue the work for the development of new products. A challenge for research will be to select more efficient microorganisms by taking better account of their ecological competence, the stability and the durability of their efficacy. For the already existing products, it is necessary to identify the perimeters of their efficacy and to ensure their integration into complex farming system in order to guarantee optimal use of these products by farmers, for example by creating decision support tools.

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Chapter 14
Biological Control Agents for Control of Pests in Greenhouses

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Abstract First we describe the different types of biocontrol used in greenhouses and present examples of each type. Next we summarize the history of greenhouse biocontrol, which started in 1926, showed a problematic period when synthetic chemical pesticides became available after 1945, and flourished again since the 1970s. After 1970, the number of natural enemies becoming available for commercial augmentative biocontrol in greenhouses grew very fast, as well as the industry producting these control agents. Biocontrol of the most important clusters of greenhouse pests is summarized, as well as the taxonomic groups of natural enemies that play a main role in greenhouses. More than 90% of natural enemy species used in greenhouses belong to the Arthropoda and less than 10%, many belonging to the Nematoda, are non-arthropods. This is followed by sections on finding and evaluation of potential biocontrol agents, and on mass production, storage, release and quality control of natural enemies. Since the 1970s, production of biocontrol agents has moved from a cottage industry to professional research and production facilities. Many efficient agents have been identified, quality control protocols, mass-production, shipment and release methods matured, and adequate guidance for farmers has been developed. Most natural enemy species (75%) are produced in low or medium numbers per week (hundreds to a hundred thousand), and are applied in

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situations where only low numbers are needed, such as private gardens, hospitals, banks, and shopping malls. The other 25% of the species are produced in numbers of 100,000 to up to millions per week and regularly released in many of the greenhouse crops. Microbial pesticides are predominantly used as corrective treatments in greenhouse crops where natural enemies are providing insufficient control. Europe is still the largest commercial market for arthropod greenhouse biocontrol agents, and North America is the largest market for microbial control agents. We then continue with a discussion on the pros and cons of use of polyphagous predators, and the use of semiochemicals. Finally, we summarize factors that indicate a positive future for greenhouse biocontrol, as well as developments frustrating its implementation.

Keywords Natural biocontrol · Conservation biocontrol · Classical biocontrol · Augmentative biocontrol · Inundative biocontrol · Seasonal inoculative control · Polyphagous predators · Semiochemicals · Mass production

14.1 A Short History of Natural Enemy Use for Pest Control in Greenhouses

Different types of biological control – here defined as the use of a population of one organism to reduce the population of another organism – are used in greenhouses. Natural biological control (NatBC), whereby natural enemies which occur in the environment reduce pest populations, is observed in countries where greenhouse structures are often partly open like in the Mediterranean Basin, tropics and semitropics. Surprisingly, natural biological control is even observed in temperate climates. Examples are (1) natural control of exotic leafminer species by native parasitoids (e.g. *Dacnusa sibirica* Telenga (Hymenoptera: Braconidae), *Diglyphus isaea* (Walker) (Hymenoptera: Eulophidae), and *Opius pallipes* Wesmael (Hymenoptera: Braconidae)), pest mites that are controlled by naturally occurring gall midges (*Feltiella acarisuga* (Vallot) (Diptera: Cecidomyiidae)), and lepidopterans controlled by naturally occurring parasitoids (e.g. *Euplectrus* sp.) (van Lenteren 2010; van der Ent et al. 2017). Other spontaneously occurring parasitic wasps, such as *Cotesia* spp., *Eulophus* spp., *Euplectrus* spp., and *Necremnus artynes* (Walker) (Hymenoptera: Eulophidae) can make an important contribution to the biocontrol of native and exotic lepidopteran pests in the Mediterranean region (van der Ent et al. 2017). NatBC can be improved by growing plants near greenhouses that provide nectar, pollen or refuge for natural enemies, or by placing such plants inside the greenhouse. In that case we speak about conservation biological control, which consists of human actions that protect and stimulate the performance of naturally occurring natural enemies. Conservation biological control (ConBC) is currently receiving a lot of attention and is expected to be used increasingly, also for control of pests in greenhouses (see other chapters in this book). Further, we may use classical biological control (ClasBC), where natural enemies are collected in an exploration area (usually the area of origin of the pest) and then inoculated, i.e. released in low numbers in areas where the pest is invasive. However, in classical biological control the aim is permanent pest population reduction and this is not easy to obtain in greenhouse crops that are grown for short periods only. Still ClasBC may play a role in reducing pests outside the greenhouse area on wild plants, thereby contributing to lower pest pressure inside the greenhouse. An example is the generalist parasitoid *Lysiphlebus testaceipes* (Cresson) (Hymenoptera: Braconidae), which was introduced from Cuba in 1976 into Spanish citrus orchards for control of *Toxoptera aurantii* Boyer de Fonscolombe (Hemiptera: Aphididae) (Jacas et al. 2006). After introduction, this parasitoid established throughout the Mediterranean agricultural area where its parasitic action on natural populations of *Aphis gossypii* Glover (Hemiptera: Aphididae) has resulted in a lower impact of this pest aphid on horticultural and ornamental crops. Some greenhouse crops – e.g. roses and gerberas – are grown during several years and situations can be created that resemble classical biological control: natural enemies of exotic origin are released in low numbers (inoculated) at the start of a production cycle and exert control during many pest populations. In this case we speak about seasonal inoculative releases, and it differs from inundative releases, whereby large numbers of natural enemies are released for immediate pest control in crops with a short production cycle. Often seasonal inoculative and inundative are addressed under the umbrella of augmentative biological control (ABC), the form of biocontrol where natural enemies are mass reared for periodic releases (Van Lenteren et al. 2018a). ABC has always been the most used type of biocontrol in greenhouses, but as said above the use of ConBC is growing.

The documented history of biocontrol in greenhouses goes back to 1926. Biocontrol might have been used long before, for example by having cats for control of mice in protected structures where food was produced or stored. In 1926, a tomato grower observed black pupae among the normally white nymphs of the greenhouse whitefly, *Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodidae), and later, adult parasitoids emerged that were identified as *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) (Speyer 1927). A research station in England started to mass rear the parasitoid and a few years later, it was annually supplying 1.5 million parasitoids to about 800 nurseries in Britain. During the 1930s *E. formosa* was shipped to other countries in Europe, Australia, Canada and New Zealand. Mass production was discontinued for a short period after 1945 because synthetic pesticides became available. Due to quick development of resistance to pesticides in greenhouses, particularly in spider mites, interest in biocontrol revived. First a predatory mite (*Phytoseiulus persimilis* (Athias-Henriot) (Acari: Phytoseiidae)) of the spider mite (*Tetranychus urticae* Koch (Acari: Tetranychidae)) was found and put into practice with great success in the 1960s (Hussey and Bravenboer 1971). Later, the use of the parasitoid *E. formosa* became popular again in the 1970s. Also biocontrol of other pests, such as aphids, thrips, and exotic invasive and native leafminers was developed, and successful mass-rearing and distribution systems emerged. This was for a large part the result of very good collaboration between researchers and the natural enemy industry within the two working groups "Integrated Control in Protected Crops" in Mediterranean and temperate climates of the European section of the International Organization of Biological Control (www.IOBC-WPRS.org). These working groups published (and are still publishing) bulletins with a wealth of information on greenhouse IPM topics. For a detailed review of development of IPM in greenhouses up to 1985, we refer to van Lenteren and Woets (1988); for the period up to 2000 to van Lenteren (2000), who also provides an IPM programme for tomato, the largest greenhouse vegetable crop worldwide. IPM programmes for other vegetables and ornamentals, and biocontrol agents used until the end of the 1990s can also be found in Cavalloro and Pellerents 1989; Albajes et al. (1999). Arnó et al. (2018) highlight major landmarks in the development of biocontrol programmes for tomato greenhouses in the Mediterranean.

During the period 1970–2000 the number of natural enemies becoming available for commercial augmentative biocontrol grew very fast (Fig. 14.1). After 2000 and until today, a much lower number of new natural enemies came to the market. The decrease was for one part due to various positive developments as (1) the availability of complete sets of biocontrol agents managing the key pests and diseases in

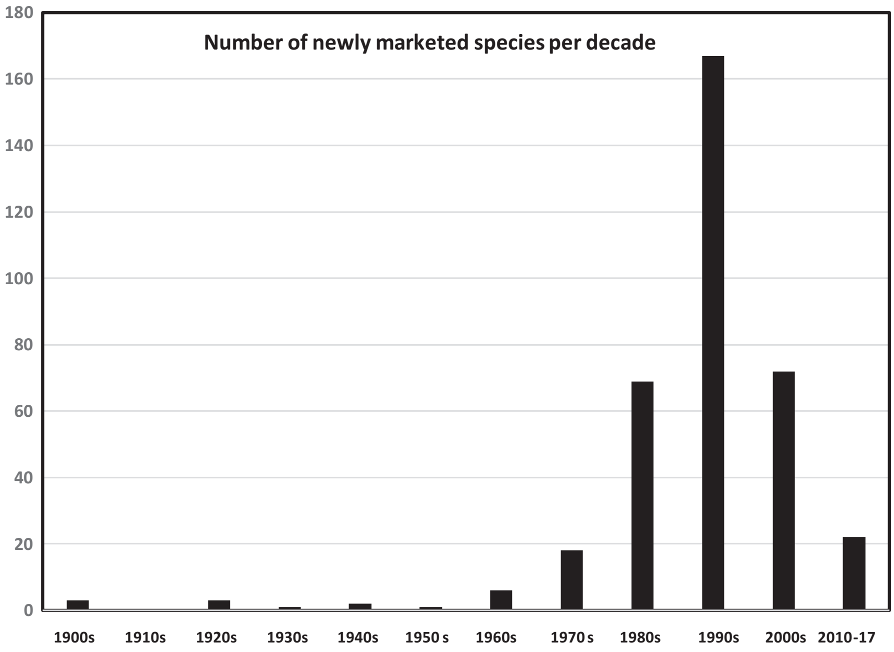

Fig. 14.1 Number of newly marketed invertebrate natural enemy species per decade for augmentative biocontrol (based on tables and supplementary material in van Lenteren et al. 2018a and with recent updates)

greenhouses, (2) the increased use of generalist predators and (3) the growing popularity of conservation biocontrol approaches. However, the reduction was for another part due to stronger regulation of import of exotic natural enemies, increased demands concerning registration of biocontrol agents, and the Access and Benefit Sharing paragraph in the Convention of Biological Diversity resulting in the Nagoya Protocol which recently came into force (Secretariat of the Convention on Biological Diversity 2011). All these new measures have negatively affected market penetration of new biocontrol agents and, whether they are of indigenous or exotic origin, now usually undergo an environmental risk assessment (Cock et al. 2010; van Lenteren et al. 2006). Due to the current evaluation and registration requirements, a trend has developed to first look for indigenous agents, even when a new exotic pest establishes. Until a few years ago, prospecting for new, exotic natural enemies after accidental introductions of exotic pests was common practice, but particularly the Access and Benefit Sharing process has resulted in an almost complete stop of foreign natural enemy exploration programmes (Cock et al. 2010). We can illustrate this trend by the number of natural enemies that have been used in augmentative biocontrol for the first time in Europe (Fig. 14.2). Until 1970, the only two species commercially used in European greenhouses – *P. persimilis* and *E. formosa* – were exotics. During the period from 1960 to 1999, more new exotic species (77) were used than indigenous species (58). As of 2000, this trend changed and for the first time more indigenous species (18) were commercialized than exotic species (6).

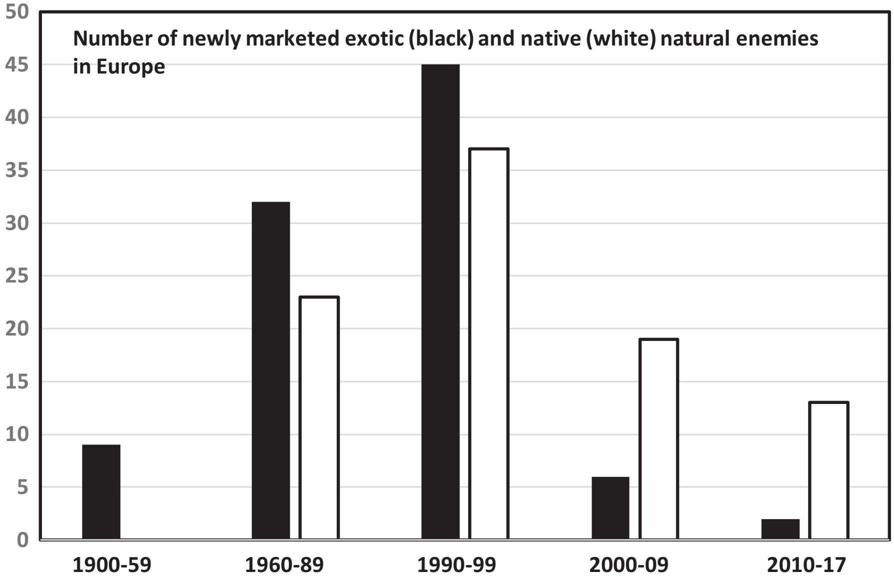

Fig. 14.2 Numbers of new exotic (black) and indigenous (white) invertebrate natural enemies introduced for augmentative biocontrol to the European market. (Based on tables and supplementary material in van Lenteren et al. 2018a and with recent updates)

The majority (>90%) of natural enemy species used in ABC belongs to the Arthropoda and less than 10% of the species, many belonging to the Nematoda, are non-arthropods. Within the arthropods, four taxonomic groups provided most natural enemies expressed in number of species: Hymenoptera (>50%), Acari (about 15%), Coleoptera (about 12%) and Hemiptera (about 8%) (van Lenteren 2012; van Lenteren et al. 2018a). The large number of hymenopteran species used in ABC can be explained by the fact that they have, compared to predators, a much more restricted host range, which is considered important in preventing undesirable side effects (e.g. Bigler et al. 2006). Acarid predators are popular because they can cheaply be mass reared, can be released by mechanical means, may control several pest species, do not spread actively over large distances, which reduces the risk of undesirable effects. An example of a recent acarid species becoming very popular in use is *Amblyseius swirskii* Athias-Henriot (Acari: Phytoseiidae) (e.g. Calvo et al. 2012a). Interestingly, polyphagous heteropteran predators have become increasingly popular in ABC during the past two decades (see Table 14.1 in van Lenteren 2012, and Table 14.2 in van Lenteren et al. 2018a). This was a somewhat unexpected development as several of the currently used heteropteran species have a very wide prey range and some of them are (facultatively) phytophagous (Wheeler 2001; Pérez-Hedo et al. 2015). See Sect. 14.5 of this chapter for a more detailed discussion of the use of polyphagous predators in greenhouse IPM.

Most natural enemy species (75%) are produced in low or medium numbers per week (hundreds to a hundred thousand) (van Lenteren 2012; van Lenteren et al. 2018a). They are applied in situations where only low numbers are needed (private gardens, hospitals, banks, shopping malls, etc.), or when occasionally needed in large cropping systems for control of minor pests. An example of a taxonomic group mainly used in niche markets is the Coleoptera; more than 90% of the species are

Table 14.1 Major biocontrol agent producers providing beneficial organisms and information on greenhouse pest management. For lists with more producers, see e.g. http://www.ibma-global.org/en/all-ibma-members, and http://anbp.org/index.php/members-products

Name of company	Area where active	URL
Agrobio	Global	www.agrobio.es
Applied Bionomics	NAFTA	www.appliedbio-nomics.com
BASF	Global (EPNs)	www.basf.com
Beneficial Insectary	NAFTA	www.insectary.com
Biobee	Global	www.biobee.com
Biobest	Global	www.biobest.be
Bioline Agrosciences	Europe, NAFTA	www.biolineagrosciences.com
Biological Services	Australia	www.biologicalservices.com.au
Bioplanet	S. Europe	www.bioplanet.eu/it/
Bugs for bugs	Australia	www.bugsforbugs.com.au
Dudutech	E. Africa	www.dudutech.com
Enema	Global (EPNs)	www.e-nema.de
Koppert Biological Systems	Global	www.koppert.com

Table 14.2 Most important biocontrol agents used for control of pests in greenhouses

Target pests → target →	Thrips	Whitefly	Mites	Aphids	Lepidop	Scales	Beetles	Diptera	Heterop	Hemip
Biocontrol ↓ agents									Bugs	Psyllid
Invertebrates										
Acari										
Amblydromalus limonicus Garman and McGregor (Acari: Phytoseiidae)	++	+								+
Amblyseius swirskii Athias-Henriot (Acari: Phytoseiidae)	++	+	+							
Macrocheles robustulus (Berlese) (Acari: Macrochelidae)	+							+		
Neoseiulus californicus (McGregor) (Acari: Phytoseiidae)			++							
Neoseiulus cucumeris (Oudemans) (Acari: Phytoseiidae)	++		+							
Phytoseiulus persimilis (Athias-Henriot) (Acari: Phytoseiidae)			++							
Stratiolaelaps scimitus (Womersley) (Acari: Laelapidae)	+							+		
Transeius montdorensis (Schicha) (Acari: Phytoseiidae)	+	+								
Coleoptera										
Adalia bipunctata L. (Coleoptera: Coccinellidae)				+						
Cryptolaemus montrouzieri Mulsant (Coleoptera: Coccinellidae)						++				
Delphastus catalinae (LeConte) (Coleoptera: Coccinellidae)		+								
Rhyzobius lophantae Blaisdell (Coleoptera: Coccinellidae)						+				
Diptera										
Aphidoletes aphidimyza (Rond.) (Diptera: Cecidomyiidae)				++						
Episyrphus balteatus (De Geer) (Diptera: Sirphydae)				++						
Feltiella acarisuga (Vallot) (Diptera: Cecidomyiidae)			+							
Sphaerophoria rueppellii (Wiedemann) (Diptera: Syrphidae)				++						

(continued)

Table 14.2 (continued)

Target pests → target →	Thrips	Whitefly	Mites	Aphids	Lepidop	Scales	Beetles	Diptera	Heterop	Hemip
Biocontrol ↓ agents									Bugs	Psyllid
Hemiptera										
Macrolophus pygmaeus (Rambur) (Hemiptera: Miridae)		++	+	+	+					
Nesidiocoris tenuis (Reuter) (Hemiptera: Miridae)		++								
Orius insidiosus (Say) (Hemiptera: Anthocoridae)	+									
Orius laevigatus (Fieber) (Hemiptera: Anthocoridae)	++									
Orius strigicollis (Poppius) (Hemiptera: Anthocoridae)	+									
Hymenoptera										
Anagyrus pseudococci (Girault) (Hymenoptera: Encyrtidae)						+				
Anaphes iole Girault (Hymenoptera: Mymiridae)									+/–	
Aphelinus adbominalis (Dalman) (Hymenoptera: Aphelinidae)				+						
Aphidius colemani Vierek (Hymenoptera: Braconidae)				++						
Aphidius ervi Haliday (Hymenoptera: Braconidae)				+						
Aphidius matricariae Haliday (Hymenoptera: Braconidae)				+						
Aphytis melinus DeBach (Hymenoptera: Aphelinidae)						+				
Dacnusa sibirica Telenga (Hymenoptera: Braconidae)								++		
Diglyphus isaea (Walker) (Hymenoptera: Eulophidae)								++		
Encarsia formosa Gahan Hymenoptera: Aphelinidae)		++								
Eretmocerus eremicus Rose and Zolnerowich (Hymenoptera: Aphelinidae)		++								
Trichogramma spp. (Hymenoptera: Trichogrammatidae)					+					
Trissolcus basalis (Wollaston) (Hymenoptera: Scelionidae)									+/–	

Nematoda										
Heterorhabditis bacteriophora Poinar (Nematoda: Heterorhabditidae)							+			
Steinernema carpocapsae (Weiser) (Rhabditida: Steinernematidae)		+			+			+		
Steinernema feltiae (Filipjev) (Rhabditida: Steinernematidae)		+						+		
Neuroptera										
Chrysoperla carnea (Stephens) (Neuroptera: Chrysopidae)				+						
Micro organisms										
Bacteria										
Bacillus thuringiensis Berliner (Bacillales: Bacillaceae)					++					
B. thuringiensis spp israelensis								+		
Fungi										
Beauveria bassiana (Bals.-Criv.) Vuill. (Hypocreales: Clavicipitaceae)	+	+	+	+	+	+	+			
Lecanicillium muscarium Zare & Gams (Hypocreales: Cordycipitaceae)	+	++								
Metarhizium anisopliae (Metsch.) Sorokin (Hypocreales: Clavicipitaceae)	++						++			
Isaria fumosorosea (Wize) Hypocreales: Clavicipitaceae)		++								
Baculoviruses										
Helicoverpa armigera NPV					+					
Spodoptera exigua NPV					+					
Spodoptera littoralis NPV					+					

produced in small numbers. Twenty five percent of the natural enemy species are produced in numbers of more than 100,000 per week and are either frequently applied in many of the greenhouse crops (hymenopterans and heteropterans), and/or need to be released in very large numbers per unit area for sufficient control (acarids and heteropterans).

Microbial pesticides are predominantly used as corrective treatments in greenhouse crops where natural enemies are providing insufficient control, except for the use of *Bacillus thuringiensis* Berliner (Bacillales: Bacillaceae) against caterpillars which is a standard measure. Fungal microbial control agents against whitefly and thrips are applied locally in hot spots or as blanket treatment besides the use of parasitoids or predators. The same is true for use of baculoviruses against caterpillars. Except for *B. thuringiensis*, the markets for these microbials are relatively small. Insect-pathogenic nematodes are used in ornamental crops, mainly in chrysanthemum, for control of thrips and are then a major part of an IPM programme.

Europe is still the largest commercial market for ABC with invertebrate biocontrol agents, with a well-functioning, highly developed biocontrol industry. The next largest market is North America, followed by Asia, Latin America, Africa and the Middle East (Dunham 2015; Research and Markets 2016a). According to the latest marketing reports (e.g. Research and Markets 2016b) North America is now the largest market for microbial pesticides, followed by Europe. Since the start of application of biocontrol in greenhouses almost 100 years ago, we see a slow increase in use until the 1970s, followed by a period of strong growth to the year 2000, a stagnation in growth until 2010, with a new period of market expansion of biocontrol today (e.g. van Lenteren et al. 2018a).

14.2 Biological Control of the Main Groups of Pests

We do not aim to provide a complete overview of the biology and application methods of biocontrol agents currently used in greenhouses in this chapter. Instead, we will mention the major species that are applied for pest control in greenhouses today, and refer to published information in journals, books and on the world wide web. The number and importance of pest species is changing continuously due to intensified international tourism, trade and transport of crops. Two recent examples of invasive pests spreading all over the world are the South American tomato pinworm *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) and the spotted-wing Drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae). Such new pests initially may very negatively interfere with well working, pesticide independent IPM programmes, but also create research activities resulting in identification and use of new biocontrol agents. For the most recent IPM programmes for various greenhouse crops we refer to the websites of the biocontrol agent producers (Table 14.1) and crop specific chapters in this book.

14.2.1 Major Groups of Biocontrol Agents Available for Greenhouse Pest Management

In Table 14.2 we present the major groups of biocontrol agents used for control of pests in greenhouses. Many other species of beneficial organisms may be used in special situations and for the control of minor pests. Van Lenteren et al. (2018a) provide lists of all agents known for use in ABC, together with the region where used, target pests, first year of use and market value. According to these authors: "The largest European biological control companies are still getting the main part of their income from sales of invertebrate biological control agents, but the contribution of microbial biological control agents is steadily increasing." Commercial ABC is used in protected crops and high-value outdoor crops (e.g. strawberries, grapes), contributing to about 80% of the market value of invertebrate biocontrol agents. Biocontrol programmes for each of these crops may involve up to 10–20 different species of natural enemies (van Lenteren 2000). Almost 40% of the income of the European biocontrol companies originates from sales of invertebrate biocontrol agents for control of thrips, another 30% for control of whitefly, 12% for control of spider mites, 8% for control of aphids, and the remaining 10% for control of various other pests (Bolckmans K, personal communication 2016). We will present the biocontrol agents used in greenhouses per taxonomic group, but not go into detail about their biology. Van der Ent et al. (2017) provide summaries of the biology, behaviour, population development, life cycles, development times at a range of temperatures, photographs and drawings of all natural enemies used in greenhouses, as well extensive information about the pests these natural enemies control.

14.2.1.1 Acari

As of 2005, predatory mites have contributed enormously to the growth of the market for invertebrate biocontrol agents as a result of the (re)discovery of (1) their use for control of whiteflies (e.g. Nomikou et al. 2001), (2) finding more efficient species for thrips control (e.g. Messelink et al. 2006), (3) the development of techniques to enhance dispersal and establishment of predatory mites in crops (e.g. Messelink et al. 2014); and the development of new highly economic mass-production technologies (e.g. Bolckmans et al. 2005). Since the 1960s, *Phytoseiulus persimilis*, the second commercially available biocontrol agent, was the champion invertebrate natural enemy when expressed in numbers produced per week, but around 2010 *Amblyseius swirskii* took over the pole position. The following predatory mites are most often used in greenhouse biocontrol (within brackets the year of first use): *Amblydromalus limonicus* (Garman and McGregor) (Acari: Phytoseiidae) (1995), *Amblyseius swirskii* (2005), *Macrocheles robustulus* (Berlese) (Acari: Macrochelidae) (2006), *Neoseiulus californicus* (1985), *Neoseiulus cucumeris* (Oudemans) (Acari: Phytoseiidae) (1985), *Phytoseiulus persimilis* (1968), *Stratiolaelaps scimitus* (Womersley) (Acari: Laelapidae) (1990) and *Transeius* *montdorensis* (Schicha) (Acari: Phytoseiidae) (2004). These predatory mites are aimed at reducing populations of phytophagous mites, thrips, whiteflies, dipterans and psyllids (see Table 14.2). Although applied with much success in different crops, several of the important predatory mites species, like *A. swirskii*, *N. californicus* and *P. persimilis*, do not perform well on tomato due to the presence of sticky hairs. For a background article about several of the predatory mites mentioned above we refer to McMurtry and Croft (1997).

14.2.1.2 Coleoptera

Ladybird beetles are since long known as efficient predators of many different phytophagous pest insects. Actually, the first "modern" case of very successful biocontrol was obtained by introducing the exotic Australian ladybeetle *Rodolia cardinalis* (Mulsant) (Coleoptera: Coccinellidae) in the 1880s into the United States of America for control of the invasive cottony cushion scale, *Icerya purchasi* Maskell (Hemiptera: Monophlebidae). Since its first release, the *Rodolia* beetle has controlled the *Icerya* scale pest on citrus worldwide for more than 100 years in more than 50 countries without causing any negative side effect (Cock et al. 2010). Also in greenhouses, several species of ladybird beetles (Coleoptera: Coccinellidae) are used with success, like *Adalia bipunctata* L. (since 1998)*, Cryptolaemus montrouzieri* Mulsant (1980)*, Delphastus catalinae* (LeConte) (1985) and *Rhyzobius lophantae* Blaisdell (1980), for control of aphids, mealybugs, scales and whiteflies (Table 14.2). Though not very recent articles, Hagen (1962) and Obrycki and King (1998) are still excellent introductions to the biology of ladybird beetles.

14.2.1.3 Diptera

The gall midge *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) has been used in greenhouses for control of aphids since 1989. Gall midge larvae prey on many aphid species. *Feltiella acarisuga* gall midge larvae, applied in greenhouses since 1990, are specific spider mite predators and used for reducing high density mite concentrations. The syrphid fly *Episyrphus balteatus* (De Geer) (Diptera: Sirphydae) has been used in greenhouses since the late 1990s for the control of different species of aphids. Recently, *Sphaerophoria rueppellii* (Wiedemann) (Diptera: Sirphydae) has replaced the use of *E. balteatus* in some crops (i.e. sweet pepper), because it is adapted to a wider range of temperatures. General information about gall midges can be found in Dorchin (2008).

14.2.1.4 Hemiptera

Hemipteran predators have recently become very popular and important biocontrol agents, although *Orius insidiosus* (Say) (Hemiptera: Anthocoridae) is already used since the 1980s, and *Macrolophus pygmaeus* Rambur) (Hemiptera: Miridae) and

O. laevigatus (Fieber) (Hemiptera: Anthocoridae) are used since the 1990s in greenhouses. These polyphagous predators are applied mainly against thrips, whiteflies, mites, and lepidopterans, but will prey on many other pest species. Currently, *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae) is often used for control of whiteflies and lepidopterans in the Mediterranean area. There is one potential drawback associated with the use of hemipterans, and that is the zoophytophagous behaviour of several species (see Sect. 14.5 of this chapter). An important positive characteristic of the mirid species *M. pygmaeus* and *N. tenuis* is that they function very well on tomato and have no problem with its sticky hairs (Wheeler and Krimmel 2015). *Orius strigicollis* (Poppius) (Hemiptera: Anthocoridae) is a recent addition to the list of hemipteran predators and is used for control of thrips. Wheeler (2001) provides background information about hemipteran predators.

14.2.1.5 Hymenoptera

Parasitoid wasps have always been popular biocontrol agents, because of their host specificity. Contrary to many predators, these parasitoids usually attack only a few species and are, therefore, considered safer since they will not parasitize non-target species. Many species of parasitoids are used for pest control in greenhouses. The first commercially available natural enemy for greenhouse use was the whitefly parasitoid *Encarsia formosa*, which is applied since 1926. The species *Eretmocerus eremicus* Rose and Zolnerowich (Hymenoptera: Aphelinidae) (since 1995) is also used for whitefly control, in particular to reduce *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) populations. A suite of parasitoids is used for control of aphids, among which the species *Aphelinus adbominalis* (Dalman) (Hymenoptera: Aphelinidae) (since 1992), and three *Aphidius* (Hymenoptera: Braconidae) species *A. colemani* Vierek (1991), *A. ervi* Haliday (1996), *A. matricariae* (1980). Often, parasitoids alone are not enough to reduce aphid populations, which is, in part, caused by hyperparasitoids invading the greenhouse and attacking the primary parasitoids listed above. Most important dipteran leafminer species occurring in greenhouses can be successfully controlled with the parasitoids *Dacnusa sibirica* (since 1981; effective against *Liriomyza bryoniae* (Kaltenbach) and *L. huidobrensis* (Blanchard) (Diptera: Agromyzidae)), and *Diglyphus isaea* (1984, effective against the previously mentioned two species and *L. trifolli* (Burgess) and *L. sativae* Blanchard). The parasitoids *Anagyrus pseudococci* (Girault) (Hymenoptera: Encyrtidae) (since 1995) and *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae) (1980) are applied against mealybugs and scales, respectively. The heteropteran bug *Lygus hesperus* Knight (Hemiptera: Miridae) can be controlled with the parasitoid *Anaphes iole* Girault (Hymenoptera: Mymiridae) (since 1990) and *Trissolcus basalis* (Wollaston) (Hymenoptera: Scelionidae) can partially reduce populations of *Nezara viridula* L. (Hemiptera: Pentatomidae) (1995). *Trichogramma spp.* parasitize eggs and are used since the 1990s for control of various lepidopterans in greenhouses. Godfray's (1994) book entitled "Parasitoids" gives an overview of the biology of parasitoids.

14.2.1.6 Nematoda

Nematodes that parasitize insects are known from the genera *Heterorhabditis* and *Steinernema,* and have been used for control of beetles, lepidopterans, sciarid and shore flies and leaf-mining flies since the 1980s. Killing of the host insect occurs through bacteria that are released into the insect after nematode infection. In greenhouses mainly *Heterorhabditis bacteriophora* Poinar (Nematoda: Heterorhabditidae) (since 1984) is used for control of various beetle species, and *Steinernema carpocapsae* (Weiser) (Rhabditida: Steinernematidae) (since 1984) and *Steinernema feltiae* (Filipjev) (Rhabditida: Steinernematidae) (1984) are applied for control of sciarid and shore flies. A good introduction into the biology and use of entomopathogenic nematodes is provided by Poinar and Grewal (2012).

14.2.1.7 Neuroptera

Many species of Neuroptera, and particularly those of the genus *Chrysoperla*, are commercially available for biocontrol for control of aphids and whitefly. In greenhouses the species *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) is often used for control of aphids since the 1980s. Information on predatory Neuroptera is presented by McEwen et al. (2001).

14.2.1.8 Microorganisms

Microbial control of pests with viruses, bacteria and fungi is a strongly growing market. In greenhouses mainly three species of microbial control agents are often used, while in the field many more species are applied. Information about the biology and commercialization of microbial control agents can be found in Ravensberg (2011).

Bacteria

The bacterium *Bacillus thuringiensis* is used since the mid 1980s for control of young lepidopteran caterpillars. The strain *B.t.* var. *israelensis* is used on a small scale for control of sciarids.

Fungi

The fungus *Beauveria bassiana* (Bals.-Criv.) Vuill. (Hypocreales: Clavicipitaceae) is one of the oldest known entomopathogenic organisms, is applied in greenhouses since the 1990s, and can be used for reduction of populations of a wide array of pests (see Table 14.2). *Lecanicillium muscarium* Zare & Gams (Hypocreales:

Cordycipitaceae), applied since 1980s in greenhouses, is mainly used for control of whitefly, but also kills thrips. *Isaria (Paecilomyces) fumosorosea* (Wize) Hypocreales: Clavicipitaceae) is solely used for control of whitefly and available since 1999; a second strain reached the market in 2014. *Metarhizium anisopliae* Sorokin (Hypocreales: Clavicipitaceae) is used for control of black vine weevil and thrips since 2010.

Baculoviruses

Three species of baculoviruses have been approved for control of noctuid caterpillars (Lepidoptera: Noctuidae) in protected crops: the *Spodoptera exigua* nucleopolyhydrosis virus against the beet army worm (*S. exigua* (Hübner)), the *Helicoverpa armigera* nucleopolyhedrovirus against the cotton boll worm (*H. armigera* (Hübner)), and the *Spodoptera littoralis* nucleopolyhedrovirus against the cotton leaf worm (*S. littoralis* (Boisduval)).

14.3 Searching for and Evaluation of Biological Control Agents

In this chapter we will not describe the process of collection and evaluation of biocontrol agents in detail. Information concerning these factors for invertebrate biocontrol agents can be found in Cock et al. (2010) and for microbial biocontrol agents in Ravensberg (2011). When searching for natural enemies, it is not unusual to find dozens or more species of predators, parasitoids, parasites and pathogens attacking a certain pest, but criteria such as population growth rate, host range, and adaptation to crop and climate can often be used to quickly eliminate clearly inefficient species (van Lenteren 2010, 2019). Next, the most promising species can be compared by using characteristics such as efficacy of pest control under crop production conditions, potential environmental risks and economy of mass rearing. For the screening of microbial control agents, large collections of hundreds or thousands of isolates may be established for high throughput screening assays to assess important traits such as cold tolerance, metabolite production and efficacy against the target pest. The whole process from searching for potential biocontrol agents up to commercial use may take up to 10 years for invertebrate natural enemies and even longer for microbial control agents, which is particularly due to long registration procedures. Ways to simplify registration of microbials are currently considered in the EU. Due to the recent implementation of the Nagoya Protocol with respect to Access and Benefit Sharing issues, prospecting for exotic biocontrol species has practically come to a stands still and seriously limits finding biocontrol solutions for new invasive pests (see Sect. 14.1 of this chapter). On the other hand, it stimulated searching for native natural enemies which, in some cases, appeared to be able to sufficiently reduce invasive pests.

14.4 Mass Production, Storage, Release, and Quality Control of Biological Control Agents

About 500 companies commercially produce invertebrate biocontrol agents worldwide, although most of these employ a handful of personnel. Less than ten producers employ more than 50 staff. In addition to commercial producers, there are hundreds of government-owned production units, particularly in China, India and Latin America. Also, and especially in Latin America, some large-scale growers are involved in producing their own natural enemies. Together, these companies and grower or government-owned production facilities produce at least 350 species of invertebrate natural enemies and 209 strains from 94 different species of microbial control agents (van Lenteren et al. 2018a). Microbial biocontrol agents are produced by approximately 200 manufacturers, which is an underestimate as no data are available for China or India (Dunham 2015). Companies, the majority of which are small to medium sized, are often specialised in one or two types of microorganisms and production methods. Large multinational agro-chemical companies are now getting involved in the production and marketing of microbial control agents, mainly through the acquisition of the small to medium-sized companies.

Since the 1970s, ABC has moved from a cottage industry to professional research and production facilities. Since then, many efficient agents have been identified, quality control protocols, mass-production, shipment and release methods matured, and adequate guidance for farmers has been developed (van Lenteren 2003, 2012; Cock et al. 2010; Ravensberg 2011). Mass production of natural enemies is described in detail in various chapters in van Lenteren (2003), including obstacles encountered in setting up and running large scale rearing programmes, mass-production schemes, storage procedures, methods for collection, shipment and release of natural enemies, and quality control techniques and protocols. All the elements related to mass production just mentioned have undergone a very fast development since the 1970s. Not only are many more species and much higher numbers produced per week, also mass-rearing methods have been developed that are no longer based on rearing on the target pest and target crop, but on other hosts or prey species and inert substrates (see e.g. Bolckmans et al. 2005). These improvements have led to a decrease in price of several important biocontrol agents. Shipment in climate controlled containers, development of slow release sachets for natural enemies and mechanized delivery methods (see e.g. Lanzoni et al. 2017) have all resulted in improved biocontrol results in greenhouses. Still, there is great demand for cheaper ways of mass production, strongly improved methods for natural enemy storage during longer periods and with better survival, and for simpler and more reliable quality control protocols. For mass-production, storage, application methods and quality control of microbial control agents, we refer to Ravensberg (2011).

14.5 Recent Popularity of Polyphagous Predators: Pros and Cons

Historically, the development of biocontrol in greenhouses has been characterized by using specialized natural enemies, mainly parasitoids (see introduction of this paper). However, during the development of biocontrol programmes in southern Europe the spontaneous presence of generalist predators was often observed, mainly of mirids in tomato greenhouses (Fauvel et al. 1987; Albajes et al. 1980; Arnó et al. 2018). Initially, they were considered with scepticism, because of being generalists they might cause unwanted side effects by preying on other beneficial insects. Nevertheless, experience has shown during the past decades that generalists can be effective biocontrol agents under many circumstances (DeClerq 2002; Symondson et al. 2002). Their polyphagy is in a number of situations even advantageous as it allows them to survive when the target pest is reduced to low densities, which is to supposed to happen in successful biocontrol programmes (Albajes and Alomar 1999). Nowadays, generalist predators are recognized to be valuable biocontrol agents and several of them have been incorporated successfully into the portfolio of biocontrol agents (see Table 14.1 and Sect. 14.2 of this chapter and see other chapters in this book). Several of the generalist predators used in greenhouse biocontrol are also omnivores (or zoophytophages). They not only feed on animal prey, but complement or supplement their nutritional needs profiting from plant resources (pollen, nectar, seeds or plant juices). Further to this, plant tissues (phloem and xylem) may provide a source of water as well as nutrients. Overall phytophagy in predators results in improved life-history traits such as survival, development time, fecundity and longevity (Coll and Guershon 2002; Wäckers et al. 2005; Albajes and Alomar 2008). A well-known example of a positive effect of phytophagy is the requirement of pollen for the establishment of *Orius* predators.

Omnivory may actually make these predators preferred candidates for effective pest control, because plant feeding allows them to survive and bridge periods of low pest presence. As a consequence, they may establish on crops early in the growing season when prey is scarce or absent. This enables them to respond quickly to new pest infestations. Additionally, it may contribute to sustain predator populations while target pests are under control and occur at very low densities. At present, the positive effects of the ability to feed on plants is well acknowledged, and non-crop plants may be added to the crop to improve the presence and establishment of predators. Not only do these non-crop plants offer shelter or alternative food, but they also provide breeding sites for development of predator populations (Messelink et al. 2014; Perdikis et al. 2011; Lambion et al. 2016). In practice however, few growers use such plants.

Probably the most successful example of using polyphagous predators in greenhouses is the combined use of the predatory mite *A. swirskii* together with the anthocorid *O. laevigatus* in protected sweet peppers (see chapter 18). If properly managed, release and conservation of both natural enemies can successfully reduce populations of the key pepper pests; sweet potato whitefly, *B. tabaci*, greenhouse whitefly, *T. vaporariorum* and western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) (Sanchez and Lacasa 2002; Calvo et al. 2012a; van Lenteren 2012; van Lenteren et al. 2018a). Moreover, the polyphagous behaviour of *A. swirskii* and *O. laevigatus* contributes to the management of secondary pests, such as spider mites and Lepidoptera (Park et al. 2010; van Maanen et al. 2010). The use of these two predators in sweet pepper in Murcia and Almería (Southeast Spain) is a paradigmatic example: the area under biocontrol increased from a mere 200 ha in the 2005–2006 season to about 7,500 ha in 2008–2009, and in the 2015–2016 season the area exceeded 10,000 ha (almost 100% of the sweet pepper aea) (Calvo et al. 2015; van der Blom 2017).

Amblyseius swirskii is native to the Mediterranean-Middle East area and is commercially available as a biocontrol agent of whitefly and thrips in different crops since 2005 (Nomikou et al. 2001, 2002; Messelink et al. 2008; Calvo et al. 2011, 2015). In Spain alone, during the 2012–2013 season, the total greenhouse area sunder biocontrol using *A. swirskii* reached 18,000 ha (Calvo et al. 2015). The ability of *A. swirskii* to establish even before the appearance of the pest, owing to its capability of feeding on alternative food sources such as pollen, nectar, small insects and mites as *T. urticae* and *Polyphagotarsonemus latus* (Banks) (Acari: Tarsonemidae) and other non-prey food, including eggs of the Mediterranean flour moth *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), decapsulated dry cysts of the brine shrimp *Artemia franciscana* Kellogg (Anostraca: Artemiidae), enhanced its efficiency as biocontrol agent.

Orius laevigatus is a key predator of thrips, but also preys on *B. tabaci* (Chambers et al. 1993; Hamdan and Abu-Awad 2008). In addition, *O. laevigatus* can consume other arthropod pests such as aphids and mites (Alvarado et al. 1997; Venzon et al. 2002). The generalist anthocorid predator *O. laevigatus*, is a western Palaearctic species, widespread along Mediterranean and Atlantic coasts (Tommasini 2004). Many characteristics contribute to its success, including the absence of diapause, high fecundity, a long life span and polyphagy (Tommasini and Nicoli 1996; Tommasini et al. 2004). Like many other anthocorids, the predator *O. laevigatus* is also able to exploit plant resources, including pollen and plant juices, and use the plant as egg-laying substrate (Cocuzza et al. 1997; Lattin 1999). Adults may feed on mesophyll and xylem, and Lundgren et al. (2008) reported that neonate *O. insidiosus* were able to feed on the nutritious phloem, allowing them to survive on plant materials for several days. Feeding from plants by anthocorids helps predator establishment and survival when protein-rich animal food lacks. Until today plant-feeding by *Orius* has not resulted in complaints by growers such as in the case of *N. tenuis*, but it is an interested phenomenon deserving further study. Recently Bouagga et al. (2018a) investigated the importance of *O. laevigatus* feeding on sweet pepper compared to other behaviour: it spends almost 40% of its time on feeding, mainly on apical meristems and apical fresh leaves, which are also favourite residence locations. This information indicates that plant feeding is common and ecologically relevant for omnivorous *Orius* bugs.

Biocontrol by predatory mirids in greenhouses is another example of successful use of omnivorous, plant-feeding species. One of these mirid species, *Macrolophus pygmaeus*, spontaneously colonizes tomato crops where IPM is used, and contributes to the control of several important pests, including whiteflies, aphids, thrips, mites, leafminers and moths. This mirid species now has been used in commercial greenhouse tomato production in Europe for almost 30 years. When spontaneous presence is not sufficient, releases are made, primarily to control whiteflies and the exotic tomato leaf miner *Tuta absoluta*. Yet, under specific circumstances, plant-feeding by predatory mirids may cause injury to the crop, which does not necessarily have to result in yield loss when injury is limited. Injury is predator species and crop specific, and may vary dependent on crop species and variety, growth stage and affected plant part (Castañe et al. 2011). In many cases the injury zoophytophagous mirids may cause to the crop phytophagy was compensated by their beneficial value as pest control agent (Gabarra et al. 1988). In fact, *M. pygmaeus* has been said to cause some yellowish discoloration and deformed tomato fruits, especially at extremely high population levels resulting from too high initial release rates and application of adding supplementary food too frequently (Moerkens et al. 2016), but this has not stopped it from being used on a large scale all over Europe. Albajes et al. (2006) provide guidance as to how to assess risk of damage.

Another group of successfully used zoophytophagous mirids are *Dicyphu*s (Hemiptera: Miridae) species, and also here the fact that they may feed on plants does not prohibit their application. *Dicyphus tamaninii* Wagner is spontaneously present in field and greenhouse crops, and injury to tomato fruits only arose when excessive predator populations were observed after controlling high whitefly densities (Gabarra et al. 1988). Injury might result in economic damage due to yield reduction, requiring measures to control high densities of the predator. Development of decision thresholds related to predator–prey ratios avoided the appearance of injury in commercial fields after pests were controlled (Alomar and Albajes 1996). The above reported results highlight the success of proper strategies to manage natural populations of mirids for successful biocontrol. *Dicyphus errans* (Wolff), another zoophytophagous mirid, occurs naturally and is the most abundant dicyphine in tomato crops in Northwestern Italy. It is considered a major contributor to the control of *Tuta absoluta*. A strategy to manage *D. errans* populations in greenhouses now aims to identify specific companion plants that either boost predator populations but not the pest *T. absoluta*, or to control *T. absoluta* on the companion plants during the off-season period (Ingegno et al. 2017). Both *Dicyphus* species have not yet been commercialized, but are under evaluation for use in several crops (Messelink et al. 2015). Two other European species, *D. geniculatus* (Fieber) (Beitia et al. 2016) and *D. maroccanus* (Wagner) (Abbas et al. 2014) are currently tested for their pest control capacity. *Dicyphus hesperus* Knight was identified as an effective natural enemy of whitefly and spider mites in Canadian greenhouses (Gillespie et al. 2007), and was later used to control several other pests in tomato. It does not damage fruits unless its numbers are high and prey density is low. Recently Calvo et al. (2016) have been looking at the potential of *D. hesperus* to control new invasive pests, such as the potato psyllid *Bactericera cockerelli* (Šulc) (Hemiptera:

Triozidae). Other recent activities concern the evaluation and use of three Neotropical mirids (Hemiptera: Miridae), *Campyloneuropsis infumatus* Carvalho, *Engytatus varians* Distant and *Macrolophus basicornis* Stål, for control of various lepidopteran pests and whiteflies in greenhouse tomatoes in Brazil (Bueno et al. 2013) and, interestingly, during laboratory and greenhouse tests these three mirids seem to cause much less plant and fruit injury than the two commercially used European mirids (Silva et al. 2017; van Lenteren et al. 2018b).

Another important zoophytophagous mirid used for biocontrol in greenhouses is *Nesidiocoris tenuis*. This predator was not native to Europe, but invaded the Mediterranean area in 1985, spontaneously colonized greenhouses and contributed to pest control (Pérez-Hedo and Urbaneja 2016). In some Mediterranean regions *N. tenuis* has become an important player in the battle against whitefly and *Tuta absoluta*, and, in most cases, the benefits of pest reduction outweigh plant damage. In areas where *M. pygmaeus* does not establish well, *N. tenuis* has been mass reared, commercialized, and released with success, and several commercial biocontrol companies offer *N. tenuis* in their portfolio. Indeed, tomato production in Southeast Spain is currently managed using *N. tenuis* as the main pest control method, and *T. absoluta* is a major problem on tomatoes when *N. tenuis* is not released. In other parts of Europe this bug is considered a problem, especially after pest control has been achieved with *M. pygmaeus*. Its plant-feeding results in necrotic rings on the stem, shoots, leaf petioles and flower stalks, that may cause abortion of flowers and young fruit and reduced growth of the plant. Serious injury is observed with large *N. tenuis* populations in the crop, when few or no prey is available, and specially on sensitive crops and varieties, like cherry tomatoes and small-truss tomato types. In France, entomopathogenic nematodes are advised for control of *N. tenuis* resulting in significant reduction of mirid populations and plant damage (https://www.koppert.fr/conseils-de-culture/gamme-nematodes-gel-koppert-de-nouvelles-cibles-dans-le-viseur-des-biosolutions/). *Nesidiocoris tenuis* mainly preys on the eggs of *T. absoluta*, which means that preventive releases have to be made to ensure *T. absoluta* control as soon as the pest appears (Calvo et al. 2012b). Due to slow establishment when weather conditions are not favourable during winter, *N. tenuis* is also released in seedling nurseries before the transplant. This shortens the establishment period, and improves the distribution of the predator in the crop. Such pre-transplant releases may influence biocontrol even in other ways than direct predation on the pest. Puncturing of plants by these zoophytophagous bugs can induce defence related responses that reduce the performance of other herbivores and may also attract other natural enemies (see next section of this chapter). And this, again, shows that generalist, omnivorous predators should not be classified simply as bad or good. Careful study of positive and negative impacts, and next, a well-balanced evaluation of effects may result in proper use of mirid predators and enhance sustainability in pest control (Pappas et al. 2016; Bouagga et al. 2018b).

The success of zoophytophagous mirids in biocontrol programmes in European greenhouses resulted in increasing interest in the search for these mirids as candidates for biocontrol of pests outside Europe (van Lenteren et al. 2016; Silva et al.

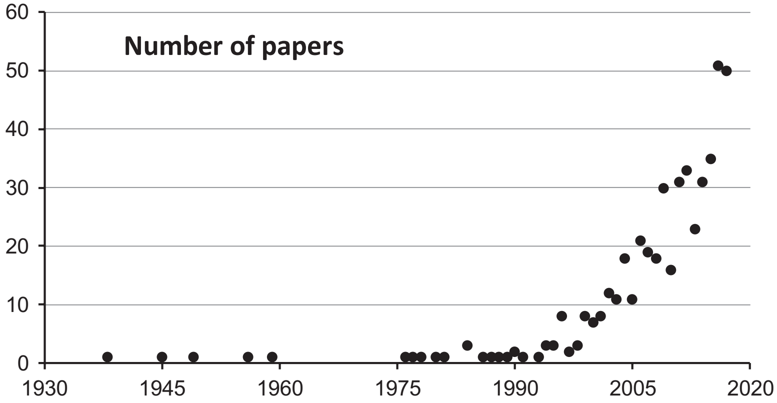

Fig. 14.3 Number of papers indexed in the Web of Science that include the search terms '*Macrolophus*', '*Dicyphus*' or '*Nesidiocoris*'

2017; Pineda et al. 2016). Overall, the number of research papers that appear in the Web of Science mentioning either '*Macrolophus*', '*Dicyphus*' or '*Nesidiocoris*' has steadily increased since early work with mirids on tomato published in France and Spain (Fauvel et al. 1987; Gabarra et al. 1988) (Fig. 14.3).

Most papers are related to the assessment of new species, testing them in crops, and to basic research on plant-feeding habits etc., but not so much on how to control them when considered 'pests'. This highlights to what extent their management is considered beneficial within IPM programmes. Still, when an omnivorous predator species may pose a risk of injury to the target crop, any measure promoting their establishment, augmentation or persistence should be carefully tested in order to avoid excessive predator populations at critical times during the cropping period. Unrestricted augmentation strategies may facilitate migration between successive or neighbouring crops (Castañe et al. 2004), thereby enhancing the risk that recently transplanted crops may receive too high populations. Conversely, screens used to avoid pest entrance may also concentrate too high predator populations in the greenhouse. In addition, too frequent use of supplemental foods may result in fast population growth and damage (Moerkens et al. 2016). Further, banker or companion plants should be selected or managed in such a way that they are useful for the target predator (e.g. *M. pygmaeus*), but less so for less desirable species (e.g. *N. tenuis*).

In order to optimize pest control while minimizing plant damage, more research is needed on the mechanisms behind the effects of feeding behaviour of these zoophytophagous species. Of particular interest is the effect of plant feeding on plant quality for herbivores (induced resistance), and on attraction and repellence of herbivores and predators/parasitoids (Durán-Prieto et al. 2017).

14.6 Use of Semiochemicals in Greenhouse IPM

Although application of semiochemicals is not strictly considered a form of biocontrol (the use of a population of one organism to reduce the population of another organism), these chemicals might play an important role in increasing the efficacy of natural enemies. Communication among arthropods and between arthropods and their surrounding ecosystem is for a large part based on chemical information. Knowledge about chemical communication in insects has increased enormously during the past 70 years and some of the findings are used in greenhouse IPM. Chemical compounds playing a role in communication between organisms are generally addressed as semiochemicals (Vet and Dicke 1992).

One group of semiochemicals has been used in agriculture since the 1970s: insect pheromones (Baker 2009). A pheromone is a chemical compound that evokes a responses in an organism of the same species and they often play a role in communication between the sexes. The composition of many of these sex pheromones has been analysed and can be synthetically produced. Pheromones are applied in agriculture to discover whether pests are present (monitoring technique), to attract and trap pest insects (mass-trapping technique), or to confuse communication by releasing pheromones in such concentrations that sex partners can no longer find each other (mating disruption technique). In greenhouses, mainly the monitoring technique is used, for example to detect the presence of several lepidopteran pests (e.g. *Tuta absoluta*, and several noctuids (Lepidoptera: Noctuidae) as *Chrysodeixis chalcites* (Esper), *Lacanobia oleracea* (L), *Ostrinia nubilalis* (Hübner), and *Spodoptera exigua* (www.biobest.be, www.koppert.com). The mass-trapping technique is used for control of *T. absoluta* (www.koppert.com). Interestingly, natural enemies of pests can spy on the sexual communication used by pest insects. They use the sex pheromone to detect if and where pest insects are present (e.g. Fatouros et al. 2008), but this knowledge is not yet commercially applied. In this case, the pheromone is used by the parasitoid as a kairomone, because not the emitting organism (the pest producing the pheromone) is benefitting, but an organism of another species, the parasitoid.

Natural enemies use chemical compounds of other natural enemies, pests, plants and other players in (agro-) ecosystems in many different ways to obtain information on the presence of refugia, food or hosts for reproduction. In this paragraph we concentrate on the effects of chemical information produced by plants, particularly after they have been attacked by pests. Plants have evolved with different types of defense mechanisms to minimize attack by phytophagous pests. These defenses can, among other phenomena, cause the production of secondary metabolites and proteins that have toxic, repellent and/or anti-nutritive effects on herbivores (direct defenses) (Kant et al. 2015), and these chemical compounds are then addressed as allomones, because they benefit the emitter of the volatile – the plant – but not the receiver, the herbivore. Furthermore, production and release of plant volatiles (Herbivore Induced Plant Volatiles; HIPVs) is triggered by attack of plant-eating arthropods, and this can modify the behaviour of both phytophagous pests and their natural enemies (indirect defenses) (Dicke 2016). These plant volatiles, such as the green leaf volatiles (GLVs) and others as terpenoids, play an important role in signaling information for natural enemies to be attracted to the damaged plant (Peterson et al. 2016), and in this case we speak about synomones, because the volatiles produced by the plant are benefitting both the emitter, the plant, and an organism of a different species, the natural enemy. Therefore, HIPVs, if properly managed, could offer an excellent tool to increase the presence of natural enemies in crops. There are two possible ways in which the use of HIPV's could attract and promote natural enemies within a greenhouse crop: (i) intercropping plant species that emit endogenously HIPV's and (ii) applying exogenously HIPV's on the crop. Conservation biocontrol strategies based on endogenously and exogenously HIPV's have been tested mainly in outdoor crops with promising results (James 2005; Mallinger et al. 2011). However, few studies concern greenhouse crops, while we expect this approach could be even more exploited than in outdoor crops. Recently, several studies indicated that HIPV's might already be playing an important role in the pest management of several horticultural crops where zoophytophagous predators are actively used. Pérez-Hedo et al. (2015) demonstrated that phytophagy by the mirid predators *N. tenuis* and *M. pygmaeus* activated the metabolic pathway of jasmonic acid (JA) in tomato, which made them more attractive to the whitefly parasitoid *Encarsia formosa*. The HIPVs involved in the defensive responses of tomato induced by *M. pygmaeus* and *N. tenuis* and responsible for parasitoid attraction have been identified: six green leaf volatiles (GLVs) and methyl salicylate (Pérez-Hedo et al. 2018). In general, plants exposed to *N. tenuis* emitted more volatiles than plants exposed to *M. pygmaeus*. In sweet pepper, phytophagy by the anthocorid predator *O. laevigatus* also triggers defensive responses and also here *E. formosa* attraction is induced; *O. laevigatus* attack results in the release of a mixture of volatiles (5 terpenes, 2 GLV's, methyl salicylate and one to be identified) and the activation of the JA and salicilic acid (SA) metabolic pathways (Bouagga et al. 2018a). Also phytophagy by *N. tenuis* and *M. pygmaeus* in sweet pepper caused attraction of *E. formosa* and resulted in production of volatiles similar to those produced by *O. laevigatus* (Bouagga et al. 2018b). Altogether these results show how the plant's response to zoophytophagous predators increases emission of HIPV's which can modulate the behaviour of other arthropods, both pests and natural enemies. Indeed, these induced defenses could partially explain the great success achieved by IPM programmes based on the release, establishment and conservation of zoophytophagous predators in crops as sweet peppers and tomatoes (Fig. 14.4). Some authors recommend the use of zoophytophagous predators as vaccines, so that releases of these predators on seedlings can activate the the defense mechanism of the plants at the moment of transplantation to the greenhouse (Pappas et al. 2015; Bouagga et al. 2018b). Furthermore, because some HIPV's might be elicitors of the induction of indirect defenses in horticultural crops, recent results have demonstrated that activation of JA pathway in intact tomato plants is possible by simply exposing them to a HIPV of synthetic origin (Pérez-Hedo et al. personal communication). Therefore, imitating the defenses induced by zoophytophagous predators with elicitors of synthetic origin may be an effective natural alternative to induce defenses in

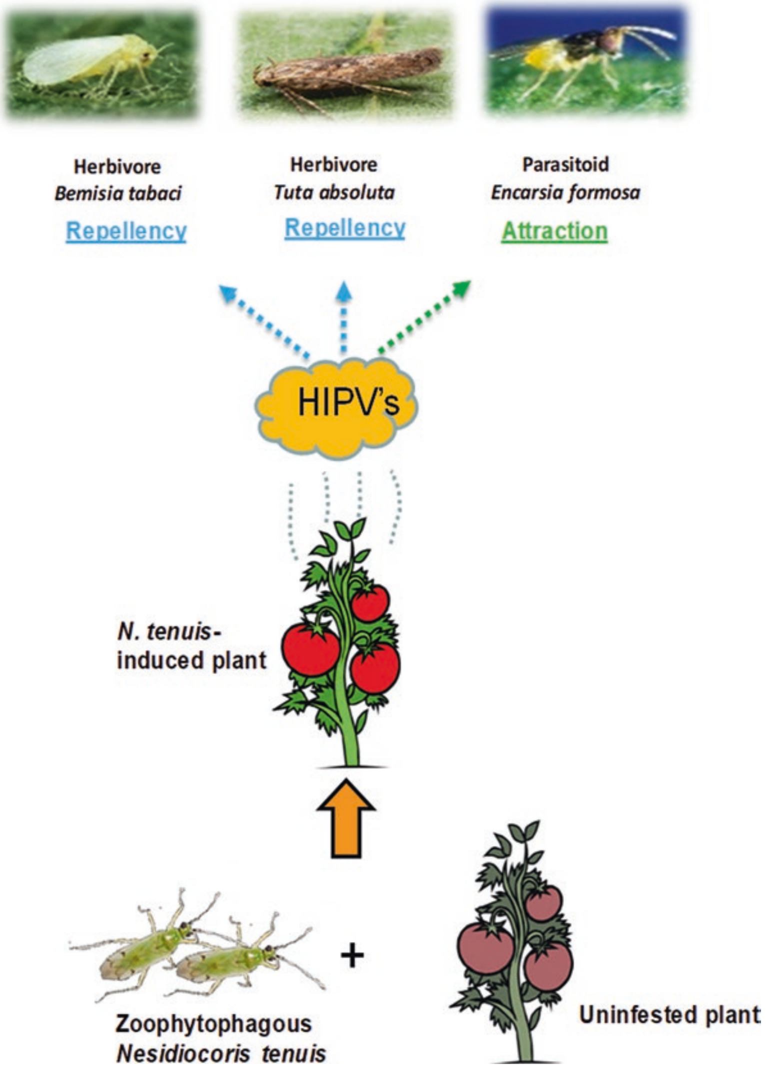

Fig. 14.4 A conceptual model of how HIPV's triggered by the zoophytophagous predator *Nesidiocoris tenuis* can attract or repel arthropods. In the model, an uninfested tomato plant is activated by *N. tenuis* feeding. Activated plants produce HIV's resulting in (i) a repellent effect on the whitefly *Bemisia tabaci* and the lepidopteran *Tuta absoluta*, and (ii) in attraction of the whitefly parasitoid *Encarsia formosa.* (Adapted from Pérez-Hedo et al. 2015)

greenhouse crops. Finally, the rapid advance of gene editing technology allows us to speculate that in a future not too far away the production of plants with an increased ability to attract natural enemies after pest attack will be possible (Gurr and You 2016).

14.7 Future Developments of Biological Control of Greenhouse Pests

We are very positive about the future of biocontrol in greenhouses. Growth percentages for sales of biocontrol agents have during the past 10 years been considerably higher than for conventional synthetic pesticides (Dunham 2015) and this is for a large part due to the inherent positive characteristics of biocontrol agents. These agents are basically harmless to the health of farm workers and persons living in farming communities. Also, they do not have a harvesting interval or re-entry period as do pesticides. Further, they are more sustainable, as there has been no development of resistance against arthropod ABC agents. In addition, the large majority of biocontrol agents do not cause phytotoxic damage to plants and, as a result, most farmers report better yields and healthier crops after switching to biocontrol-based IPM. Consumers continue to express concerns about food safety and environmental impact issues in relation to synthetic pesticide use. Food retailers and supermarkets often have stricter demands about pesticide use and MRL levels than governments do. The current EU approach to stimulate development and adoption of IPM programmes, in which biocontrol is a cornerstone, has increased interest in and application of ABC (Lamichhane et al. 2017). The decision by the EC (2009) that a large number of pesticides will be legally discontinued will also lead to increased requests for ABC solutions. The development of new and better biocontrol solutions during the past decades, improved and more stable formulations for microbial biocontrol agents and their use as seed treatments, and more convenient application methods for invertebrate biocontrol agents have resulted in increased respect for biocontrol as a reliable alternative for synthetic pesticides. More important, biocontrol provides a solution for quite a number of pests in greenhouses that can no longer be controlled with synthetic pesticides due to lack of efficacy and development of resistance. Moreover, biocontrol agents are usually the only option for real IPM programmes and in many cases displaced failing chemical pest control.

There are, however, also developments that may hamper or delay implementation of biocontrol in IPM. We have already mentioned the increased regulatory requirements and the strongly negative effects of the implementation of the Nagoya protocol concerning Access and Benefit Sharing issues. We are, of course, in favour of the fair and equitable sharing of benefits arising from the utilization of genetic resources, but implementation of the protocol without availability of clear guidelines has resulted in a bureaucratic nightmare for researchers. International harmonization of regulations concerning environmental risk analyses and registration would result in faster implementation and lower costs of biocontrol agents. The following might be a surprising statement for many, but also researchers may frustrate implementation of biocontrol by publishing “immature or speculative” papers stating that their findings show as a result of laboratory research under highly standardized conditions that certain natural enemies are very promising candidates for biocontrol. We agree with Brownbridge (2017) that: “True measures of performance (- of a natural enemy, authors -) need to be done with this framework (- the production environment, authors -) in mind and the contribution and fit of the biocontrol agent considered within a defined production system. … Yet bridging the gap between discovery to implementation and integration is critical to the broader uptake of biologically-based IPM. …. Studies should be designed to duplicate commercial environments and data interpreted using appropriate statistical analyses" (end of quote).

On the positive side, there are also research developments aiming to result in improved practical biocontrol, such as the BINGO project, whose main objective is to deliver improved biocontrol agents genetically selected for optimal trait values (https://subsites.wur.nl/en/bingo.htm). This would allow to improve the efficacy of these natural enemies obtained through selective breeding in a broad range of agricultural systems and environmental conditions (Lommen et al. 2018).

Finally, those working in practical biocontrol of arthropod pests are hoping for several contributions from those working in pure and applied science. First, improvement of methods for finding and quick evaluation of natural enemies is of high priority (Ravensberg 2011; van Lenteren et al. 2019). Currently, still a lot of time is spent on studying potential candidates that appear to be inefficient after having spent a considerable amount of time and money. Fast, but meaningful evaluation methods would be very helpful in speeding up the trajectory from discovery to marketing (van Lenteren et al. 2019). Secondly, perfection of quality control protocols is needed (van Lenteren 2003). Some of the presently used quality criteria are not really telling a lot, others that do so are often time consuming. A simple to determine, but reliable characteristic would be appreciated. Thirdly, progress in storage methods is of great importance as most arthropod can only be stored for a few days without loss in performance. Finally, methods and equipment for large scale release without quality loss of the natural enemies are essential, but this problem might be solved rather quick as developments in the field of mechanical distribution and releases with drones are fast.

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Chapter 15
Chemical and Natural Pesticides in IPM: Side-Effects and Application

Maria Lodovica Gullino and Luciana Tavella

Abstract The regulation for the registration and use of pesticides, also including natural products, currently in place in the different countries, although not completely normalized, has become very stringent in all industrialized countries, leading to a strong reduction in the number of active ingredients available on the market and to a severe reorganization of the agrochemical industry, which is shrinking. Most of greenhouse crops are ranked among minor crops, and some pesticide usages, such as seed dressing, are considered a minor use. Although the use of pesticides for the management of most pests and diseases of greenhouse crops remains important and often crucial, in general, a limited number of them is available for minor crops and/or minor uses. The choice of the chemical and its application methods is very important in order to guarantee its compatibility with the use of other control methods, particularly biocontrol agents, its control efficiency, and prevention of residues being above the maximum residue level (MRL). Aspects such as selectivity, phytotoxicity, development of pesticide resistance, and residues are critically discussed. Special attention is also devoted to fumigants and natural products, including resistance inducers.

Keywords Chemicals · Regulation · Selectivity · Phytotoxicity · Resistance · Residues · Natural products · Resistance inducers

Although the use of pesticides for the management of most pests and diseases of greenhouse crops remains important and often crucial, the choice of the chemical and its application methods is very important in order to guarantee its compatibility with the use of other control methods, particularly biocontrol agents, its control

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efficiency, and prevention of residues being above the maximum residue level (MRL). The regulation for the registration and use of pesticides, also including natural products, currently in place in the different countries, although not completely normalized, has become very stringent in all industrialized countries, leading to a strong reduction in the number of active ingredients available on the market and to a severe reorganization of the agrochemical industry, which is shrinking (Oliver and Hewitt 2014). In the European Union, for instance, the Regulation No 1107/2009 concerning pesticide registration, which is accompanied by a Directive on the Sustainable use of pesticides (Directive 2009/128) and by National Action Plans for reduction of their usage, is strongly regulating pesticide registration and application. As a result, about 50% of the pesticides available in the 1990s have been withdrawn. The aim is to eliminate all active ingredients that pose a particular hazard to the public or the environment. One of the most targeted effect is the so called "endocrine disruption", typical of many insecticides. In comparison with just a few decades ago (Blumel et al. 1999), much more attention is currently paid, during the development of a new pesticide, to the evaluation of its possible side-effects, in order to tackle them since the start of its application. The EU regulation currently in place, introduced the concept of "substitution" of "hazardous" compounds with products with the same or similar crop protection properties (Leadbeater and Gisi 2010). While many of pesticide classes in use in the 1990s are still providing good value, several new classes, including the quinone outside inhibitors (QoIs) and succinate dehydrogenase inhibitors (SDHIs) among fungicides and the ryanodine receptor modulators and the selective feeding blockers or inhibitors among insecticides, have been introduced.

In general, a broad arsenal of pesticides is still available for major crops, while often a limited choice represents a constraint for minor crops and/or minor uses. Unfortunately, most of greenhouse crops are ranked among minor crops, and some pesticide usages, such as seed dressing, are considered a minor use. By contrast, since greenhouses are considered as a confined environment, some pesticides, which have been banned from using in the field, are still allowed in greenhouses, such as the recent case of most neonicotinoids. However, Europe is faced with having to produce profitably and sustainably using fewer pesticides (Hillocks 2012). Most of the crops considered in this book are left with few or no registered crop protection products (Hillocks 2012). In Europe, a database with the current status of any pesticide or active ingredient (EU Pesticides database), as well as a list of databases on registered plant protection products (https://www.eppo.int/PPPRODUCTS/information/information_ppp.htm), are available. While addressing readers to specific reviews and books on pesticides currently available and their modes of action (Isman 2006; Ishaaya et al. 2007; Krämer et al. 2012; Oliver and Hewitt 2014), this chapter will focus on the main aspects related to pesticide application under integrated pest and disease management in greenhouse crops. Special attention is also paid to possible negative side-effects, such as selectivity, resistance and limited availability of pesticides for minor crops and minor uses, also including natural products.

15.1 Side-Effects

15.1.1 Selectivity

In the frame of integrated pest and disease management, one of the most important characteristics of the pesticide choice should be its selectivity, expressed by its activity against a limited range of target specific pests with a minimal impact on non-target organisms (Heitefull 1975). Such characteristic permits to ensure its activity against the target pests and diseases, with a minimum effect on non-target and potential useful organisms and microorganisms (Hull and Beers 1985). During the past decades, selectivity has been particularly exploited during the process of pesticide development. The increasing use of biocontrol agents in the practice requires, in order to permit their establishment and survival, a strong selectivity of the pesticides applied. The selectivity of action and toxicity of a pesticide depends on its physiological selectivity and/or the application methodology and timing (Blumel et al. 1999). The physiological selectivity is expressed by reduced sensitivity of an organism to the pesticide, due to pesticide metabolism and to the availability of the enzymes capable of breaking it down in the target organisms (Hassall 1982).

Plant protection products may adversely affect beneficials via (a) direct contact during spray application or spray residues on the plant tissue surface, (b) ingesting contaminated plant tissue or fluids, and (c) being exposed by feeding on contaminated hosts (Richter et al. 2016). Most pesticides have lethal effects on natural enemies of plant pests, and mitigation of such undesired side-effects can be achieved by selecting the product with the least non-target activity, even if most insecticides have a broad spectrum of action and very few are completely selective (Messelink et al. 2014). Several studies have been performed on side-effects, achieving variable results depending on active ingredients, formulations, insect species, developmental stages and habitat (Talebi et al. 2008; Horowitz et al. 2009; Cloyd 2012).

Besides lethal effects, sub-lethal effects affecting physiology and behaviour of natural enemies (development, longevity, fecundity and fertility, mobility, etc.) must also be considered as a risk of viability reduction (Stark et al. 2004; Desneux et al. 2007; De Franca et al. 2017). Several pesticides are known to cause sub-lethal effects on biocontrol agents largely used in greenhouses, such as the predatory mite *Phytoseiulus persimilis*, the minute pirate bug *Orius laevigatus*, the green lacewing *Chrysoperla carnea* and the ladybird *Adalia bipunctata* (Nadimi et al. 2011; Biondi et al. 2012; Garzón et al. 2015).

Undesired side-effects on natural enemies can be reduced by adapting the timing, place and mode of pesticide application, by creating refuges or by developing new release methods. Moreover, persistence of residuals must be considered especially for pesticides with a high level of persistence, which can disrupt natural enemy establishment over long periods. For example, synthetic pyrethroids applied against several crop pests can be lethal for predatory mites (i.e., Phytoseiidae) over 2 months (Bostanian and Belanger 1985).

15.1.2 Phytotoxicity

Another important aspect related to pesticide use of particular relevance in the case of ornamental crops, relates to the broad range of genera, species and varieties grown. For instance, just as an example, in the case of rose (*Rosa canina*), thousands of varieties have been developed, with a very quick evolution of consumer's taste. The same active ingredient, while effective against the target pathogen, can cause phytoxicity on some varieties. Since testing all varieties of ornamental crops grown during pesticide development is almost impossible, in addition to being extremely costly, the application of any active ingredient on a new variety in the case of ornamental crops should be done only after previously testing it on few plants.

There are many examples of phytoxicity observed and reported. Plants can manifest several phytotoxic reactions to insecticides including chlorosis, necrosis, burn, leaf distortion, and abnormal growth or stunting (Short 1981; Ebel et al. 2000). Moreover, phytotoxic effects of pesticides can vary in relation to the water quality (Vukovic et al. 2014), and to the temperature and relative humidity conditions within the greenhouse.

The risk of phytotoxicity represents, especially for ornamentals, one more constraints to the registration of new chemicals, thus often letting the sector with limited choice of available chemicals, particularly after the loss of the old ones.

15.1.3 Pesticide Resistance and Strategies to Counteract It

Pesticide resistance represents, since the 1970s, the most severe challenge to pesticide usage. Its appearance and spread are linked to the commercialization and repeated use of pesticides having a specific mode of action. Pathogens and pests may overcome the effect of pesticides with different mechanisms: by modifying the target site, by metabolizing the active ingredient into less toxic compounds, by reducing the adsorption of the active ingredient or by avoiding the exposure to it. Greenhouse crops, because of their susceptibility to a number of pathogens and pests and because of the closed environment, which provides favourable conditions for both the spread of resistant strains and the rapid pest population growth, are most prone to be subject to this problem.

In the case of fungicides, resistance did develop in many pathogens (e.g., *Botrytis cinerea,* different causal agents of downy and powdery mildews, *Alternaria* spp.) towards several classes of fungicides (e.g., benzimidazoles, dicarboximides, phenylamides, sterol biosynthesis inhibitors, QoIs). Fungicide resistance spreads quite easily and quickly in the confined greenhouse environment.

The phenomenon of resistance development has been and is particularly serious and frequent in the case of *B. cinerea*, a high risk pathogen in terms of fungicide resistance development (Brent and Hollomon 1998), which also very often requires frequent application of fungicides. Evolution of resistance in this pathogen to different classes of fungicides has been frequently reported on many crops (Katan 1983; Gullino 1982; Moorman and Lease 1992; Dianez et al. 2002; Baroffio et al. 2003; Zhang et al. 2009; Stylianos et al. 2011; Veloukas et al. 2011; Zhang et al. 2011; Gullino et al. 2012). Multiple fungicide resistant phenotypes of this pathogen are predominant in most greenhouse crops (Myresiotis et al. 2007; Fan et al. 2017; Fernandez-Ortuno et al. 2017; Rupp et al. 2017; Weber and Entrop 2017). A recent study carried out on greenhouse crops in Cyprus revealed the resistance profile and genetic structure of *B. cinerea*, and showed that less than 9% of the isolates tested were sensitive to all botryticides (Kanetis et al. 2017). Such situation poses a major threat to the chemical control of grey mould. *B. cinerea* also showed its capability to adapt to pyrrolnitrin, an antibiotic identified in many biocontrol agents active against it (Ajouz et al. 2010).

Also different powdery mildew agents of greenhouse crops (e.g., cucurbits, rose) developed resistance to different classes of fungicides (benzimidazoles, DMIs, and more recently to QoI and SDHI fungicides. The same happened with several causal agents of downy mildews (e.g., cucurbits, basil), which became resistant to phenylamides first and more recently in some cases to QoIs.

As experienced in the 1970s with benzimidazoles, site-specific inhibitors such as QoI fungicides, which are widely applied due to their broad spectrum of activity on a number of crops, carry a high risk of resistance development in many pathogens. In fact, shortly after their introduction, in the late 1990s, resistance to QoIs developed in cucumber and melon powdery mildew (*Podosphaera fusca*) and in cucumber downy mildew (*Pseudoperonospora cubensis*) (Ishii 2006). *Pseudoperonosora cubensis* also developed resistance to systemic carboxylic acid amides (CAA) fungicides, such as dimetomorph and flumorph (Zhu et al. 2007). QoI resistance is quite widespread also in *B. cinerea* on many crops (Stylianos et al. 2011) as well as in *Colletotrichum acutatum* on strawberry (Forcelini et al. 2016). In the case of *Didymella bryoniae,* the causal agent of gummy stem blight of watermelon, resistance to benzimidazoles, QoIs and boscalid has been observed (Thomas et al. 2012).

Fungicide resistance is much less widespread in the case of soil-borne pathogens, also due to a much more limited use of fungicides for soil treatments and to the fact that in general soil-borne pathogens are less prone to developing resistance.

In the case of insecticides, resistances to conventional insecticides are widespread and well documented, while those to bio-insecticides have raised less attention, and resistance management is frequently neglected (Siegwart et al. 2015). There are different types of resistance: (1) multiple resistance, to several insecticides of different classes by multiple mechanisms; (2) cross resistance, to one insecticide leading to resistance to another yet unused insecticide; (3) negative cross-resistance, resistance to insecticide A leads to susceptibility to insecticide B and vice versa.

In the Mediterranean basin, an example of multiple insecticide resistance to a wide range of insecticides (e.g., pyrethroids, organophosphates, insect growth regulators, spinosad) is well represented by the tomato borer *Tuta absoluta*, which thanks to its rapid spread has become of major concern in Europe (Haddi et al. 2012; Ferracini et al. submitted). Moreover, it is known that most of the noxious greenhouse pests, including thrips (*Frankliniella occidentalis* and *Thrips tabaci*), whiteflies (*Bemisia tabaci* and *Trialeurodes vaporariorum*), and aphids (*Aphis gossypii* and *Myzus persicae*), developed insecticide resistance to several insecticides (IRAC 2018).

Often, resistance to different classes of pesticides in the same pathogen or pest, as mentioned above, causes the presence in the field of strains of pathogens and pests showing multiple resistance. This phenomenon, particularly frequent for instance, among fungal pathogens, in the case of *B. cinerea* on many crops (e.g., tomato, lettuce, basil, rose, cyclamen) and among insects, makes difficult the control of important pathogens and pests.

Under IPM, pesticides not only must be applied only when strictly necessary and as last defense barrier, but also by mixing or even better by rotating active ingredients having different modes of action (van den Bosch et al. 2014). This is the most important principle to be adopted in order to reduce the risk of development of field resistance. In this context, the Fungicide Resistance Action Committee (FRAC) and the Insecticide Resistance Action Committee (IRAC) play an important role by promoting the development and implementation of pesticide resistance management strategies to maintain efficacy and support sustainable agriculture and improved public health. A key function is the development of the Mode of Action classification scheme, which provides up-to-date information on the modes of action of new and established pesticides and serves as the basis for developing appropriate pesticide resistance management strategies for crop protection (Sparks and Nauen 2015). However, in the case of some greenhouse crops, the limited availability of chemicals with different modes of action, caused by the current legislation, may pose problems to the possibility of a good rotation among pesticides belonging to different chemical classes.

Some suggestions about using high dosages of pesticides for reducing the risk of resistance, which seem to have come from insecticide resistance literature, do not apply to fungicides. Insect pests are mostly diploid and reproduce sexually: in this case high dosages are likely to delay resistance emergence by removing the majority of resistance genes from the population, as they initially contained within heterozygote individuals (provided the resistance is sufficiently recessive) (Mikaberidze et al. 2016). However, this situation does not apply to most fungal pathogens, which are either haploid or clonal (van den Bosch et al. 2011).

15.1.4 Residues

The correct usage of pesticides, respecting dosages and timing of application, permits to avoid the presence of residues higher than those admitted by National and International Regulation. At European level, the data annually collected and elaborated by the European Food Safety Authority (EFSA), regularly made available to the public (EFSA 2017) show, by analysing the last available report, which elaborates the data of 2015, that 97.2% of the samples analysed fell within the limits permitted by EU legislation. Interestingly, 53.3% of the samples tested are free of quantifiable residues, while 43.9% contain residues not exceeding legal limits. Such data show the progress done in industrialized countries thanks to an improved usage of pesticides, coupled with good regulation. Some concern is still related to imported products, which often show residue levels of some pesticides higher than those admitted. In 2015, 5.6% of imported products exceeded legal limits, down from 6.5 in 2014. Unfortunately, in many third world countries no set MRLs and no market control for legal residue content are in place. Such situation poses local consumers under risk of consuming illegal amount of pesticide residues and put at risk the export from these countries. Although washing solutions for decreasing residue levels in vegetables are available, providing good results in removing the residues to values below the MRL in most cases, as shown for instance with mychlobutanil, fenhexamid and boscalid residues in sweet pepper and cherry tomatoes in Egypt (Sherif et al. 2010), a long term approach relies on programmes aimed at controlling the residue levels.

15.2 Fumigants

A type of pesticides very much regulated lately are the fumigants employed for soil or substrate disinfestation or in post-harvest, pre-shipment treatments. In particular, soil fumigation consists of applying volatile, wide spectrum biocides that act as vapor and liquid phases. For many years, fumigants have been used to control a wide spectrum of soil pathogens and pests and weeds, on many greenhouse crops. The most frequently applied one, methyl bromide, due to its inclusion in the list of chemicals that deplete the ozone layers has been phased out (Colla et al. 2014; Chap.12 in this book. Under the current European regulation, very few fumigants are available, with stringent rules in terms of dosages and frequency of application. In the future, their use will be further restricted (Colla et al. 2014), posing serious problems in the management of soil-borne pathogens and pests (see Chap. 12 in this book).

15.3 Influence of Mode and Timing of Pesticide Application

The mode and timing of application of pesticides can influence their activity, selectivity as well as resistance development. Such aspect is of special importance in the relative small area of greenhouses, in comparison to open field. Due to the high plant density, manually operated spraying equipment is often adopted, with optimal distribution of the active ingredient and best results in terms of pest and disease control. In the meantime, the optimal distribution of the pesticide can adversely affect the biocontrol agents, such as antagonistic fungi and beneficial arthropods, as well as pollinators such as bumble-bees (Blumel et al. 1999). Much improvement in the application of soil fumigants, with the use of virtually impermeable plastic films, led to a significant reduction in the dosages applied as well in more limited emissions into the atmosphere (Colla et al. 2014), as well pointed out in Chap. 12 in this book.

Mode, timing and place of pesticide application can be adjusted to reduce undesired side-effects on natural enemies (see Chap. 15 in this book). For example, insecticides must be applied when beneficials are at the most insecticide-resistant life stage. In case of augmentative biological control, natural enemies must be released after insecticide applications and when insecticide residuals are harmless. Also site-specific or precision pest management, i.e. targeting applications only in fields or parts of the field with high pest pressure, can be useful to protect natural enemies from insecticide exposure. In conservation biological control, alternative-row and border-row spraying preserves beneficial populations at a landscape level, since as the spatial scale of insecticide application increases, the potential for re-colonization by natural enemies declines (Roubos et al. 2014).

Depending on their mode of action, insecticides can be applied by foliar spray or to the soil/growing medium; in this case, material can be drenched as a liquid, distributed into pots or sub-irrigation system, or surface applied as granules (Cloyd et al. 2011). Systemic insecticides are adsorbed by plant roots and then translocated in the vascular system, and their movement within plant tissue depends on their chemical characteristics (Byrne et al. 2010).

Improvement in application technology is leading to a strong reduction in pesticide losses into the environment. In recent years, such improvements interested also greenhouse crops. Manufacturers of field crop and orchard sprayers did progressively introduce new and improved devices, taking advantage of the last developments in computers, electronics, and global positioning systems (Llop et al. 2015). Those improvements consist in safer and more effective use of pesticides, with less risk of contamination, adapting the dosage to the canopy structure and the leaf area index of the crop plant, and improving traceability. However, the implementation of the new technologies under greenhouse is not yet so widespread, and handled sprayer and knapsack are still very popular (Nilsson and Balsari 2012). Spraying techniques alternative to handled sprayers have been tested: the use of vertical boom sprayers for instance improves spray distribution under greenhouse conditions (Sanchez-Hermosilla et al. 2012), also reducing labor cost and worker exposure (Nuyttens et al. 2009). Also navigation systems and autonomous vehicles with ultrasonic sensors or machine vision have been tested (Balsari et al. 2012). Unfortunately, the use of such equipment is strongly limited by their high cost. A study carried out on greenhouse tomato with the aim of evaluating the influence of air-assistance on spray application showed improved results in terms of deposition and uniformity of distribution (Llop et al. 2015).

Considering the economic importance of greenhouse production, there is indeed a need to improve pesticide application process, at the moment still hindered by a lack of advanced technologies as well as by constraints in their application in comparison to other agricultural sectors.

15.4 Natural Products, Including Resistance Inducers

During the past years, many so called “natural compounds”, mainly salts, oils, extract have been increasingly exploited for pest and disease management. Some of them derive from organic agriculture, where they have been applied for many years, often without a thorough scientific knowledge about their mode of action. Recent studies carried out in order to improve knowledge concerning the products applied in organic farming led to a better understanding of the potential of some natural products. In particular, a number of products with different structure and of organisms from different origin sharing the ability to induce resistance in the host have been tested and in some cases applied in practice (da Rocha and Hammerschmidt 2005; Walters and Fountaine 2009; Deliopoulos et al. 2010; Alexandersoon et al. 2016).

The increasing interest in their use relies on their broad spectrum of activity, since they often act on the host instead of on the pathogen, as well as on the possibility of reducing, with their use, the number of synthetic fungicide sprays, due to their long lasting action. In general, the resistance inducers are able to activate the inducible signalling pathways of the host, thus strengthening plant defence (Shoresh et al. 2010; Walters et al. 2013). However, their efficacy is rarely complete (Walters and Fountaine 2009) because it is generally influenced by several factors such as the target pathogen (i.e., biotrophic or necrotrophic), the plant genotype and its development stage, the environmental conditions (temperature, relative humidity, disease pressure), the timing, formulation and type of application (Walters et al. 2013). Additionally, biostimulants, which consist of different substances from a broad range of source materials and microorganisms able to enhance plant growth, have received an increased attention (Calvo et al. 2014; Yakhin et al. 2015; Le Mire et al. 2016).

Biopesticides used to control pests and diseases in organic greenhouse crops are commonly based on botanicals, microbials and minerals (Horowitz et al. 2009). They vary in their mode of action, chemical families and formulation. Some natural substances, such as oils and plant extracts, are usually non-specific when applied on insects; however, after drying, residues of oils are usually harmless. Effects of botanicals such as pyrethrins and azadirachtin, while being harmful, are short term, and in the field, at least a proportion of the natural enemies survive apparently by being in the right place and the right time, thereby avoiding direct exposure to the pesticide and to sprayed surfaces (Castagnoli et al. 2002; Raguraman and Kannan 2014).

Research on commercially available microbials and the applied use of combinations of arthropod natural enemies and microbials have remained relatively under explored despite their use for a quite long time. Recently, the current uses of entomopathogenic fungi (e.g., *Beauveria bassiana*, *Isaria fumosorosea*, *Lecanicillium muscarium*, *Purpureocillium lilacinus*), bacteria (e.g., *Bacillus thuringiensis*) and viruses, and their possible direct and indirect effects on arthropod natural enemies in European greenhouses has been reviewed (Gonzales et al. 2016). Moreover, the possibilities of using other microorganisms for biological control, such as endophytes, and the need to understand the effect of insect-associated microorganisms, or symbionts, on the success of biological control should be further exploited (Gonzales et al. 2016).

Other methods include the use of organic soil amendments such as compost (Bonanomi et al. 2007; Pugliese et al. 2015; Gilardi et al. 2016), biochar (Bonanomi et al. 2015), *Brassica* green manure and defeated dried pellet and their possible effect under soil solarization conditions (Garibaldi et al. 2014). They have been considered in Chap. 12 in this book.

15.5 Concluding Remarks

Most of the crops grown under greenhouse belong to the so called "minor crops", due to the overall low acreage interested worldwide, though having a very high economic impact at local level and requiring a large amount of pesticides. As a consequence, in many cases a limited availability of registered pesticides often represents a challenge to growers and extension services. Such situation represents a further suggestion to pursue a reduction in the use of chemicals, as suggested under IPM. Disease and pest management with less pesticides has been carefully described for lettuce (Barriere et al. 2014) and is possible for many crops, provided that a good extension service is available to assist growers. The new developments in research, the availability for many greenhouse crops of varieties with a good level of resistance permit to limit the use of pesticides to the most critical situation.

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Part III
Implementation of IPM in Major Greenhouse Crops

Chapter 16
Implementation of Integrated Pest and Disease Management in Greenhouses: From Research to the Consumer

J. Riudavets, E. Moerman, and E. Vila

Abstract Chapters 6 to 15 in this book provide a complete view of the feasibility of Integrated Pest and Disease Management (IPDM) in protected crops. Within the framework of an advanced sustainable production system, IPDM is the primary response for the growers facing consumer demands of high quality products while at the same time addressing environmental, health/safety and socio-economic issues. Most examples of successful IPDM commercial systems have started with appropriate planning of the necessary research. However, the fact that researchers have developed an IPDM programme does not necessarily mean that growers will automatically implement it. In this chapter, we have summarized the entire process to transfer the innovative knowledge from research to practical application, with special emphasis on the application of biological control (BC) of pests and diseases and the commercial development of biological control agents (BCAs).

Keywords IPDM development · Demonstration trials · Field application · Innovation · Transfer · Extension services · Training · Education · Biological control market · Biological control products

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16.1 Research on and Development of BCAs in the Framework of IPDM Programmes

During the past 50 years, BC has become the most important issue of research in the field of IPDM. BC research, both with public and private funding, has experienced a major boom and has produced a large amount of published information. For example, there are more than 17,000 citations in Google Scholar during the period 2013–2017 about the use of BC in greenhouses. Of these, only a few correspond to studies focused on the BC of plant diseases. In comparison, most citations correspond to research studies focused on the control of insect and mite pests. The use of predatory insects and mites as BCAs account more than 7500 citations. There is a lot of information about their biology, natural occurrence and efficacy in the laboratory and in greenhouse conditions. Regarding parasitoids, there are more than 7000 citations in Google Scholar about their biology, host range and performance against key pest species. The number of citations about entomopathogenic fungi, viruses, bacteria and nematodes only exceeds 3000 citations.

Using a worldwide coverage search of national patents offered by the European Patent Office (https://worldwide.espacenet.com/), a total of 159 patents have been found concerning compositions, methods and/or uses of natural enemies, including insect and mite predators or parasitoids. The highest percentage are Chinese patents, representing 57%, with 41 patents describing at least a mass rearing systems, 34 patents about storage and/or releasing systems and 14 patents exclusively about methods of biological control of pests on crops. In the rest of the countries a total of 47, 13 and 8 patents have been published concerning these 3 categories.

Research on BC on greenhouse began in the 1960s, when the main pest of vegetable crops were the spider mite *Tetranychus urticae* and the whitefly *Trialeurodes vaporariorum* (Westwood) (van Lenteren and Woets 1988). Since then, various other pests have occurred into the greenhouse agroecosystem, and in all cases, research aimed at finding BCAs (predators, parasitoids and pathogens) to control these pests (Stiling and Cornelissen 2005). All this previous research now enables us to find relatively easy for most common pest species commercially available BCAs able to replace pesticides (van Lenteren et al. 2018). However, for a number of new invasive or emerging pest species and diseases we do not know the best natural enemy (NE) candidate yet. An example is the problems in tomato, the largest greenhouse crop worldwide: effective biological control is not yet available for *Tuta absoluta* (Meyrick), *Aculops lycopersici* (Tryon) and *Oidium neolycopersici*. Moreover, there is still a very strong demand for applied and commercial studies, because much work is limited to laboratory research. New pest management strategies must be made available to growers to improve existing cultivation methods, otherwise poor pest control may lead to over reliance on chemical pesticides. Expected climate change and increased global trading may impact on the complexity of pest species and diseases present in the different growing areas, which will require the adaptation of innovative methods to prevent the spread of new or emerging pests and diseases.

16.1.1 Fundamentals of BC

Basic research generally involves experiments conducted under controlled conditions to explore and understand the biology and ecology of pests and their NE, and the interaction and relationship between them. Measuring some basic features, such as the reproductive biology, prey/host preference or prey consumption with traditional methodology is generally a tedious procedure. However, from an applied point of view it is very useful to know basic aspects such as the suitability of the host species, whether a population of the introduced NE is properly establishing in the crop, or the quality of mass-rearing insects prior to be released in the field. Also, climatic change, intensification of commercial exchanges and modification of agricultural methods, result in an increased occurrence of invasive, emerging and re-emerging pests and in a need for continuous research to provide the biological basis for their control.

To fully exploit the control potential of NE, it is important to understand their abiotic requirements, and how they match with local conditions. With this aim, laboratory studies under controlled conditions are very useful to determine the biology of the different BCAs at different constant and fluctuating temperatures and at different light regimes and other culture measures. These studies have showed the best environmental conditions at which these NE can be effective to control the target prey.

The study of predator-prey and parasitoid-host relationships is rather complicated. Over the past years, the development of new molecular and chemical techniques to analyse trophic relationships have been developed (Traugott and Symondson 2008). For example, the use of specific molecular markers allows prey DNA detection in sucking insects in which morphological remains cannot be found in their gut in order to identify what they have been feeding on. Those preys may include insect pests, non-pest insects or even other NE (parasitoids or predators) (Moreno-Ripoll et al. 2012). In this way it is possible to know which is the most suitable NE for a particular pest species and which prey/host species is fed/parasitized by a particular NE, and therefore to be able to evaluate the real impact of the NE in field conditions.

Foraging and reproductive behaviour of NE are also an important basic research topics. They include habitat location and host location, and host suitability. During these phases, NE can use physical, biochemical, and mainly semiochemical cues (Godfray 1994; Chap. 16 Biocontrol agents). The evaluation of NE response to these semiochemicals has been a valuable tool to learn how to manipulate their behaviour improving their impact on pest populations in agroecosystems (Vet and Dicke 1992).

Regarding generalist predators, their polyphagia is seldom evaluated in spite of being one of their most appreciated characteristics (Albajes and Alomar 1999; Chap. 14 Biological control agents for control of pests in greenhouses). Studies have been conducted on plant and prey preference of several predatory species in the laboratory, as well as the control capacity of two or more coexisting pest species by one predatory species in the crop. Some species of generalist predators could also show a different degree of plant feeding. Studies have been focused in determining and characterizing the risk of crop damage posed by predatory natural enemies in crops such as tomatoes and cucurbits (Arnó et al. 2010; Chap. 14 Biological control agents for control of pests in greenhouses).

16.1.2 Application of BCAs Under Practical Conditions

The simulation of arthropod food webs at crop level and a broad knowledge on the ecology of pest species and their NE under practical conditions are crucial for the development of an IPDM programme. However, it is not so easy to understand and integrate the diversity of situations in a commercial greenhouse ecosystem. Greenhouse growing areas are landscapes characterised by the coexistence of several annual crops, grown simultaneously all year round. Greenhouses tend to be only partially closed, and the boundaries between greenhouses and open field crops often become blurred, particularly in (semi-) tropical climates. As many crops share the same pests (e.g. whitefly, aphids and thrips) problems are exacerbated, as there is a continuous carry-over of the pests that is hardly interrupted, even in winter (Castañé et al. 2000).

The first step for implementing any IPDM programme is to know how to evaluate pests and BCAs densities to decide on control measures. Research has focused to develop sampling protocols to decide the BCAs and the optimum time to be released (Shea and Possingham 2000). The introduction of commercially produced BCAs in crops is based in the synchronized development of both pest and BCA populations when they are still at low densities. This process has a critical (weak) point that corresponds to the ability of the BCA to establish of the colony of BCA in the crop. Another strategy involves overkill introductions of BCAs to ensure that pest populations never approach damage thresholds. Also, research has focussed to assess different factitious prey or added foods with the aim of improving the establishment of the released BCA in the greenhouses.

The development of mass rearing techniques for producing BCAs and at a reasonable cost is one of the cornerstones for the broad spread of BC. Several groups have been working in developing protocols for mass rearing different BCAs, (see proceedings of the IOBC working group on Mass Rearing and Quality Assurance http://www.iobc-global.org/global_wg_mrqa.html). These studies have focused on issues such as the effect of BCA density per plant on the fecundity of the colony, the genetic drift of the colony, or in developing different diets for predators as a factitious prey, some of them with a considerable reduction in the cost. Another important topic is the behaviour of commercially produced BCAs once they are released in the crop. Mass production conditions are completely different to those that the BCAs should face when released. If the behaviour of the BCAs has changed dramatically due to rearing conditions, it may be less effective in controlling the target pest. Maintaining a high quality of mass reared BCAs is a major concern for producers and end-users. Therefore, quality control guidelines for a number of natural enemies have been established to evaluate their quality in relation to wild populations of the same species (van Lenteren et al. 2003). These guidelines are a result of an intensive cooperation between researchers and the BCAs industry, and are reviewed regularly in the framework of the IOBC Global Working Group on Quality Control of Mass Reared Arthropods and the European and American associations of natural enemies producers (IBMA and ANBP, respectively).

Both researchers, the BCA industry and the agrochemical companies have promoted intense laboratory work to determine the side effects of most pesticides on the commercial BCAs, also due to the increasing dossier requirement for agrochemicals registration (see proceedings of the IOBC working group on Pesticides and Beneficial Organisms https://www.iobc-wprs.org/expert_groups/01_wg_beneficial_organisms.html). Detailed and update information can be found on the web pages of most BCAs producers (i.e. Biobest, Koppert or Agrobio). A positive development is that, the majority of recently developed active chemical compounds are showing less negative effects on BCAs, making their integration easier within the existing IPDM programmes. Fewer side effects of the active compounds increasingly is a criterion during the registration of chemical pesticides in most countries.

16.1.3 Commercial Development of BCAs

Hussey (1985) and van Lenteren and Woets (1988) give detailed descriptions of the first two decades of the history of commercial BC starting in the 1960s. Since the 1960s, BC grew from a scientific activity to a commercially interesting venture and a technically reliable way of pest management. Years of fundamental and applied research, together with considerable investments in the private sector, has been necessary before the BCAs could be used commercially. Today, there are about 500 commercial producers of BCAs worldwide (van Lenteren et al. 2018). The majority of producers are small to medium-sized companies and only less than 10 producers employ more than 50 staff. In addition, there are government-owned and growers association production units.

In a number of countries, supermarkets, their service providers and cooperatives require growers-suppliers to produce their vegetables according to strict guidelines and standards (stricter than the legal standards!), only allowing minimal use of pesticides from a restricted list and in some cases with zero detectable residues in the final product. This has had a strong influence on the implementation of BC and a pressure on the horticulture industry to reduce the use of pesticides (van der Blom 2010). In the past, certification of the safety and quality of products has typically come from government organizations (Hatanaka et al. 2005). Nowadays, retailers put high pressure on growers to reduce their pesticide use. Third party private certifiers have become widely used to audit growers and most horticultural products are endorsed with various labels providing consumers with guarantees that what they purchase has been produced according to particular standards. The role of governments is now much more the encouragement through legislation and other means, and even stimulating the development of new BC strategies (i.e. EU Directive 2009/128/EC on the Sustainable Use of Pesticides).

Large agrochemical companies have started investing in acquisition of biocontrol manufactures, especially of microbial biocontrol agents, semiochemicals and natural products (van Lenteren et al. 2018). This will eventually help in filling the gap between chemical and biological control. Although BCAs represent niche markets that are smaller for large companies, their interest in their development could speed up their usage in practice. Ad hoc regulations in Europe for biopesticide registration and use and particularly BCAs would encourage a faster development of BC.

16.2 Transfer of New IPDM Technology to Extension Services and Growers

The ultimate goal in the development of an IPDM programme is to bring it to the end users. First, basic and applied information produced by researchers is published in scientific journals after a peer review process. In addition, researchers usually present their results at scientific conferences to share their work with potential users. There are a number of international (e.g. International Congress of Entomology, ICE; International Congress of Plant Pathology, ICPP; International Symposium on Biological Control of Arthropods, IOBC workshops), national and regional meetings that bring together the scientific community, pest management professionals, and policy-makers/regulators and provide an opportunity to update and share the knowledge on IPDM. In the West Palearctic Regional section of IOBC, several working groups (International Organization for Biological and Integrated Control of Noxious Animals and Plants, http://www.iobc-wprs.org/index.html) meet once regularly and the proceedings are published as the IOBC/WPRS Bulletin (http://www.iobc-wprs.org/pub/index.html). Topics covered in these conferences include biological and other alternative control methods of pests and diseases.

However, to complete the effective transfer of technology it is necessary to cover the gap between researchers and the end users (i.e. growers, technicians and advisors) promoting the alignment of science, business and society. There are a number of instruments to disseminate and facilitate access to training opportunities related to technology transfer and innovation such as networking events, seminars, articles and reports in technical journals, courses and demonstration pilot projects.

16.2.1 Demonstration Trials

The development of sustainable systems of pest control has to be based on the study of the ecology and management of agro-ecosystems. The development of effective and practical BC pest programmes is quite complex and often needs to be done at a local scale according to particular environment/crop/pest conditions. This makes IPMD rather knowledge intensive. For example, many types of structures can be found in different regions (i.e. screenhouses, greenhouses, plastic tunnels or glasshouses), influenced by the local climate, technology development and economy, and this diversity has a direct influence on the approach to design an appropriate pest management programme.

Demonstrations and field trials are effective tools through which researchers directly show the efficacy of new innovative solutions and technologies to the end users with appropriate examples. Moreover, demonstration trials allow close collaboration during the whole research and innovation process among scientists, extension services, growers, producers of BCAs and policy makers in order to better align both the objectives addressed with the needs and expectations of the end users. Demonstration trials also permit careful evaluation of the technical limitations that can make IPDM challenging under practical conditions (van Lenteren 1995 and Chap. 8 IPM methods and considerations).

Governments and EC support close-to-market activities and demonstration projects with the aim to give a strong boost to breakthrough innovations. However, it is crucial to increase the implication of the private sector through direct investment (co-funding) in research and innovation to reduce time from research to market. In Europe, the European Innovation Partnership has recently launched funding support for research in the field of ‘Agricultural Productivity and Sustainability’ (EIP-AGRI) (https://ec.europa.eu/eip/agriculture/). These funds shall be distributed via a European cooperative network to be formed by working groups (Operational Groups). These working groups shall be responsible for setting up research and innovation projects that promote productivity and sustainability in agriculture. These working groups shall be set up by greenhouse growers, researchers, advisers and companies in the farming sector to run projects aimed at testing and applying innovative processes, products and technologies. The priority innovations to be implemented include increasing agricultural productivity, production and efficiency of resources, for which advances in the fields of IPDM and BC are needed. For this reason, it is hoped that the establishment of integrated pest management working groups will help in the near future to enhance IPDM programmes currently based on conventional plant protection products with alternative control systems that are both effective and safer for the environment and human health.

16.2.2 Technical Support and Role of the Extension Service

For IPM to be successful, regular and reliable technical support is essential. It is evident that extension services played a major role in most countries providing the necessary link between application and research, and promoting agricultural productivity and increasing food security (Chap. 6 Integrated Pest Management methods and considerations concerning implementation in greenhouses). There were professional teams, on the national and local levels providing training to greenhouse growers and producing applied knowledge through field experiments and observations. Extension activities to assist growers included the spread of information throughout specialized journals, lectures to growers' groups, seminars and conferences, technical booklets and posters. Nowadays, the role of the extension service have been privatized in many countries and private Pest Control Advisers (PCAs) and specialists from BCA suppliers partly fulfill this need now, with the problem that they are not independent and objective, with their advice influenced by the product line of their company.

To date, IPDM and BC without technical support from a specialist very seldom works and in any case takes longer to become applied. For this reason, it is essential to maintain and further develop the role of PCAs, to help achieve the objectives of IPDM. Some PCAs may work independently and some are employed by grower associations, especially in the vegetable and ornamental industry. Chemical companies and BCAs producers also have advisers who work for them and suggest the right solution that they manufacture, or even a complementary solution from the competition. Hence, growers do not really buy only products but a pest management service.

Independent governmental PCAs have served as a reference in assisting growers when providing recommendations on alternative control techniques. PCAs are responsible for training growers and/or some of their staff in scouting crops and identifying pests and diseases that can affect the crops and the damage that they are causing. Based on their observations they then make recommendations on treatments and suggest alternative methods to control or prevent problems. When applying BC, they teach to check the level of natural enemies and their effect on the pests, discuss the situation with the growers, and advise on the timing and quantities of BCAs to introduce, which pesticides to use (or not to use) and how and where, among other tasks. In many cases, they are the responsible of the planning and implementation of the whole IPDM programme, including ad hoc cultural practices, and the coordination and management of experimental trials to test new solutions. They can also provide training to greenhouse growers as needed and speak in events on topics that are of interest to growers.

Advisors should be capable to manage growers' expectations about what will happen in the crop in the period after first releases of BCAs: it may take some weeks before effects become visible. For this, beginning users of IPDM need frequent contacts (and visits) of advisors to assure them they are on the right track. Advisors should be willing to learn together with growers, considering the grower's (future) objectives and interests.

Advisors must have the skills to observe, scout the crop, check monitoring tools (like sticky traps and pheromone traps) and write a comprehensive advice report (poor and good examples in Table 16.1) with specific observations and concrete recommendations, which both grower and advisor should be willing to sign.

16.2.3 Training and Education

Recent years have witnessed the rapid development of IPM's training and education system at all levels. An IPM programme has to provide effective pest prevention based on a generally knowledge and skills-intensive approach and training on the tools employed for maintaining an acceptable level of control. Training is essential to the success of IPM by producing qualified interdisciplinary professionals (Wardlow 1992). A comprehensive review of the role of education and training in IPDM has been given by Jeger (1995), who stresses the importance of all formal instruction, ranging from short courses to training programmes, including master's, doctoral and postdoc programmes, and continuing education programmes. Well-instructed and motivated growers, crop managers and employees are crucial for effective IPM. The basic instruction of the young grower and others involved starts at agricultural schools and continues with refreshment courses organized by the extension service and by local growers' associations (Chap. 6 Integrated Pest Management methods and considerations concerning implementation in greenhouses). In addition, technicians working in the extension service should be regularly updated, in order to make sure that they will be able to provide growers with the most advanced and recent technologies. However, teaching is an important limitation in some countries where there are few possibilities for formal professional education and it is often identified as a major need or bottleneck in IPM projects in those countries.

Table 16.1 Poor and good report examples with observations and recommendations

Poor (non-specific, vague)	Good (specific, concrete)
Visit report 3rd visit	*Visit report 2 February 2017*
Whitefly	**Whitefly**
Infection increases, but signs of parasitism are visible. Predatory bugs are established well. Continue introduction of Encarsia	Average 10–20 whiteflies per sticky trap week 4. Few whitefly larvae found on oldest leaves, but >50% is parasitized by Encarsia. Continue introductions of Encarsia at 5 parasitoids per m^2 per week
Red spider mite	**Red spider mite**
Lower infection than last visit. Good establishment of predators	Only 10–15 infested spots in the entire compartment, all just 3–4 plants. Over 75% of infested leaves have predatory mites. No action needed for the moment

New technologies and internet are useful aids that have totally transformed the way to teach IPDM and the possibility to reach a higher number of professionals and the consumers by means of online education and training. Many governmental organizations and entities approved by the competent authorities provide online courses that reflect the newest advances in pest management and related topics. One leading supplier in the greenhouse sector runs a recognized training institute (www.universidadceickor.mx/). Short certified courses on IPDM performed by various Dutch suppliers are officially recognized options to update the compulsory crop protection licences (www.beekenkamp.nl/plants/kennisbijeenkomst-geintegreerde-gewasbescherming-poinsettia-kwekers/). Courses cover the identification of pests and natural enemies, alternative control methods and the sustainable use of pesticides, including application equipment and calibration. The objective is to offer certification training and updates for those who apply pesticides about the safe and legal use of pesticides and pest management alternatives.

16.3 The Market for Biological Pest Control in Greenhouses

16.3.1 Area of Protected Crops

The world area of protected crops (glasshouses, plastic houses, walk-in plastic tunnels and multi-span structures) is estimated at around 447,825 Ha, excluding China, which on its own has by far the biggest coverage with about 2,760,000 Ha. Excluding the Chinese market, Europe has the biggest area of protected crops, with 206,046 Ha, followed by the Asian markets with 149,532 Ha, whilst each one of the remaining countries/continents represents less than 1% of the total greenhouse area (Marc Ruijs, Wageningen Economic Research, personal communication). More than 60% of the European protected area lies in the Mediterranean area, with about 78,407 Ha's in Spain and 43,000 in Italy.

Between 70% and 95% of the protected crops is made up of vegetables and fruits, while ornamentals plants make up between 5% and 30%. The most important greenhouse vegetable crops are tomatoes, peppers, cucumbers, melons and eggplants, with tomatoes accounting for about 30% of the European greenhouse vegetables. The ornamental plant sector includes a very wide range of products, including the production of floral crops such as cut flowers and cut foliage, flower bulbs, potted flowering as well as foliage plants and bedding plants.

16.3.2 Biological Control Products

The biological control programmes of pests in most of the greenhouses are based not only on the natural control of the spontaneously colonizing natural enemies, but also on augmentative biological control. This means making releases of BCAs that have been mass reared by bio-manufacturers to suit both the individual crop as well as seasonal changes. Cock et al. (2010) lists more than 170 species of invertebrate natural enemies that are used in augmentative biological control in Europe; a database that increases to about 219 arthropod species when considering the worldwide scenario (van Lenteren 2012). Although, of these, only about 31 species are in common use in protected crops. Van Lenteren (2012) listed the 25 most frequently used natural enemies. His list is updated in Table 16.2 but now excludes *Eretmocerus mundus* (Mercet), a very successful parasitoid which is no longer available due to problems in the productions systems, but does include a further eight species which have come into favour since 2012 and have been used quite frequently in the last 5 years in at least in five European countries.

Five of the eight new additions are predatory mites – *Amblydromalus limonicus* (Garman and McGregor), *Transeius montdorensis* (Schicha), *Euseius gallicus* Kreiter and Tixier, *Amblyseius andersoni* (Chant) and *Macrocheles robustulus* (Berlese). Two are parasitoids: *Trichogramma achaeae* (Nagaraja & Nagarkatti) (Cabello et al. 2012) and *Aphidius matricariae* (Haliday), and one is a predatory bug, *Nesidiocoris tenuis* (Reuter) (Table 16.2).

In recent years, the increase in the use of predatory mites, resulting in the introduction of several new species, is a clear indication of the major focus that has been engendered by the industry in developing new rearing and releasing systems for these species, most of which have been patented (Table 16.3).

Past reasons accounting for the limited use of commercial natural enemies, together with the main factors which subsequently have stimulated their use have been discussed by van Lenteren (2012) and van Lenteren et al. (2018). One of the important factors that has obviously contributed to the success of biocontrol are the major advances made to the methods for rearing and releasing systems of the insects and mites currently used in augmentative programmes (Vila and Cabello 2014).

Regarding registered microbial BCAs, van Lenteren et al. (2018) provided the first published list with 209 microbial strains from 94 different species. The list includes bacteria, bacteriophage, fungi, yeast and viruses that target different pests and diseases. In protected crops, only a few species of microbial control agents are often used: The bacterium *Bacillus thuringiensis*; the fungi *Beauveria bassiana, Lecanicillium muscarium, Isaria (Paecilomyces) fumosorosea* and *Metarhizium anisopliae;* and the viruses *Spodoptera exigua* nucleopolyhydrosis, *Helicoverpa armigera* nucleopolyhedrovirus, and *Spodoptera littoralis* nucleopolyhedrovirus (Chap. 14 Biological control agents for control of pests in greenhouses).

Table 16.2 List of the most important invertebrate biological control agents used in augmentative biological control in the world

Natural enemy	Family	Target(s)	Year of first use
Amblyseius swirskii	Phytoseiidae	Whiteflies, thrips, mites	2005
Aphidius colemani	Braconidae	Aphids	1991
Aphidoletes aphidimiza	Cecidomyiidae	Aphids	1989
Dacnusa sibirica	Braconidae	Leafminers	1981
Diglyphus isaea	Eulophidae	Leafminers	1984
Encarsia formosa	Aphelinidae	Whiteflies	1926
Macrolophus pygmaeus	Miridae	Whiteflies	1994
Nesidiocoris tenuis	Miridae	Whiteflies, tomato leaf miner	2001
Neoseiulus cucumeris	Phytoseiidae	Thrips	1985
Phytoseiulus persimilis	Phytoseiidae	Mites	1968
Steinernema feltiae	Steinernematidae	Sciarids	1984
Aphidius ervi	Braconidae	Aphids	1996
Orius laevigatus	Anthocoridae	Thrips	1993
Cryptolaemus montrouzieri	Coccinellidae	Coccids, pseudococcids	1989
Galeolaelaps aculeifer (=*Hypoaspis aculifer*)	Laelapidae	Sciarids	1996
Feltiella acarisuga (=*Therodiplosis persicae*)	Cecidomyiidae	Mites	1990
Leptomastix dactylopii	Encyrtidae	Pseudococcids	1984
Stratiolaelaps miles (=*Hypoaspis miles*)	Laelapidae	Sciarids	1995
Aphelinus abdominalis	Aphelinidae	Aphids	1992
Heterorhabditis bacteriophora	Heterorhabditidae	Coleopterans	1984
Heterorhabditis megidis	Heterorhabditidae	Coleopterans	1990
Neoseiulus californicus	Phytoseiidae	Mites, thrips	1985
Eretmocerus eremicus	Aphelinidae	Whiteflies	1995
Episyrphus balteatus	Syrphidae	Aphids	1990
Trichogramma evanescens	Trichogrammatidae	Lepidopterans	1975
Transeius montdorensis	Phytoseiidae	Whiteflies, thrips, mites	2003
Amblydromalus limonicus	Phytoseiidae	Whiteflies, thrips, mites	1995
Amblyseius andersoni	Phytoseiidae	Mites, thrips	1995
Euseius gallicus	Phytoseiidae	Whiteflies, thrips, mites	2014
Trichogramma achaeae	Trichogrammatidae	Lepidopterans	2009
Aphidius matricariae	Braconidae	Aphids	1980
Macrocheles robustulus	Macrochelidae	Dipterans, thrips, lepidoptera	2010

Modified after van Lenteren (2012)

Table 16.3 European Patents about compositions and methods for rearing predatory mites developed by biomanufacturer companies

Patent number	Applicant	Factitious prey species	Predatory mite species	Granting date
EP1686849B1	Koppert BV	Family Carpoglyphidae	*Amblyseius swirskii*	Oct 8, 2008
EP1830631B1	Koppert BV	Family Carpoglyphidae	Phytoseiidae species other than *A. swirskii* from members of the subfamilies Amblyseiinae and Typhlodrominae	May 5, 2010
EP1965634B1	Koppert BV	Family Glyciphagidae	Phytoseiidae species other than *A. swirskii*	Aug 4, 2010
EP2042036B1	Koppert BV	Orden Astigmata	*Amblyseius swirskii*	Jun 22, 2011
WO2008/015393A2	Bioline Agrosciences	*Thyreophagus entomophagus*	All predatory mites	Aug 20, 2014
EP2124573B1	Certis Europe BV	Family Suidasiidae	*Amblyseius swirskii*	May 4, 2011
EP2380436B1	Agrobío SL	Species from the order Astigmata not alive	Phytoseiidae species	Oct 3, 2012

16.3.2.1 Changes of the Mass Rearing Systems

Development of more efficient cost-effective rearing techniques are urgently needed so that augmentation can become a standard competitive strategy. This unfulfilled need partially explains while despite many species being described by academic researchers as promising candidates, only a few species have been successfuly commercialized on a broad scale. To resolve this problem steps must be taken to reduce the cost to the producer and in turn to the grower. The most important development has been the introduction of a rearing system in which a factitious prey/host, together with the predator/parasitoid, is introduced into carrier materials thus eliminating the need to grow plants on which to rear the natural prey of the agent, for example, members of the stored food group of species belonging to the Astigmata are factitious hosts to the plant dwelling phytoseiid predators. Secondly, the utilization of artificial diets which avoids the need to use any arthropod prey component, yet to be perfected.

Several reviews have been published in the scientific literature pertaining to factitious preys and artificial diets, three good examples are – Thompson (1999) and Thompson and Hagen (1999), both covering the period up to 1998, and Riddick (2009), examining data from 1999 to 2007. Despite many works being published, very few examples have been transferred to commercial industry: just a few new astigmatid factitious hosts for commercially rearing mite predators; and a few examples of generalist predatory bugs [*Macrolophus pygmaeus* Rambur, *Nesidiocoris tenuis* (Reuter) and *Orius laevigatus* (Fieber)] being reared in climatic controlled rooms without whole plants and being fed on eggs of the moths *Ephestia kuehniella* Zelle or *Sitotroga cerealella* (Olivier), the dipteran larvae of *Ceratitis capitate* (Wiedemann), crustacean cysts of *Artemia*, or combinations thereof.

The predatory mites of the family Phytoseiidae, which have received little or no attention in these past reviews, have now become an essential element of augmentative programmes. Due to the combination of a predator with a live prey, selected from one of a few species of astigmatid mites, collectively known as 'stored food mites', as factitious prey, then reared using carrier substrates in plastic boxes placed in climatic controlled rooms, has made it possible to boost productions and so increase the quantities affordable to growers. This has resulted in five of the most commercially important phytoseiid predator species being released over much larger areas into a greater variety of crops. A good example is *Amblyseius swirskii* Athias-Henriot, which now represents the largest single species production, and is introduced into most of the protected vegetables except tomato, generally at more than 100 individuals/m^2. The production of this species was the first to be patented and soon other systems were developed by the main three or four manufacturers, resulting in six species being cited in patents granted by the European Patent Office (Table 16.3), with some others in application.

Despite the success achieved using living astigmatid mites as factitious hosts, a recurring problem is that frequently, the introduction of a new suitable predator is thwarted by the fact that when presented with a strange factitious prey it refuses to predate. A possible factor operating here is the mechanisms of defense of the prey mites, which use active fast jerky movements or alarm pheromone defense systems, or both. This problem has been overcome by emulating techniques for fast freezing food for human consumption. The factitious host is frozen and after de-frosting is presented to the predatory mites as an inert diet (EP 2380436 B1; Table 16.3).

Artificial foods are not as yet adopted on a commercial scale, although there are about 100 species of predators and parasitoids which could be reared on an artificial diet media (Grenier 2009). Specifically, artificial foods for predatory mites have been studied for mass rearing (e.g. Patent US006129935A; Nguyen et al. 2014; Vangansbeke et al. 2016), but none have been established commercially. The only exception of a natural enemy being produced artificially in large quantities is the production of *Trichogramma* sp. by some Chinese producers. It seems obvious that the use of entirely artificial diets is the way forward for the bio-control production industry. Nutrigenomics, a very innovative tool already in progress, must be further developed in the near future (Coudron et al. 2006).

16.3.2.2 Improvement of Releasing Methods

Linked to the recently accelerated improvements in the development of mass productions of phytoseiid mites is the significant improvement of 'releasing' techniques which are now used in augmentative programmes, including providing alternative food, prey or hosts and oviposition sites or shelters (Messelink et al. 2014), development of machinery to release biological control agents in crops, among others. Development of reliable, repeatable distribution methods is a key issue for mites with a low dispersal ability (Buitenhuis et al. 2010; Amoah et al. 2016). A further major aim for the improvement of biocontrol programmes has been the discovery of a method which will ensure the strong establishment of BCA populations before an invasion of a pest arises. For this reason, the actual timing and ratios of releases of generalist predators have and are being modified in many crops. The introduction of plant defensive responses that may result in attraction of natural enemies is another area requiring attention (Naselli et al. 2010; Bouagga et al. 2018; Chap. 14 Biological control agents for control of pests in greenhouses).

One of the main advances both for distribution and preventive establishment of mites has been the formulation *á la carte* of individual sachets that are hung in the crop, which include a reproducing population of prey and predatory mites, with a capacity for using either controlled quick or slow release systems. The controlled release system can release mites for up to 8 weeks and, at present, the main producers of *A. swirskii* are delivering sachets which produce high numbers of mites, with claims of up to some 8000 departing mites per sachet, whilst 5 years ago the mean number used to be no more than 600–800 individuals (Vila et al. 2013). Specific designs have been developed and commercialized to improve the resistance of the sachets to overhead water applications (Patents US10901545 and WO2017/123094A1).

Further developments have been the modification of overhead watering systems or heating pipes that are mounted high above the crop and used of transport rails for introducing predators on to cut flowers, such as chrysanthemums crops.

Other methods of introducing mites which have been in operation for some time, mainly in plant nurseries and/or high-tech greenhouses, is the use of blower machines or rotating disc devices to spread loose material. The first blower machines were used as leaf gatherers, but were later adapted for distributing BCAs by the addition of a reservoir to hold the predator substrate (Opit et al. 2005). These machines now have evaluated to robot-like automotive systems (Airbug, https://www.koppert.com/products/distribution-appliances/airbug/) that move throughout the greenhouse and distribute the biocontrol agents with minimum manual labour requirement.

More recently, an automatic device commercialized under the name Biospreader has been designed in the Netherlands, in cooperation with a group of Dutch growers to spread both prey and predatory mites, which is based on mechanical distribution and which guarantees an even distribution onto different protected crops, saving labour cost (https://royalbrinkman.com/crop-protection-disinfection/biological-crop-protection/sticky-trap-rolls-and-sheets/accessories/biospreader-210102877). Other specific release systems have been developed and commercialized to resolve distribution problems for potted plants (e.g., sachets on sticks; www.biolineagrosciences.com/2015/08/14/launching-amblyline-and-swirskiline-stick/).

A further strategy, being increasingly implemented in biocontrol programmes, is the addition of alternative or complementary foods to encourage the early establishment, and subsequent conservation of BCA populations which may be present in the crop during periods of prey scarcity, and several commercially produced factitious foods are now being occasionally introduced into certain crops (Messelink et al. 2014). An example is the introduction of eggs of *E. kuehniella* or cysts of *Artemia* to feed predatory bugs on tomato crops. This feeding technique is also applied in a similar procedure where the bugs *Nesidicoris tenuis* or *Macrolophus pygmaeus* is released directly on to the seedling before it is transplanted out. This technique has resulted in a major improvement when trying to establish *N. tenuis* on tomatoes in the south of Spain (Calvo et al. 2012).

Some other foods have been tested, for instance sugars (Urbaneja-Bernat et al. 2015), but so far none are used extensively in commercial situations.

Relative to the use of additional foods, the most researched subject is that of adding pollen grains to the crop surface. Examples of publications are: Goleva and Zebitz (2013), Leman and Messelink (2015), Samaras et al. (2015), and Vangansbeke et al. (2016). Recently, a system to feed predatory mites in different crops using pollen from *Typha*, has been developed and is commercialized with the name of Nutrimite (Pijnakker et al. 2016).

Other authors have described that introducing prey mite populations to the litter below the crop may favour the development of certain predatory mites which operate both on the plant and in the soil beneath the plant. Whilst they are living in both situations, they predate thrips as well as alternative preys (Munoz-Cardenas et al. 2017). Following the publication of these exploratory trials, a producer of mites evaluated the idea of applying commercially available factitious astigmatid prey mites directly to the plant canopy instead of to the soil (www.agrobio.es). Based on experience, different combinations of predator/prey species were tested using this new technique and from the results obtained various adjustments were made to programme timings, and mite ratios, which produced satisfactory protocols for use in a variety of crops, including ornamentals and vegetables (Vila et al. 2016, 2017). Following these results, the system has been taken up commercially also by other main producers. More research is needed in the near future to evaluate specific nutrients and whether mixtures of different food sources would favour the establishment of generalist predators. For some species a benefit has been stated when they can commute between different food sources (Messelink et al. 2008; Muñoz-Cárdenas et al. 2014).

Some approaches of feeding the predator mites with early releases of both predators and preys combined with other foods before transplanting have given significant improvements in the ability to control arthropod pests in commercial crops, in particular the control of thrips in Chrysanthemums (Vila et al. 2017). These combinations may help implementation in the near future.

The use of banker plants is a further strategy aimed at favouring the establishment of natural enemies which is currently attracting the attention of commercial bio-manufacturer companies (Messelink et al. 2014). But so far it is a technique not yet taken up to any extent commercially. An exception is the use of banker plants for supporting parasitoid populations of aphids (Frank 2010), but this procedure is now confined mainly to southern Europe, since the system is losing favour in northern European markets because it is believed to encourage hyperparasitism.

Many papers have been published evaluating banker plants which favour the establishment of predators and parasitoids to control pests other than aphids, including some for predatory mites (ex. Xiao et al. 2012), and predatory bugs (Nguyen-dang et al. 2016; Zhao et al. 2017).

16.3.3 Actual Biological Control Market

In 2015 the International Biocontrol Manufacturers Association (IBMA) estimated that between 2013 and 2015 there was a global increase of around 10–20% in the total sales of macro-organisms, natural-biochemical products, semiochemicals and micro-organisms, with the market value of the natural enemies increasing to about 155 million euros.

Global wide micro-organisms are the most sold BCAs, and sales increased from 250 million euros in 2013 to about 325 million euros in 2014, but then decreased in 2015 to about 305 million euros. The natural-biochemical products have increased to about 115 million euros, but the semio-chemicals have increased more slowly to about 50 million euros in 2015.

Europe has the biggest market share of natural enemies, with more than 100 million euros sales in 2015, with further sales of about 35 million euros in NAFTA (USA, Canada and Mexico), and outside Europe and NAFTA, another 20 million euros. In contrast, the micro-organisms have the highest market share in NAFTA, with more than 160 million euros. Also, outside Europe and NAFTA, the largest market share is taken up by micro-organisms (75 million euros). Until 2006, the main market in BCAs in Europe was confined to the northern European countries, chiefly Holland, Belgium and UK, but then in 2007 came a very fast expansion of the biocontrol industry in Spain, which came to be known as the ‘green revolution of Almería’ (van der Blom 2010). The development and adoption of IPM programmes in the Southeast of Spain where, excluding China, the largest concentration of protected crops of the world has developed, has become a reference model for other areas, especially those with Mediterranean climates. The main reasons for such a rapid replacement of chemical usage in Spain was the same as reported earlier in northern Europe: an excessive use of chemicals and the resulting onset of pest resistance to insecticides, the use of too high dosages resulting in too high residue levels, as well as use of illegal pesticides. The selection of new natural enemy species was a prerequisite needed to cope with the local conditions. After years of research three important BCAs were selected and developed for the commercial market, namely, *A. swirskii, E. mundus* and *N. tenuis*. Currently, about 25,700 ha of protected cultivation in the Mediterranean area are using augmentative releases of natural enemies, about 75% of this total surface have peppers and tomatoes as main crops.

Vegetables are still the main market for biocontrol, but ornamental crop producers are increasingly using biological control, especially in northern European countries, although development may soon speed up in southern countries, especially

Spain. In Holland, for instance, biocontrol is used in 100% of rose crops amounting to some 250 ha followed by 80% for gerbera crops on about 200 ha's. In chrysanthemum the tendency to use BCAs has increased sharply, so that now more than 75%, i.e. 345 out of a total of 460 ha's are under biocontrol. For pot plants, about 20% of an estimated surface of approximately 1500 ha is under BC, and 100% of the 60 ha crop of *Alstroemeria* uses bio-control programmes.

The same tendency to increase the adoption of BC systems has occurred for vegetable and some ornamental crops in non-European countries, especially in the USA and Canada. In Canada, 80% of the greenhouse vegetables are using augmentative releases for BC (Shipp et al. 2007). For ornamental plants the strategy of using BC systems is increasing in Canada as well (Summerfield et al. 2015).

The percentage of growers adopting BC in the USA is still low although almost 50% of the growers producing ornamental crops use or have used BC, and 55% of interviewed growers indicated that they would like to learn more about biocontrol whilst 42% of the respondents indicate they will increase the use in the coming 5–10 years (Marsh and Gallardo 2009).

BC is increasing in Mexico, with about 12,000 ha of vegetables under glass or plastic greenhouses, of which, in 2014, some 29% was estimated to receive augmentative releases for biocontrol (Lomelí-Flores et al. 2014). Ornamental producers still rely heavily on chemicals. This same 'pesticide attitude' occurs in other Latin American greenhouse productions where protected ornamentals occupy the largest area under cultivation, although such applications are in general made with less enthusiasm (Bueno 2005; Bueno and van Lenteren 2010).

China, with the highest glass/plastic house based production in the world, is steadily establishing the use of biological control systems, but the market for BCAs, mainly in greenhouse vegetables, is still quite small, despite the fact that there are already seven commercial companies producing 21 species of natural enemies, most of them available countrywide. It is difficult to get information on total sales figures, but it is known that at least six species are sold in large numbers. Estimates suggest 35 million of *Encarsia formosa* Gahan individuals, 2 million of *Harmonia axyridis* (Pallas), and 12 billion of *Amblyseius cucumeris* Oudemans are produced per year, whilst in the 1990s it was estimated that more than 45% of the greenhouse hectarage was using *Phytoseiulus persimilis* Athias-Henriot (Yang et al. 2014).

Augmentative biological control in Africa is still rather limited, and is mainly confined to the northern countries, especially Morocco and Tunisia. In the rest of the continent, in general, most programmes employ systems of classical control involving inoculative releases (Greathead 2003), except for some ornamental crops where augmentative releases are applied on a relatively small area, mainly of predatory mites, in several African countries, including Kenya and Ethiopia.

16.4 Marketing, Distribution and Logistics

Marketing products, or rather systems for IPDM is probably more challenging compared to the marketing of agrochemical products to control pests and diseases. One of those challenges is to motivate growers willing to spent resources before they experience a problem in their crop. IPDM often requires preventive or timely action, while chemical interventions are often only taken when a pest or disease problem is clearly visible in the crop. Other challenges are storage, shipment and release of BCAs, demanding more careful treatment than chemical pesticides (see Sect. 16.4.2).

IPDM requires a concise and holistic plan of action how to manage all pests and diseases in the crop: ideally in a biological way when feasible, only using (compatible!) chemicals where really needed (Chap. 6 Integrated Pest Management methods and considerations concerning implementation in greenhouses). What is feasible depends not only on technical possibilities, but also on availability of the BCAs in the area. Such a paradigm shift from a reactive to a proactive approach is often experienced as difficult, especially in the first crop(s) grown after the start of implementing an IPDM programme.

IPDM on the greenhouse level will only work with a firm commitment of owner, grower and employees. New tasks appear in the greenhouse, such as systematic scouting of pests and diseases, handling and application of natural enemies and biopesticides, and checking their effectivity in the crop. Comprehensive information in text, photos and videos are one way to support users/stakeholders to become more familiar. But also (especially in the beginning) greenhouse visits and detailed advice on the spot from experienced advisors are a pre-requisite for growers to do the right things in the right way, and to gain trust in the new approach. Obviously, growers do not want to take chances with the health and condition of crop and source of income.

Despite all the positive ecological effects of IPDM, technical and/or economic benefits are the strongest drivers that motivate growers to shift, the main ones being:

1. Pests that have developed resistance against available chemicals and can only be controlled effectively with IPDM (e.g. *T. absoluta, Frankliniella occidentalis* (Pergande)*, Tetranychus urticae* (Koch) and whitefly); and
2. Gowers and buyers (retail) that demand healthy products with limited or no chemical residues.

16.4.1 Conditions for Success with IPDM

Designing an effective, affordable and reliable IPDM programme is specialist work, and this is one way a biocontrol company can distinguish itself in the market. Such a programme must be feasible at greenhouse level: the biocontrol supplier chosen must be able to provide the products needed in the programme for every week they are scheduled.

Effectivity of such a programme not only depends on the right choice of appropriate BCAs and their introduction strategy (numbers and timing). The way of packaging of biocontrol products can largely contribute to their easy, simple and faultless application. Think about slow release sachets of predatory mites, or BCAs mixed with carrier materials that can easily be applied with mechanical distribution devices etc.

The products with fragile mites and insects must be transported from the place of production to their final destination in the greenhouse within a number of days. The condition, and hence potential performance, of the BCAs in the crop can suffer during transport when this takes too long and/or they travel outside the optimal temperature range for significant time. Isolating packaging, icepacks and refrigerated means of transport are ways to prevent too high temperatures in transports with relative warm ambient conditions. Preventing loss of quality in colder ambient conditions is more complicated. The biggest challenge is faced when colder and warmer ambient conditions occur during the shipment. Dataloggers are often used today to monitor product temperature during transport, and they provide information to adjust materials of packaging or modes of transport.

For some products, there is a second parameter next to temperature that needs consideration in transport: the concentration of carbon dioxide (CO_2) inside insulating boxes or in the transport vehicle. Astigmatic (feeder) mites produce significant amounts of this gas. Its accumulation can cause high CO_2 concentrations in the space for BCAs travelling in the same space, leading to reduced vitality or even mortality.

16.4.2 Local or Central Production of BCAs?

The complex logistics described above may trigger the idea that local production of BCAs seems the best option. However, in real life, production of BCAs for augmentative release or use as bio-pesticide mostly takes place in a centralized way. There are clear reasons for this:

- Efficient and reliable production systems for BCAs are expensive to develop, build and maintain. Therefore, it is more economic to manage few big systems for the production of large quantities, compared to many small ones.
- The demand for certain products in one single country or region can fluctuate enormously from week to week, depending on crop calendars, pest pressure, climate conditions, etc. It would take enormous investments in each local production capacity to avail sufficient numbers at the right time. Clustering demands for more regions or countries together creates a more stable demand by definition (law of big numbers).
- Centralized production of a big portfolio offers versatile choice to customers worldwide to design the best possible IPDM programme for their particular requirements.

Of course, all rationales have their exceptions or limits. For instance, winter production of BCAs that require vitally growing plants can be more effective in the Mediterranean than in northern Europe. Production of BCAs that can only be transported as fragile adults may only be feasible when done locally. Production of non-indigenous organisms may not be permitted in certain countries. Some local cooperatives have set up rearing facilities for BCA's that are very important for their members (ex. SELMAR in Catalonia, Spain, www.federacioselmar.com/, or Savéol in Bretagne, France www.saveol.com/).

16.4.3 The Value Chain in IPDM

There is a value chain for IPDM: the producer of BCAs, the logistic service provider(s)/distributors and advisors all put effort in delivering a product (or rather a system) that should meet growers' expectations. All stakeholders deserve a fair reward for their efforts: investments in time, energy and money or taking certain risks. One should not underestimate the total costs of these efforts, so it often pays to plan introduction schedules properly, communicate timely and collaborate wherever possible. This contributes to efficient use of resources.

It is also important to understand the different stakeholders' positions: distributors that sell agrochemicals at interesting margins may be biased in their advice. Advisors that feel inexperienced with IPDM may not want to sacrifice their expert image on agrochemicals.

16.5 Benefits from the Replacement of Pesticides by Biological Control

For people working with growers this question sounds familiar. It is not always easy to explain that all efforts to produce and deliver effective BCAs bring costs for products, such as costs for production, packaging, transport, customs duties, etc.

There are also service components that bring costs: advice, identification, and scouting services. In many cases, all cost components for product and service are accumulated to a 'price per package'. Many growers then consider the biological option more expensive than the chemical one.

But this is not the complete story! Many other economic parameters on the greenhouse need to be brought into the equation in order to come to a fair cost/benefit analysis:

– Effective biological control always reduces the number of pesticide applications. Crops that are sprayed less grow better, and often produce more and better quality. Biological control of *T. urticae* in roses is a classic example: IPDM may increase total yearly pest control material cost by € 10,000/ha, but production easily increases with 20%. Depending on the region where production takes place, this can increase yield with € 40,000/ha, resulting in a net-gain of € 30,000 gain per hectare. So one should rather talk of 'cost of ownership' of IPDM rather than just the BCAs' price per package or per treatment.

- When pests or disease develop resistance, biological control is often more effective than agrochemicals. Moreover, crops perform better at lower pest density.
- When agrochemical use is limited, natural control by native BCAs may work more efficiently, avoiding the use of additional measures of management.
- The effect of augmentative releases of BCAs often persists for a longer time. Hence, the application frequency of such releases reduces after time. Application of agrochemicals often shows the opposite dynamics. In time, more frequently applications are needed when pests or diseases develop resistance.
- More and more retail chains set lower (than legal) thresholds for residue levels (MRL) on the produce supplied. And recently and increasingly not only for edible products but also for cut flowers and pot plants. Here restricted use of agrochemicals is a license to deliver to the retail chain.
- The quantities (and thus costs) of BCAs are often highest in the 1st year after transition from a total chemical to an IPDM programme. This is due to chemical residues in various construction parts of the greenhouse (ground cover, benches, poles, etc.) that break down slowly. But also the learning effect for grower, staff and advisors play a role. Generally, costs go down in following seasons. Stopping the use of broad-spectrum pesticides creates friendly conditions in crop for BCAs from the local ecosystem that increasingly come into the greenhouse and support IDPM. Fully chemical strategies rather show increasing costs in consecutive years as a result of pests/diseases developing resistance.

Some suppliers try to overcome the hurdle of IPDM programme *perceived* to be more expensive by offering a complete programme of BCAs needed during a crop or season at a more or less fixed price per hectare, payable in several installments.

Other benefits of IPDM are more difficult to express directly in terms of money, but nevertheless important considerations in the cost/benefit analysis.

- Reduced use of agrochemicals creates a cleaner and safer working environment, which is more attractive for workers. This creates a competitive advantage on the labor market for growers practicing IPDM.
- Application of BCAs can easily be trained and learned, and is not subject to license for the applicators as it is for application of agrochemicals. In addition, there is no re-entry interval nor harvest interval after application of BCAs. So all employees can potentially perform this task at any time, which makes the work planning much simpler.

16.6 Regulatory Issues

Currently, the possibility to develop and expand the use of biological control, specifically the use of arthropod natural enemies, is better than ever, with strong positive changes taking place in Europe. The EU Directive 2009/128/EC, together with the increasing demand by retailers and NGOs for products in which the level of residues is far below the national or international legal requirements, has been mainly responsible for this welcome upsurge in biological control usage.

In the European Union, each country had to develop a National Action Plan (NAP) aimed at reaching the common objectives of this Directive, where IPM is not an alternative but has mandatory recognition. IPM is defined based on the principles of the IOBC in which alternative non-chemical methods are the priority and must be applied whenever possible (Boller et al. 2004). Other areas, worldwide are also following similar sustainable approaches to pest control (Peshin et al. 2009).

However, tough regulations governing the import, export, research and release of invertebrate biological control agencies (BCAs) often delay implementation of biological control. For example, when considering exotic species, the risk assessment procedures are frequently misunderstood, and mismanaged, leading to high costs and, potentially, the inability to market a promising natural enemy (van Lenteren 2006). Whilst it is unanimously agreed that deliberate, unsanctioned, releases must be clearly avoided there is a risk that overly too stringent regulations will deter the development of promising agents. Thus, there is a fine balance between the application of these two opposing needs, as yet unresolved by many countries (De Clercq et al. 2011).

In 2001, there were about 25 countries, which have implemented policies relating to the importation of exotic biological control agents (Lockwood et al. 2001). Some countries have a long experience of dealing with requests for introducing exotic species such as Australia, Canada, New Zealand, South Africa, Switzerland and the USA. However, in Europe the situation is more complicated in that some countries have regulations, some do not, and still others only have plans to introduce regulations (Bale 2011; Barratt and Ehlers 2017). Indeed, there are countries in which the decision to regulate or not to regulate has been ongoing for many years without a clear decision. Examples of some initiatives which have dealt with registration issues are two EU-funded projects (1) ERBIC = Evaluating environmental risks of biological control introductions into Europe, and (2) REBECA = Regulation of biological control agents, http://www.rebeca-net.de). Also international organizations such as the International Organization for Biological Control – West Palearctic Regional Section (IOBC-WPRS) and the European and Mediterranean Plant Protection Organization (EPPO) have been active in the field of regulation. Some of the difficulties leading to a fragmented system of regulation across Europe are: inconsistency in information requirements between countries; no general, official agreement on a format for environmental risk assessment (ERA), and no guidance for implementing methods to be applied. Additionally, there is a limited number of biocontrol experts able to perform and evaluate an ERA in some countries, together with the lack of knowledge on the applicability of ERA methods involving different taxonomic groups.

The REBECA project produced a standardized application form for use by companies when applying for a license to release a non-native BCA, which can be used also for native species, both for research or release purposes (Bale 2011). There is no legislation at the EU level regarding the import and use of invertebrate BCAs although some, but not all, countries have adopted the REBECA protocol or something similar.

The lack of a Directive for arthropod natural enemies is seen by the International Biocontrol Manufacturers Association (IBMA) as an advantage, since it is believed, based on experience with regulation of microorganisms that a Directive may well increase bureaucratic interference and is certainly likely to increase registration costs, which might be limiting for a small and medium-sized type industry with its limited resources for investment in R&D.

However, requirements need to be unified, since at present companies have to prepare separate license applications (dossiers) depending on the information requirements of individual member states. For this reason, the IBMA has prepared a Position Paper on Regulation of invertebrate BCAs (http://www.ibma-global.org/en/position-papers-1). One of its recommendations is that 'Proper definitions of terms (exotic, established, native, etc.) should be developed between IOBC and IBMA'. Another recent concern in a few countries is that only local populations collected in the area are considered to be native, which means that local strains are relevant for permissions of releases. Accordingly, the IBMA has published a further Position paper on the interpretation of 'a native species' relative to invertebrate biocontrol agent regulations (http://www.ibma-global.org/en/position-papers-1). Further, the industry believes that consideration of a non-native organism at the subspecies level or below will seriously hamper the future of the bioindustry activity, and makes no ecological/biological sense, nor does it provide any added protection to the local flora and fauna, as well as being contrary to the law and spirit of European free trade.

On a global level, several international organizations other than EPPO and the European Community, have also produced documents, guidelines and codes of conduct relevant to biological control. These include the Code of Conduct by the International Plant Protection Convention of the FAO, and the OECD, together with a 'Guidance for Invertebrate Biological Control Agents 2002' (van Lenteren 2006). Such regulations may delay the time between finding a natural enemy and its marketing (see Chap. 14 Biological control agents for control of pests in greenhouses). Recently, an even more limiting factor for marketing of exotic BCAs occurred: the implementation of the Access and Benefit-Sharing (ABS) provision of the Convention on Biological Diversity (CBD) after ratification of the Nagoya Protocol. BCAs are considered genetic resources and can only be exchanged between countries, but protocols for exchange have not yet been finalised and resulted in an almost complete stop of foreign natural enemy exploration programmes (Chap. 14 Biological control agents for control of pests in greenhouses). As prospecting for new non-native natural enemies has currently been suspended if not terminated in many countries due to CBD and ABS procedures, the IOBC prepared a best practices guide to assist the biocontrol community to demonstrate due diligence in complying with ABS requirements. The best practices guide includes a draft ABS Agreement for collection and study of biocontrol agents that can be used for scientific research and non-commercial release into nature by countries having signed the Nagoya Protocol (Mason et al. 2018)

16.7 Constraints and Future Considerations About Implementation of IPDM

The impact of increased use of pesticides in agricultural production is recognized as an important threat to human and environmental health. IPDM is suggested as the most suitable alternative to conventional pest management practices. The implementation of IPDM, however, encounters several challenges, especially in developing countries. Moreover, crop pest problems are projected to increase because of increasing numbers of invasive organisms due to agricultural intensification, increase in international trade of commodities, and changes in the distribution and dispersal of species due to climate change.

Many IPDM strategies would benefit from targeted research in order to be applied efficiently. To move forward in the implementation of BC in greenhouses it is necessary to improve our basic knowledge on the efficacy of the already known NE, and to develop new solutions for a number of pest species for which no efficient BCAs are available yet. The biocontrol industry has to be ready to provide well-adapted natural enemies to a large diversity of crops, growing cycles and local climatic conditions. In addition, it is necessary to generate more applied knowledge about integration of BC with selective insecticides and many other alternative methods (Chap. 6 Integrated Pest Management methods and considerations concerning implementation in greenhouses). It is also of high priority to improve our basic knowledge about strategies based on the conservation of natural enemies that are likely to be longer-term and more economical solutions (Chap. 14 Biological control agents for control of pests in greenhouses). Not only because they can provide the best solution in niche crops, but also because they represent a benefit in major protected crops where inoculative strategies are carried out. Further, development of more efficient cost-effective NE rearing techniques are urgently needed, although major advances have been made with the use of factitious preys and artificial diets that will allow reducing costs considerably. In addition, more research is needed to evaluate specific nutrients and/or whether mixtures of different food sources could favour the establishment of NE. New methods of releasing natural enemies are needed as well.

The challenges in implementing IPDM programmes and adoption of BC practices are closely linked to policy and social factors, extension methods, and training and education. Plant protection in protected vegetable and ornamental production is a changing scenario (i.e. invasive and emerging diseases and pest species, crops/plant varieties, crop practices) and require the collaboration among the producers, industry, pest control advisors, researchers and governments to implement technically and economically feasible alternatives in accordance with the legislation. Much remains to be done on building up a knowledge base on effective, affordable and reliable biological control measures against pests and diseases, but growers' motivation, legal requirements and social demands in favour of food and ornamental plants produced with less or no pesticide residues will stimulate an increase worldwide the area under IPDM.

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Chapter 17
Tomatoes

Cristina Castañé, Jan van der Blom, and Philippe C. Nicot

Abstract IPM has been developed and successfully applied in greenhouse tomatoes in several regions of the world since the 1970s. As an alternative to the exclusive application of pesticides, the cornerstone of this strategy is to use Natural Enemies (NE) to control some of the crop's key pests (whiteflies, tomato leafminer) and other pests (spider mites, dipteran leafminers, thrips, aphids and noctuid moths). Along with the development of varieties with reduced susceptibility to viral diseases transmitted by insects, such as TYLCV, TICV, ToCV and ToTV (by whiteflies), TSWV (by thrips) and PVY (by aphids), management of these problems in many affected areas has been enhanced by the use of screens in greenhouses and the use of NE to reduce vector populations region-wide (both inside and outside greenhouses). Until recently, fungicides were the only available solution for control of airborne diseases (Botrytis, Oidium, Phytophtora and Alternaria) and soilborne diseases (Verticillium, Fusarium, Rhizoctonia). A number of biological products and biostimulants now available offer a more sustainable solution, but there is yet no effective solution to some pest problems, such as russet mites, and their presence limits wider application of the programme.

Keywords IPM · Biological control · Natural enemies · Virus resistant varieties · Biostimulants · Whiteflies · Tomato leafminers · Tomato russet mite · Airborne diseases · Soilborne diseases

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17.1 Introduction

Tomato (*Solanum lycopersicum*—formerly *Lycopersicon esculentum* L.) is a widely grown vegetable, with 159 million tons harvested from 5 million hectares worldwide in 2014. In many parts of the world, tomatoes for fresh consumption are produced mainly in greenhouses. In the EU, most fresh tomatoes (80.3%) are produced in the Mediterranean region (FAOSTAT 2017).

IPM in greenhouse tomato crops is closely related to the climatic area in which the greenhouses are located. Heated glasshouses are common in cold regions (e.g. North Europe, North USA, Canada) while plastic houses predominate in warmer areas (e.g. Mediterranean Basin, Central and Latin America). Crop systems in glass- and plastic-covered greenhouses differ in a number of important respects. In general, glasshouses ensure a year-round crop and high productivity but incur a high production cost per square meter per year as a consequence of sophisticated climate management, including artificial lighting in winter. In contrast, yields of plastic-covered crops are lower but also incur far lower costs as they depend entirely on solar heat and have a shorter production cycle of 6–9 months. As production systems develop, plastic growing houses are increasingly equipped with advanced climate control, enabling higher yields and year-round production. The resulting changes in crop cycles and microclimate have important consequences for pest and disease incidence and control.

17.2 Pests and Diseases

17.2.1 *Insects and Mites*

For tomatoes, the current key pests are the whiteflies *Bemisia tabaci* (Gennadius) and *Trialeurodes vaporariorum* Westwood (Homoptera, Aleyrodidae) (Fig. 17.1a, b), the tomato leafminer *Tuta absoluta* (Meyrick) (Lepidoptera Gelechiidae) and the tomato russet mite *Aculops lycopersici* Tryon (Acari, Eriophyidae). Although spider mites, dipteran leafminers, thrips, aphids and lepidopterans may cause significant economic damage, their incidence varies considerably according to climatic area, greenhouse type and the year. (See Chap. 4 for a more detailed description of pests mentioned in this section).

In cold regions as well as in many temperate areas, *T. vaporariorum* is the most important whitefly species affecting the greenhouse tomato. *T. vaporariorum* and *B. tabaci* coexist in transitional areas while only the latter causes damage in warmer areas (Gerling 1996; Castañé 2002). *B. tabaci* is considered a cryptic species complex, involving at least 24 morphologically indistinguishable species (De Barro et al. 2011); for present purposes, the name *B. tabaci* will be used to refer to all biotypes/species. Both whiteflies are devastating agricultural insect pests that can seriously damage crops by feeding directly on plant sap and excreting honeydew. In addition, *B. tabaci*

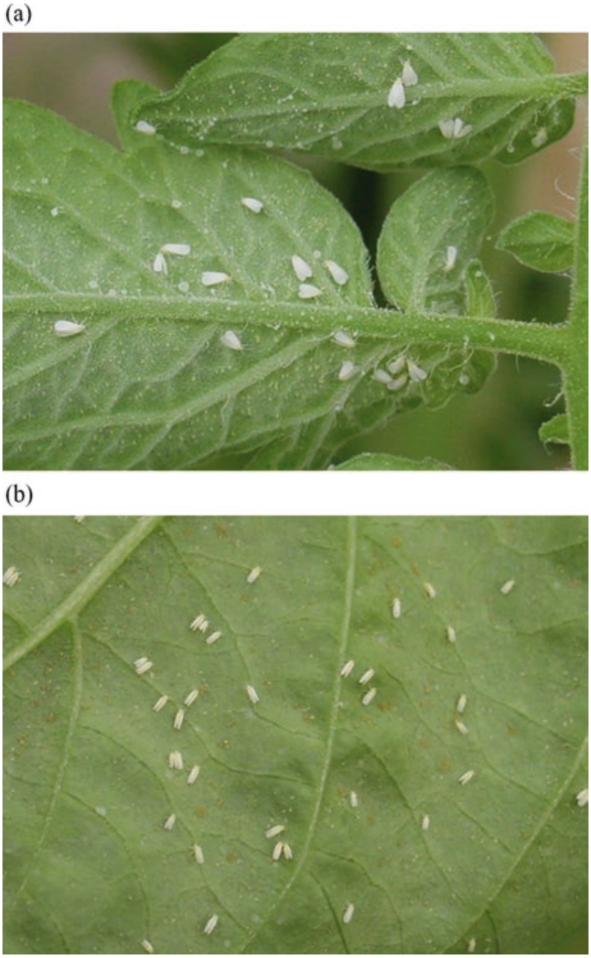

Fig. 17.1 Adults of the whiteflies *Trialeurodes vaporariorum* (**a**) and *Bemisia tabaci* (**b**)

transmits several viruses, among which Tomato Yellow Leaf Curl Virus (TYLCV) causes significant economic losses (Moriones and Navas-Castillo 2009) (See also Chap. 1). The tomato leafminer *T. absoluta,* a native pest in Latin America, was first detected in Spain in 2006; it subsequently invaded the rest of the Mediterranean and other parts of Europe and expanded rapidly into Africa and Asia. *T. absoluta* develops very large populations, and larval feeding can cause crop losses of up to 100%, attacking leaves, flowers, stems and especially fruits (EPPO 2006).

Tomato russet mite (*A. lycopersici*) is common in all areas where tomato and other Solanaceae are cultivated and has created increasing problems in both Mediterranean and Central European greenhouses. Adults and nymphs feed on the foliage, inflorescence and young fruits of tomato plants, causing shrivelling and necrosis of leaves, dropping of flowers and russeting of fruit (www.cabi.org) (Table 17.1).

Table 17.1 Greenhouse tomatoes: major pests and their natural enemies

	Biological control agents	General remarks
Whiteflies	*Nesidiocoris tenuis*	Release of *N. tenuis* in seedlings to advance installation in the crop
Tomato Leafminer	*Macrolophus pygmaeus*	Large populations of *N. tenuis* can cause damage to plants
	Dicyphus sp.	Use of companion plants (*Calendula* sp.) as refuge for *M. pygmaeus* in non-crop periods or for collecting populations from old crop to new
		Use of alternative food (*Artemia* sp. cysts, *Ephestia* eggs) to improve mirid bug installation in the crop
Whiteflies (specific)	*Encarsia formosa*	In areas affected by TYLCV, use of insect-proof netting in all ventilation structures prevents immigration of whiteflies (Bt) from outside
Bemisia tabaci (Bt)	*Eretmocerus* spp.	*E. formosa* is used only for Tv control while mirid bug populations are growing
Trialeurodes vaporariorum (Tv)		
Tomato Leafminer (specific)	*Dineulophus phtorimaeae*	Mirid bugs provide partial control of leafminer
Tuta absoluta	*Necremnus tutae*	Important natural populations of larval parasitoids
Mites	No efficient NE available. Use specific acaricides compatible with NE	Avoid contamination by eliminating wild hosts (*Convulvulus* sp., *Solanum* sp.) or debris from old infested crops
Aculops lycopersici		Detection of first foci of TRM may allow more selective chemical control
Tetranychus urticae		
Dipteran leafminers	*Diglyphus isaea*	Generally controlled by important natural populations of larval parasitoids and/or mirid bugs. Commercial NE can also be released if needed
Liriomyza sp.	*Neochrysocharis formosa*	
	Dacnusa sibirica	
	Opius pallipes	
Aphids	*Aphidoletes aphidimiza*	Generally controlled by mirid bugs. Specific NE can also be released as needed
Macrosiphum euphorbiae	*Aphidius* sp.	
	Aphelinus sp.	

17.2.2 Diseases

The major diseases of greenhouse tomatoes are presented in Table 17.2 and in Fig. 17.2. Most key **virus diseases** of tomatoes are transmitted by insect pests (mainly aphids, thrips and whiteflies). Their impact on crop health is closely related

Table 17.2 Major diseases in greenhouse tomatoes and IPM components for control

Pathogens and diseases	Control methods
Viruses and viroids	Varieties with tolerance/resistance to the virus (not available for all viruses)
Aphid-transmitted: Potato Virus Y (PVY), Cucumber mosaic virus (CMV), Alfalfa mosaic virus (AMV)	Use of pathogen-free seeds and healthy seedlings (including those used as rootstock)
Thrips-transmitted: Tomato spotted wilt virus (TSWV)	Eradication of alternative hosts. Removal of infected plants (roguing) to prevent further dissemination (taking particular care in case of contact-transmitted viruses)
White fly-transmitted: Tomato yellow leaf curl virus (TYLCV) transmitted by *Bemisia tabaci*; Tomato Infectious Chlorosis Virus (TICV) transmitted by *Trialeurodes vaporariorum*; Tomato Chlorosis Virus (ToCV) and Tomato Torrado Virus (ToTV) transmitted by both *B. tabaci* and *T. vaporariorum*	Adaptation of planting dates for a crop-free period and application of sanitation methods before establishment of a new crop to avoid carryover of virus-infected insect vectors. Disinfestation of greenhouse structures, particularly against contact-transmitted viruses
Contact-transmitted: Tobacco Mosaic Virus (TMV), Tomato Mosaic Virus (ToMV) and Pepino Mosaic Virus (PepMV)	Control of insect vectors by insect-proof netting, resistant varieties and biological control
These can also be seed-transmitted	Cross-protection with mild strains (for example, PepMV)
Viroids: Potato Spindle Tuber Viroid (contact- and seed-transmitted)	
Bacterial diseases	Resistant varieties (Ps, Xc, Rs)
Airborne: *Pseudomonas syringae* (Psy) pv. *tomato* (Bacterial speck), *Xanthomonas campestris* (Xc) pv. *vesicatoria*, (Bacterial spot)	Prophylactic methods: roguing, pathogen-free irrigation water, seeds and transplants, destruction of crop residues, eradication of alternative hosts, disinfestation of pruning tools, stakes/trellises and greenhouse structures
Soilborne: *Clavibacter michiganensis* (Cm) subsp. *michiganensis* (Bacterial canker), *Pseudomonas corrugata*, (Pith necrosis), *Ralstonia solanacearum* (Rs) (Bacterial wilt)	Biocontrol products, copper-based pesticides
	Solarization and other methods of soil disinfestation
	Avoidance of excessive fertilization (especially nitrogen)
Fungal diseases	
Airborne: *Botrytis cinerea* (Gray mould), *Oidium neolycopersici* and *Leveillula taurica* (Powdery mildew), *Phytophthora infestans* (Late blight), *Passalora fulva* (previously *Fulvia fulva*; Leaf mould)	Prevention of excess air humidity and free water on plants through use of drip-irrigation, greenhouse ventilation (and heating when appropriate), lower plant densities and leaf pruning to foster air movement

(continued)

Table 17.2 (continued)

Pathogens and diseases	Control methods
Alternaria solani (Early blight), *Alternaria alternata* f.sp. *lycopersici* (Alternaria stem canker), *Didymella lycopersici* (Didymella stem canker), *Stemphyllium* spp. (Stemphyllium leaf spot), *Septoria lycopersici* (Septoria leaf spot), *Sclerotinia* spp. (White mould)	Timing and method of plant pruning; wound protection with fungicides, biocontrol agents or clay-based products; roguing of infected plant organs and destruction of crop residues to avoid production of secondary inoculum; preventive application of fungicides; use of pathogen-free transplants
	Varieties with (sometimes partial) resistance to leaf mould, late blight, *A. alternata*, *Stemphyllium*, Septoria; rootstock resistant to Didymella
	Biopesticides
Soilborne: *Verticillium dahliae*, *V. albo-atrum* (Verticillium wilt), *Fusarium oxysporum* f. sp. *lycopersici* (Fol – Fusarium wilt) *F. oxysporum* f. sp. *radicis-lycopersici* (Forl – Fusarium crown and root rot)	Resistant varieties or grafting of resistant rootstock; destruction of crop residues, irrigation with non-saline water, weeding, solarization and biosolarization, chemical soil disinfestation, nematode control, pathogen free seeds
Colletotrichum spp. (anthracnose), *Phytophthora parasitica* (Phytophthora root rot and buckeye rot), *Pyrenochaeta lycopersici* (corky root), *Rhizoctonia solani, Sclerotinia* spp. (White mould)	Biological control

to the introduction, development and spread of the vectoring pest in the greenhouse. Over the years, several such viruses have emerged, and their geographic range has expanded, often paralleling the spread of their vector. This has often generated regulatory issues in the countries of introduction, including classification of the emerging viruses as quarantine organisms (Hanssen et al. 2010; Tsuda and Sano 2014; Moriones et al. 2017). In recent years, contact-transmitted viruses and viroids (which are often also seed-transmitted) have become increasingly prevalent in greenhouse tomatoes, as for instance in the case of Pepino Mosaic Virus, which has been reported in many countries across several continents and may be more prevalent than reported, as its symptoms and economic impact may remain discreet (Hanssen and Thomma 2010). Viruses that had become rare, such as Tomato Mosaic Virus and Tobacco Mosaic Virus, have re-emerged following renewed interest in producing "old" tomato varieties that lack the resistance genes commonly found in more modern varieties (Hanssen et al. 2010).

Prevailing **fungal and bacterial diseases** differ substantially, depending on the type of production system. In tomato crops produced in soil, the risks associated with soilborne diseases have strongly increased with the phasing out of methyl bromide, a fumigant that was widely used for soil disinfestation, and because of challenges in identifying alternative solutions (McGovern 2015; Xie et al. 2015). While tomatoes produced in substrate isolated from the soil are less likely to be affected by soilborne diseases, they can be badly damaged by certain soilborne pathogens

Fig. 17.2 Symptoms of the fungal diseases *Leveillula taurica* (**a**) and *Phytophtora infestans* (**b**), the bacterial disease *Pseudomonas syringae* (**c**) and the viral disease Tomato Yellow Leaf Curl Virus (TYLCV) (**d**)

such as the fungus *Fusarium oxysporum* f. sp. *radicis lycopersici* and the bacteria *Ralstonia solanacearum* and *Clavibacter michiganensis* subsp. *michiganensis*, which are capable of disseminating through irrigation water or an airborne phase (Shimizu et al. 2007; Frenkel et al. 2016). Both bacteria can also be transmitted via seeds and seedlings, and both are classified as quarantine organisms in various global regions. Although often considered less important, soilborne oomycetes (e.g. various species of *Pythium* and *Phytophthora*) can thrive in hydroponic systems, degrading plant root systems (Vallance et al. 2011). The re-circulation of nutrient solutions (as required by regulatory authorities in various countries) may foster multiplication and dissemination of many of these pathogens, requiring use of disinfestation systems (Vallance et al. 2011) (See Chap. 3 on soilborne diseases). Most of the airborne diseases affecting the tomato are fostered by high air humidity, and several pathogens such as *Phytophthora infestans*, *Botrytis cinerea*, and other bacteria listed in Table 17.2 are enhanced by the presence of free moisture on the plant, which allows germination or dissemination and penetration of inoculum (Fry et al. 2015; Frenkel et al. 2016; Carisse 2016). These diseases are particularly problematic in unheated plastic-covered greenhouses where there is limited management of climatic conditions; although also found in heated glasshouses, this is less common, as excess air humidity is usually avoided through careful (often computerised) climate control. For example, in humid unheated greenhouses, *B. cinerea* may cause severe leaf blight, flower and fruit rot, ghost spots and stem rot while in heated glasshouses, symptoms are generally confined to stem cankers resulting from infection of pruning wounds. However, powdery mildews can be equally problematic in all types of greenhouse, as development of their causal agents does not require high levels of air humidity.

Many other factors influence the prevalence and severity of diseases in the tomato greenhouse because of the host crop's susceptibility or the support provided by the greenhouse environment for the development and dissemination of pathogens or their vectors. For a general analysis of these factors, please see Chap. 7 (Epidemiology). The next section discusses possible means of manipulating these factors to reduce the impact of tomato pests and diseases.

17.3 Components of IPM

17.3.1 Sanitation Measures

One important factor for successful IPM is to start the cropping season without plant pathogens or pests inside the greenhouse. This can be achieved by various sanitation practices, some of which are initiated at the end of the previous crop, with careful removal and proper disposal of all potentially contaminated plant material and debris and used greenhouse consumables. (For an overview of methods, see Chap. 10 on elements of IPM). A crop-free period and/or avoiding simultaneous planting of crops hosting the same pest will reduce the risk of inoculum transfer from crop to crop. These practices are of proven efficacy, as for example when applied at a regional scale to manage *B. tabaci* and associated viral diseases (Hilje et al. 2001). As many tomato pests and pathogens can also develop or survive on weeds and in non-agricultural habitats, it is also important to keep greenhouse surroundings clean. This practice is recommended for whitefly control and has significantly delayed whitefly crop infestation in warm areas (Alomar et al. 1987).

Soilborne pests and pathogens can accumulate in substrates of soilless production systems when these are reused over successive cropping cycles (Diara et al. 2012). In both cases, solarization can be implemented as an alternative to chemical disinfestation (Diara et al. 2012; Katan 2017). Closing the greenhouse during hot summer periods to allow air temperatures to reach biocidal levels may also be useful for disinfestation of greenhouse structures and reused consumables (Shlevin et al. 2004). Soil solarization is widely used in warm areas where crops are changed or absent for part of the summer (Katan 2017); when applied immediately after a crop has finished, it is also an effective means of preventing the dispersion of pest insects that spend part of their life cycle in the soil, such as thrips or leaf miners (*Liriomyza* spp. or *Tuta absoluta*) (van der Blom et al. 2011). Other available methods of soil disinfestation include biosolarization, biofumigation and use of trap plants (Katan 2017). (See also Chap. 3 on soilborne diseases and Chap. 7 on nematodes). Finally, it is crucial to start a crop with plant material that is free of pests or diseases, whether produced by the grower onsite or purchased from a commercial nursery, making strict sanitation measures and surveillance of plant health essential in the nursery.

17.3.2 Resistant Varieties

Tomato varieties with reduced susceptibility to several diseases are commercialized in many countries. Genes conferring partial or high-level resistance originate mainly in wild species of tomatoes and have been introgressed into commercial varieties in various combinations (Blancard 2012; see also Chap. 9 on plant resistance). The most commonly available resistance or tolerance traits relate to viral diseases (with the notable exception of AMV and CMV), soilborne diseases (such as Fusarium, Verticillium or bacterial wilts) and airborne diseases caused by fungi (leaf mould, early and late blights, Septoria leaf spot, powdery mildew) or bacteria (bacterial speck, bacterial spot). Host-plant resistance to the most common viruses in the crop area is the optimal solution to virus diseases transmitted by whiteflies, and a number of varieties have been successfully commercialized (Ji et al. 2007). Nevertheless, the effectiveness of virus-resistant varieties is limited in time if vector populations are not reduced, as high levels of inoculum favour the appearance of new strains that overcome resistance (Mutschler and Wintermante 2006).

With the exception of resistance to root-knot nematodes (Barbary et al. 2015), resistance against invertebrate pests is not widely available commercially, although this situation is changing rapidly as a result of recent and ongoing research. Glandular trichomes of different types in several accessions of wild tomato species confer resistance to whiteflies by secreting toxic and repellent compounds (acylsugars, metylketones and sexquiterpenes) (Simmons and Gurr 2005). Introgression of these characters into commercial accessions is difficult when using wild parents with green fruits (*S. pennelli*, *S. habrochaites*, *S. peruvianum*) because these multigenic characters drag poor horticultural traits. However, when using wild accessions with red fruit (*S. galapagense*, *S. pimpinellifolium*) that are closer relatives of *S. esculentum*, introgression of resistance characters has proved more successful (Rakha et al. 2017a). Resistance to the vector can improve IPM of whiteflies to prevent viral plant diseases. Combining virus and vector resistance in tomato would be of value in repelling whitefly, helping to preserve the durability of virus resistance genes by contributing to slowing of begomovirus evolution. In this regard, it has been shown that selected accessions resistant to *B. tabaci* can reduce the incidence of transmitted TYLCV (Escobar-Bravo et al. 2016).

Varieties specifically commercialized for use as rootstock also offer plant resistance benefits. In many countries, greenhouse tomatoes are now produced mainly from grafted transplants—a practice originally developed in Asia (Singh et al. 2017).

Commercial rootstock varieties may exhibit resistance to a range of common soilborne pests and diseases, including root knot nematodes, corky root, and Fusarium, Verticillium or bacterial wilts, and occasionally to root pathogens such as *Fusarium solani*, *Pythium aphanidermatum* and *Phytophthora nicotianae*. In Spain and other Mediterranean countries, commercial grafting is used to control root knot nematodes *Meloidogyne javanica* Chitwood, *M. incognita* Kofoid and White and *M. arenaria* Roberts and Thomason (Verdejo-Lucas and Sorribas 2008).

Because combining a large number of resistance traits—some of which are controlled by multiple genes—is challenging for breeders, commercial varieties (whether for rootstock or fruit production) usually carry only a few of the known traits. In addition, as many tomato pathogens and pests are known for their variability and their capacity to adapt to selection pressures, the protection provided by resistance genes does not always cover all existing races of pathogens or pests, making it important that farmers opt for varieties resistant to locally prevailing strains.

17.3.3 Cultural Control During the Cropping Season

Many practices performed during the growing season may contribute to IPM by impacting directly on pests and plant pathogens, by making the microclimatic environment less favourable to their development, by making the environment more favourable for their natural enemies or antagonists, or by reducing the plant's susceptibility, even if it carries no resistance genes.

As a physical barrier to prevent entry to the greenhouse of pests such as whiteflies, aphids, leaf miners and mites, insect-proof screening nets are an integral part of IPM procedures against *B. tabaci* and TYLCV in many countries around the Mediterranean Basin and in other parts of the world. The blocking effect of these nets interferes with the insects' penetration capacity (Bell and Baker 2000; Díaz Pérez et al. 2003) and has proved to be the only effective solution for cropping tomatoes in areas with high incidence of TYLCV. Nets impregnated with insecticides or with ultraviolet blocking materials are also being developed (Díaz and Fereres 2007; Dader et al. 2014). No equivalent netting systems are available to guard against airborne plant pathogens, owing to their microscopic size. However, pathogen entry is likely to be greatly reduced in totally closed greenhouses and plant factories, a technology developed with the specific aim of maximizing resource use efficiency (Dannehl et al. 2014; Graamans et al. 2018). To prevent entry of soilborne pathogens carried on workers' and visitors' shoes, many greenhouses are equipped with foot baths or mats, impregnated with a disinfectant solution that is usually changed daily.

As most plant pathogens thrive on excessive humidity, climate management is a key control method. For this purpose, high-investment heated glasshouses have long been equipped with climate sensors and computer-controlled devices to keep relative humidity within an acceptable range. However, even in glasshouses with sophisticated climate management systems, condensation may occur on the canopy during cool clear nights as a result of radiative losses that cause plant surface temperature to drop. To avoid this problem, and to save on energy costs, thermal screening is commonly deployed on winter nights above the glasshouse canopy. Equivalent technologies are also being successfully developed for unheated plastic greenhouses (Hernandez et al. 2017). In addition to technology-based climate control, known cultural techniques can be used to support air circulation and to prevent humidity in the canopy microclimate, including row spacing, planting density and plant architecture, as well as leaf pruning (Decognet et al. 2010). Improved air circulation and reduced plant production of water vapour can also be achieved by selecting tomato varieties that develop a lower density of foliage or by fertilization and water supply schemes that avoid excessive leaf development.

Adjustments to fertilization and water supply may affect plants' physiological receptiveness to pests and pathogens. For example, high nitrogen fertilization can reduce stem lesions caused by *B. cinerea* and improve the protective efficiency of biocontrol agents (Abro et al. 2014). However, high nitrogen may also promote other diseases such as powdery mildew (Nicot et al. 2012; Hoffland et al. 2000); it is also positively correlated with adult attraction and immature development time in whiteflies, whose higher intrinsic rate of population increase makes control more difficult (Jauset et al. 2000; Idriss et al. 2015; Islam et al. 2017).

Soil and water salinity can also affect tomato plant susceptibility to various diseases and interferes strongly with genetic resistance (Bai et al. 2018). The increasing research interest in the complex interactions between abiotic and biotic stresses that affect plant physiology should lead to the development of improved IPM tools.

Finally, plant susceptibility may also be influenced by application of compounds and microorganisms that stimulate its natural defence system, typically including the biopesticides and plant biostimulants described below.

17.3.4 Biological Control, Biopesticides and Biostimulants

(See Chaps. 13 and 14 for a broad perspective on biological control of diseases and pests in greenhouses).

17.3.4.1 Insects and Mites

Biological control, which includes seasonal inoculative releases and augmentation and conservation of natural enemies, is used to manage the main pests affecting greenhouse tomato crops.

Whiteflies (*T. vaporariorum* and *B. tabaci*) are the main targets of all biological control programs for this crop. Initially based exclusively on parasitoid releases, these are now usually combined with or replaced by inoculative introduction of mirid bugs or strategies to attract these predators into the crop from the surrounding vegetation—that is, biological control by conservation. The three most important and commercially available parasitoids are *Encarsia formosa* Gahan (for control of *T. vaporariorum*), *Eretmocerus eremicus* Rose and Zolnerowich (for control of both *T. vaporariorum* and *B. tabaci*) and *Eretmocerus mundus* Mercet (which reproduces on *B. tabaci* but not on *T. vaporariorum*) (Liu et al. 2015). Predatory mirid bugs are polyphagous and have proved very successful as biological control agents of whiteflies and other tomato pests (Albajes and Alomar 1999). As they have a long immature development time when compared to other natural enemies, mirid bugs need longer to establish their populations in the crop. For this reason, supplemental foods, such as *Ephestia* eggs or *Artemia* spp. cysts (Moerkens et al. 2017) are provided to facilitate *Macrolophus pygmaeus* (Rambur) in the crop in most Central European glasshouses. In addition, *E. formosa* are released to bridge this period. In Mediterranean areas where the crop cycle starts in early spring, with abundant vegetation in the surroundings, a strategy can readily be based on the spontaneous appearance of mirid bugs, mostly *Macrolophus* spp. and *Dicyphus* spp. (Alomar et al. 2002; Castañé et al. 2004; Gabarra et al. 2004; Aviron et al. 2016). Management of companion plants (such as strips of *Calendula officinalis* L. in margins at the crop edge) is also used to preserve populations of *M. pygmaeus* between crop cycles or to provide a refuge for spontaneous populations. From these margins, predators can colonize open-field or greenhouse crops. This conservation strategy has been applied with great success in northern Spain and the south of France (Lambion 2014; Balzan 2017). In southern Spain, where crop cycles start at the end of summer, biological pest control is based mainly on the release of *Nesidiocoris tenuis* (Reuter) (Fig. 17.3a) in seedlings by the plant propagator, 1 week before the plants are taken to the final greenhouse (Calvo et al. 2012; Vila et al. 2012). When transplanted, they already contain *N. tenuis* eggs, and the population of mirids quickly builds up in the early weeks of crop development. Because mirid bugs do not feed exclusively as predators but are also partly phytophagous (*N. tenuis, Dicyphus* sp. and, to a lesser extent, *M. pygmaeus*), they may cause significant damage to the plants when populations are high and the supply of prey is low (Sanchez 2008; Arnó et al. 2010; Castañé et al. 2011). Damage by *N. tenuis* can affect young shoots and peduncles, provoking flower abortion and curtailing plant development. Mirids may also feed directly on the fruits, affecting their quality and commercial value (Lucas and Alomar 2002). To overcome this problem, a decision support system has been developed for selective treatments against *Dicyphus* sp. once the first symptoms of fruit damage are seen (Alomar and Albajes 1996); in the case of *N. tenuis*, treatments are applied when the first symptoms of plant damage are observed. The use of companion plants such as *Sesamum indicum* (L.) is a novel strategy that seems efficient in preventing damage caused to the tomato plant by *N. tenuis* (Biondi et al. 2016).

Entomopathogenic fungi such as *Lecanicillium lecanii* R. Zare & W. Gams, *Isaria fumosorosea* Wize, and *Beauveria bassiana* (Balsamo) Vuillemin have been commercialized for whitefly control. These act mainly against nymphs but require certain environmental conditions if they are to be effective. In addition, their incompatibility with most fungicides limits their application.

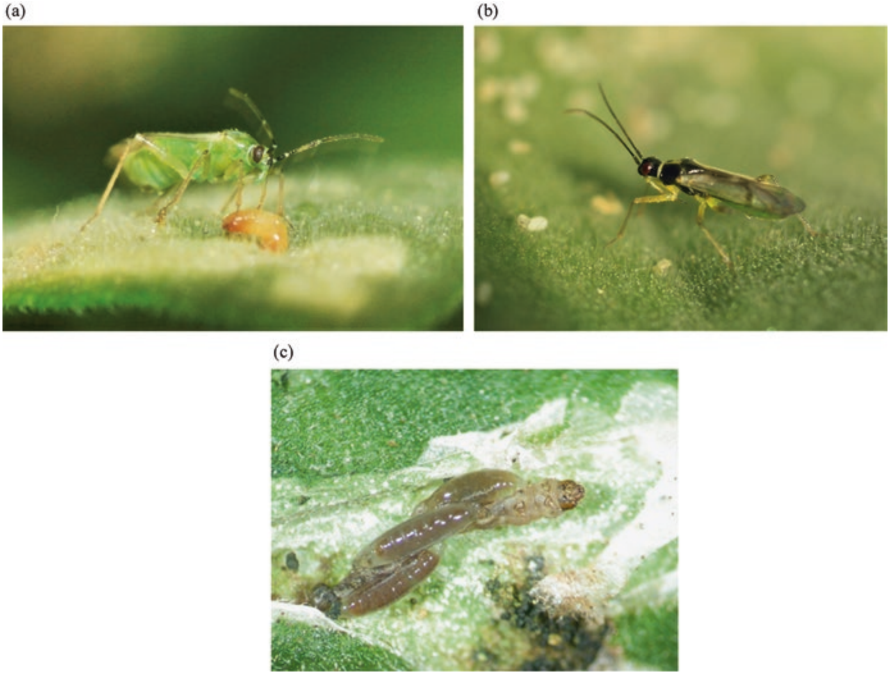

Fig. 17.3 Adults of the predatory mirid bugs *Nesidiocoris tenuis* (**a**) and *Tupiocoris cucurbitaceus* (**b**) and larvae of the parasitoid *Necremnus tutae* (**c**)

Although several natural enemies of *T. absoluta* have been reported, only a few of these are commercially available. The best documented predators belong to the family Miridae, predating mainly on eggs and small larvae; *N. tenuis, M. pygmaeus, and D. errans* are reported in Europe (Urbaneja et al. 2012; Ingegno et al. 2013, 2017) and *Tupiocoris cucurbitaceus* (Spinola) (Fig. 17.3b) has been reported in Latin America (Bueno et al. 2013). In young plantations, where *N. tenuis* and *T. absoluta* are found on the same leaves, their predatory role is more important than in old and tall plants. In mature crops, large populations of *N. tenuis* were also observed to coincide with heavy attacks of *T. absoluta*, indicating that control of the pest was clearly insufficient (Van der Blom et al. 2016). Various species of parasitoids reproduce on *T. absoluta* eggs; 17 species have been documented in Latin America and 5 species have been found in Europe (Zappalá et al. 2013). However, the most important natural enemies are larval and pupal parasitoids, with 29 different species described in Latin America and 41 different taxons already identified in the Mediterranean (Luna et al. 2012; Gabarra et al. 2014). Some Eulophidae appear particularly efficient as control agents, including *Dineulophus phtorimaeae* (de Santis) in Argentina and Chile and *Necremnus tutae* Ribes & Bernardo (originally documented as *N.* sp. nr. *artynes*) (Fig. 17.3c) in Europe and North Africa (Luna et al. 2012; Gebiola et al. 2015). *N. tutae* has shown significant capacity to control populations of *T. absoluta*, with rates of parasitism that can increase from less than 5% to almost 100% larval mortality in the course of only a few weeks. Mortality of *T. absoluta* larvae is largely caused by host feeding (Calvo et al. 2013; Van der Blom et al. 2016). As attempts to mass-produce *N. tutae* have not been successful to date, the species is not commercially available. However, *N. tutae* is so common in south-east Spain that a strategy of monitoring and conservation seems sufficient to achieve complete control of *T. absoluta*.

Several species of predatory mites are able to feed, reproduce and control **russet mites** on laboratory conditions, as *Homeopronematus anconai* (Baker), *Amblyseius andersoni* (Chant), *A. montdorensis* (Schicha)*, A. swirskii* (Athias-Henriot) and *Amblydromalus limonicus* (Garman and McGregor) among others (Haque and Kawa 2002; Fischer et al. 2005; Park et al. 2010; Steiner and Goodwin 2005). However, these are not effective in controlling heavy *A. lycopersici* infestation on large tomato plants. The small eriophid mites escape from predator control by moving up the plant and taking refuge in the dense area covered by the glandular trichomes of the growing shoots. Predatory mites have difficulty moving and establishing in this area, and biocontrol is ineffective (Lara et al. 2012; van Houten et al. 2013). The lack of efficient biological control agents leads inevitably to frequent application of acaricides, representing a bottleneck in the tomato IPM programme. Negative side effects on beneficial fauna can be limited by preventive application of sulphur, preferably in liquid form, directed to the lower parts of the plants, or by sublimation. Application of dusted sulphur should be avoided because of its negative side effects on parasitoid Hymenoptera and phytoseiids.

In Mediterranean regions, with high temperatures and low humidity, **spider mites** are a problem in many greenhouse areas, especially in dry conditions (Sade et al. 2016), the most common species being *Tetranichuus urticae* Koch. Biological control of tomato crops with inoculative releases of *Phytoseiulus persimilis* Athias-Henriot has proved largely ineffective (Gerson and Weintraub 2012), probably because of the mass rearing conditions of commercial *P. persimilis* (Drukker et al. 1997). A special strain of *P. persimilis* reared and adapted to tomato was brought to market, but this is not always commercially available. Other species of *Phytoseiulus,* such as *P. macropilis* (Banks) and *P. longipes* Evans, are also being tested (Gigon et al. 2016). Another emerging strategy involves selection of tomato resistant varieties based on the repellency to spider mites caused by exudates of glandular trichomes (Rakha et al. 2017b). Another species, *Tetranychus evansi* Baker & Pritchard, is common in Latin and North America and in many other parts of the world, including several Mediterranean regions. Promising results against *T. evansi* have been obtained with *Phytoseiulus longipes* (Ferrero et al. 2011).

Dipteran leafminers (*Liriomyza* spp.) have a broad range of natural enemies, including polyphagous larval parasitoids and generalist predators such as mirid bugs. In cold areas, inoculative releases of the larval parasitoids *Diglyphus isaea* Walker and *Dacnusa sibirica* Telenga are applied. In warm areas, natural populations of leafminer parasitoids are abundant all year round, and natural parasitism can control leafminers in the crop (Tellez Navarro and Yanes Figueroa 2004); augmentative releases of *D. isaea* are used only when natural parasitism is low. The presence of mirid bugs (*Dicyphus* sp. *Macrolophus* sp.) in the crop usually ensures good control of leafminer populations, complementing the effect of the parasitoids (Nedstam and Johansson-Kron 1999; Arnó et al. 2003).

Western flower thrips, *Frankliniella occidentalis* Pregande, can be a serious pest, causing cosmetic damage to fruits in the cherry and cocktail tomato varieties. Additionally, *F. occidentalis* is a vector of Tomato Spotted Wilt Virus (TSWV). While many tomato varieties are resistant against this virus, others are not. Although mirid bugs can be important predators of thrips, they are not always able to avoid damage. Specific thrips predators used in other crops, like *Orius* spp. and various Phytoseiid predatory mites, are unable to survive in tomato plants. The application of blue sticky traps is recommended, from the beginning of the crop cycle onwards.

The **aphid** most commonly found in tomato is *Macrosiphum euphorbiae* Thomas, which can be controlled through inoculative releases of the parasitoid *Aphidius ervi* Haliday. However, releases of parasitoids against aphids are not performed in most greenhouses, as the presence of indigenous populations of natural enemies means that aphids do not normally reach economic thresholds (Alomar et al. 1997; Alvarado et al. 1997).

The **noctuid moth** *Helicoverpa* spp. can cause severe problems in some areas by mining into fruits. While *H. armigera* (Hübner) is found in many parts of the world, *H. zea* (Boddie) is restricted to North and South America. Mirid bugs may play an important role as predators of eggs and first instars (Devi et al. 2002). Inoculative releases of *Trichogramma* sp. in combination with *Bacillus thuringiensis* can be effective against young larval stages before they enter the fruits.

17.3.4.2 Diseases

Totally absent or reported only anecdotally in greenhouse production 20 years ago (van Lenteren 2000; Nicot and Bardin 2012), biological control products and other biopesticides against diseases have now become available in many countries. Examples of products commercialized for the protection of tomato are listed in Table 17.3, which was compiled by consulting national databases on registered plant protection products in several member countries of the European and Mediterranean Plant Protection Organization (www.eppo.int), supplemented by information from other continents. Commercial biopesticides include at least 24 microbial preparations, based on 16 fungal strains (10 of which are *Trichoderma* sp.) formulated singly or in association, 10 bacterial strains (of which 8 are *Bacillus* sp.) and a hypo-aggressive strain of Pepino Mosaic Virus, which induces cross-protection against aggressive strains of the virus when inoculated to tomato seedlings. The majority of these microbial preparations are registered against fungal soilborne diseases and recommended for use as soil drench, as well as for amendment in greenhouse substrates and seed dressing or for seedling dipping. Application through the irrigation system may also be authorized (e.g. Tusal and T34 Biocontrol in France), which may facilitate their use in soilless production systems. A substantial number (predominantly based on strains of *Bacillus* sp.) have also been com-

Table 17.3 Examples of commercialized biopesticides against tomato diseases

Target pathogens or diseases	Active substance (commercial products)
Viruses and viroids	
Pepino Mosaic Virus	Hypo-aggressive strain CH2 of Pepino Mosaic Virus, isolate 1906 (**PMV-01**)
Bacterial diseases	*Bacillus amyloliquefaciens* D747 (**Double Nickel**); *Bacillus mycoides* J (**LifeGard**); *Bacillus subtilis* QST 713 (**Cease**, **Serenade**); Phages against *X. campestris* and *P. syringae* (**Agriphage Tomato spot and speck**)
	Acibenzolar-s-methyl (**Actigard, Bion**); Citric acid (**FungOUT**); Citric and lactic acids (fermentation by-products of *Lactobacillus casei* LPT-111) (**Cyclone**); Extracts of clove, thyme, cinnamon, garlic and peppermint (**BacStop**); Extract of *Reynoutria sachalinensis* (**Regalia**); Tea tree oil (**Timorex Gold**)
Fungal diseases	
Powdery mildews	*Ampelomyces quisqualis* (**AQ10**); *B. amyloliquefaciens* D747 (**Amylo-X, Double Nickel**); *Bacillus pumilus* QST2808 (**Sonata**); *B. subtilis* QST 713 (**Cease**, **Serenade**); *Streptomyces lydicus* WYEC108 (**Actinovate**)
	Acibenzolar-s-methyl (**Actigard**); Citric acid (**FungOUT**); COS-OGA (**Fytosave**); Cottonseed oil + corn oil + garlic oil (**Mildew Cure**);
	Extracts of clove, rosemary and Peppermint (**EF400**); Extract of fennel (**Bio Garden Pilz-Stopp, Fenicur**); Extract of garlic (**Influence LC**); Extract of neem oil (**Trilogy**); Extract of *Reynoutria sachalinensis* (**Regalia**, **Reysana**); Laminarin (**Vacciplant**); Maragosa (neem) oil (**Agrimorstop-Pestop**); Potassium bicarbonate (**Armicarb, Ecocarb, Kaligreen, Milstop; MycoStop Spray, Sirocco**); Potassium salts of fatty acids (**M-Pede**); Tea tree oil (**Timorex Gold**)
Phytophthora infestans (Late blight)	*B. amyloliquefaciens* D747 (**Double Nickel**); *Bacillus mycoides* J (**LifeGard**); *Bacillus pumilus* QST2808 (**Sonata**); *S. lydicus* WYEC108 (**Actinovate**);
	Extracts of clove, rosemary and Peppermint (**EF400**); Extracts of orange (**Geo-X, Limocide**); Potassium phosphonate (**Etonan, LBG-01F34, Pertinan**); Rhamnolipid biosurfactant from *Pseudomonas aeruginosa* (**Zonix Biofungicide**)
Other airborne pathogens (including *Alternaria* sp., *Botrytis cinerea*, *Didymella lycopersici,* airborne phase of *Sclerotinia* sp.)	*Aureobasidium pullulans* strains DSM 14940 and DSM 14941 (**Botector**); *B. amyloliquefaciens* MBI600 (**Serifel**); *B. amyloliquefaciens* D747 (**Amylo-X, Double Nickel**); *B. mycoides* J (**LifeGard**); *B. subtilis* GB03 (**Companion**); *B. subtilis* QST 713 (**Cease**, **Serenade**); *B. subtilis* Y 1336 (**Biobac**); *Gliocladium catenulatum* J1446 (**Prestop**); *S. lydicus* WYEC108 (**Actinovate**); *Trichoderma harzianum* Rifai KRL-AG2 (**Bora HC**);
	Extracts of clove, rosemary and Peppermint (**EF400**); extract of neem oil (**Trilogy**); extract of *Reynoutria sachalinensis* (**Regalia**); Laminarin (**Kayak, Vacciplant**); Soybean oil (**Bionatrol**); Tea tree oil (**Timorex Gold**)

(continued)

Table 17.3 (continued)

Target pathogens or diseases	Active substance (commercial products)
Soilborne pathogens (including *Fusarium*, *Phytophthotra, Pythium*, *Rhizoctonia*, *Sclerotinia*)	*B. amyloliquefaciens* D747 (**Double Nickel**); *B. amyloliquefaciens* FZB24 (**Taegro**); *B. subtilis* GB03 (**Companion**); *Coniothyrium minitans* (**Contans**); *G. catenulatum* J1446 (**Prestop**); *Gliocladium virens* GL-21 (**Soilgard**); *Pythium oligandrum* (**Polyversum**); *Streptomyces* K61 (**Mycostop**); *S. lydicus* WYEC108 (**Actinovate**); *Trichoderma asperellum* strains ICC012 T25 and TV1 (**Xedavir, Tusal**); *T. asperellum* T34 (**Asperello T34 Biocontrol**); *T. asperellum* ICC012 + *T. gamsii* ICC080 (**Bio-Tam, Cassat, Remedier, Tellus, Tenet**); *Trichoderma atroviride* IMI206040 + *T. parapiluliferum (polysporum)* IMI206039 (**Binab TF**); *T. harzianum* Rifai KRL-AG2 (**Bora WP, Rootshield**); *T. harzianum* Rifai strains T-22 and ITEM-908 (**Trianum, Triagro**); *T. harzianum* T-22 + *T. virens* G-41 (**Rootshield**)

mercialized against airborne fungi (and a few against bacterial diseases). Several of these products (e.g. Double Nickel, Serenade) appear to target a wide range of airborne tomato pathogens, which may prove useful when devising IPM schemes.

In addition to microbial products, a wide array of other biopesticides has been commercialized for the control of tomato diseases (see Table 17.3). Most are based on extracts of plants (12 preparations based on 15 botanical species, formulated singly or in mixture) or microorganisms (3 preparations), and on mineral or organic chemical compounds (5 preparations). Most of these biopesticides target powdery mildews (14 preparations), but several are also commercialized against other airborne pathogens, including late blight or bacteria. Many of these biopesticides may have direct antagonistic effects against specific pathogens—a trait that can be useful for an application in curative treatments—but their wide spectrum of action often results from the stimulation or priming of plant defence mechanisms. (For more detail, see Chap. 13 on biological control against diseases).

Plant biostimulants may also have a positive effect on plant health, with possible consequences for control of tomato diseases. These products, which are attracting interest in horticultural production (Colla and Rouphael 2015), are not usually registered as biopesticides, as they combine properties of fertilizers and plant protection preparations, involving many underlying biological processes (Colla and Rouphael 2015; Yakhin et al. 2017).

17.3.5 Selective Chemical Control

17.3.5.1 Insect and Mites

Most broad spectrum insecticides are highly toxic to natural enemies and the bumblebees (*Bombus terrestris* L) that are widely used for pollination of greenhouse tomato crops. This is also the case for many of the natural compounds permitted in organic agriculture. Nevertheless, there are many available selective products that can be used in IPM programs. Information on the compatibility of pesticides with natural enemies has been developed by the IOBC/WPRS Working Group on Pesticides and Beneficial Organisms (https://www.iobc-wprs.org/ip_ipm/IOBC_Pesticide_Side_Effect_Database.html). Information on the side effects of different active ingredients on the most important beneficial arthropods can also be found on the web pages of several companies selling natural enemies.

17.3.5.2 Diseases

The gamut of broad spectrum biocides registered for management of soilborne pathogens has declined steadily over the years. In comparison, there is a wide array of available chemicals to combat airborne pathogens, although compounds registered against bacterial diseases are mostly copper-based. While routine application of fungicides is clearly a thing of the past in most tomato greenhouses, management of airborne diseases still continues to rely on chemical control, even in production systems where biological control is predominantly used against insect pests. Like many insecticides, many fungicides may have negative effects on beneficial fauna; for that reason, it is important to consult the lists of side effects in order to choose products that are most compatible with the relevant BCAs. The increasing availability of biopesticides against pathogens, which are usually harmless for beneficial arthropods, should provide particularly useful alternatives to chemical control.

Implementation of alternative control methods should also be of value in managing fungicide resistance—a problem encountered in the case of several important tomato pathogens, including *Alternaria solani*, *B. cinerea* and *P. infestans* (Fillinger and Walker 2016; Gisi and Sierotzki 2008; Gudmestad et al. 2013). Along with reduced or stable application frequencies, lower doses may prove to be a good resistance management strategy for tomato pathogens as an increasing number of studies suggest (Jørgensen et al. 2017).

17.4 IPM Programmes

IPM programmes involve biological control of the main pests, complemented by compatible preventive and corrective measures against other pests and diseases. Application of IPM in greenhouse tomatoes has been favored by the generalised use of bumblebees for crop pollination, which is a cheap and effective means of improving yield quantity and quality. The use of bumblebees imposes strict limitations on the toxicity of pesticides that can be used on the crop. While the total area of greenhouses using IPM is not known, a sizeable majority of European greenhouses use biological control involving inoculative releases of NE or conservation strategies for pest control.

17.4.1 Factors Limiting Wider Application

As discussed previously, there are efficient non-chemical solutions for most of the arthropod pests that attack tomatoes in greenhouses. However, there is no effective biological (or chemical) solution for mites (red spider mite, tomato russet mite), and their incidence in many regions can limit the application of IPM.

The release of commercial NE often encounters problems of local availability because, in many cases, they must travel long distances from the mass rearing facility to the greenhouse destination. As these products consist of live animals, there are clear limitations with regard to shipment duration and physical conditions during transport.

Many biological control agents are subject to registration procedures that can be costly and time consuming, and the lack of harmonization of regulations governing commercialization of biocontrol agents seems a major problem. (See Chap. 20 for this and other aspects of IPM implementation in greenhouses). Additionally, there is a strong tendency in many countries to restrict the import of non-native biological control agents, which means that local solutions must be found that are often applicable only within small geographical areas. As the biological control industry is not a powerful sector, it may also prove very difficult to protect intellectual property following intensive research. Unlike chemical insecticides, beneficial arthropods cannot be patented as final products; this creates fierce competition among producers, who therefore operate with very small commercial margins.

The appearance of new pests is a challenge that requires rapid adaptation of existing IPM programmes. If the pest is also a vector of a new disease, pesticide application is often seen as the only practical solution. However, as previous invader pests confirm, populations usually become highly resistant to most pesticides, and biological control is the only sustainable solution.

Most such chemical applications aim to control plant diseases, and developing non-chemical solutions for this purpose remains a key challenge in reducing pesticide use.

17.4.2 Future of IPM in Relation to Greenhouse Tomatoes

The use of IPM based on the application of biological control is fundamental to the sustainability of the tomato industry. The international market imposes severe restrictions on chemical residues on fruits and vegetables that are impossible to meet without biological control. International retailers demand a quality standard that is only achievable through efficient IPM programmes. (See also Chap. 23 on implementation of IPDM).

Control of tomato pests using IPM is both feasible and widespread. However, continuous research is needed to address emergent problems, as in the case of control of mites, tomato leaf miner and diseases. From the grower's perspective, evidence from Spain indicates that biological control of pests is cheaper than chemical control (Van der Velden et al. 2012). However, the economics are variable, depending on the solution applied, its efficacy and where it is used. For example, conservation strategies using refuge plants for mirid bugs increase the efficacy of these natural enemies and reduce costs for growers. The release of *N. tenuis* in seedlings also reduces costs as compared to releasing the bugs in the transplanted crop. In the long term, control of new invasive pests is only effective through IPM, as observed in relation to past invasions of thrips (*F. occidentalis*), whiteflies (*B. tabaci*), dipteran leafminers (*Liriomyza* spp.) and the tomato leafminer (*T. absoluta*). Reducing the use of insecticides by applying natural enemies in regional-scale IPM programmes ensures that the range of generalist natural enemies is respected in that area, and some can easily adapt to control the new invader.

Other elements of crop management, such as the increased presence of root symbionts, can have important effects on plant robustness, reducing the need for nitrogen fertilization and enhancing defence mechanisms against many pests. In addition, these symbionts can improve plant attractiveness for some important natural enemies, with corresponding benefits for pest control, as shown by the interaction between tomato plants and mycorrhizas and increased attractiveness for the mirid bug *M. pygmaeus* (Durán Prieto et al. 2017). This illustrates the important challenge to be addressed with regard to soil management if a wide range of problems is to be avoided. In the aereal parts of the plant, as in the soil around the root system, active promotion of biodiversity rather than sterilization is the key to sustainable pest and disease control.

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Chapter 18
Sweet Peppers

Gerben J. Messelink, Roselyne Labbé, Geneviève Marchand, and Luciana Tavella

Abstract Sweet pepper is an important greenhouse vegetable crop and highly attractive to multiple pest and pathogen species. The main pests and diseases detrimental to pepper crops in various parts of the globe are reported here, along with the most effective or sustainable control strategies currently applied to manage them. Biological control of the main pest species, such as thrips, whiteflies and spider mites, is in general very successful with generalist predators, because of their ability to establish populations prior to pest invasions by using the plant-provided pollen as an alternative food source. However, other pest species, such as aphids, stink bugs and the pepper weevil, are still hard to control without pesticides and require new tools for management that do not disrupt the robust system of biological control. Most diseases can be controlled well by managing the climate, soil solarization, growing out of soil or by applying bacterial or fungal antagonists. All these tools together offer the opportunity to manage most pest and diseases with a minimal use of pesticides.

Keywords Biological control · Aphids · Thrips · Mites · Caterpillars · Whiteflies · Stink bugs · Pepper weevil · Internal fruit rot · Powdery mildew

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18.1 Introduction

Cultivated peppers generally belong to one of five *Capsicum* species, with *Capsicum annuum* L. representing the most commonly cultivated. *Capsicum annuum* includes multiple hot as well as sweet pepper varieties including bell peppers. Globally, cultivation of peppers is greatest in China, Mexico and Turkey who produced over 17.4M, 2.7M and 2.5M pepper tons, respectively in 2016 (FAOSTAT 2017). Generally, the protected cultivation of pepper represents a fraction of the total pepper production including field cultivation. Along with many European countries, Canada is an important producer of greenhouse peppers, with 135 million kg of peppers grown on 559 ha in 2016 (Statistics-Canada 2017). In Europe, the largest producer of sweet pepper in greenhouses is Spain with a production area of 12,420 ha, followed by Italy (2370 ha), Poland (1830 ha), and the Netherlands (1320 ha) (EUROSTAT 2017).

18.2 Main Pest and Disease Problems

Pepper is a highly attractive crop to multiple pest and pathogen species. Those affecting pepper crops can vary considerably in relation to geographic area and cropping system (e.g., open field or greenhouse, conventional or organic farming, etc.). At the same time, control measures adopted to reduce pests and diseases, and consequently crop losses, must be tailored to the environmental conditions, local cultural practices, and final market requirements. They must also observe national regulations on the importation of non-native agents as well as registration requirements. These apply not only to pesticides but also to biological control agents (BCAs). For instance, in some countries, only indigenous or cosmopolitan BCAs can be released for pest control regardless of their effectiveness. With this perspective, the main pests and diseases detrimental to pepper crops in various parts of the globe are reported here, along with the most effective or sustainable control strategies currently applied to manage them (Table 18.1).

18.2.1 Pests

18.2.1.1 Aphids

Aphids are among the most destructive pests of sweet pepper crops, particularly in temperate areas. The most important species known to attack pepper include the green peach aphid *Myzus persicae* Sulzer (several phenotypes ranging from green to dark red), the foxglove aphid *Aulacorthum solani* Kaltenbach and the cotton aphid *Aphis gossypii* Glover. These pests are followed in terms of importance by the

Table 18.1 Most important control agents for integrated pest management in sweet peppers

Pest/disease	Biological control agents	Supplementary measures
Aphids	Parasitoids (mainly *Aphidius* spp., *Aphelinus* spp.)	Systemic insecticides
	Predatory midge *Aphidoletes aphidimyza*	Soaps
	Lacewings (*Chrysoperla* sp.) and ladybird beetles (e.g. *Adalia bipunctata*)	Neem, natural pyrethrins
	Hoverflies (e.g. *Episyrphus balteatus* and *Sphaerophoria rueppellii*)	
	Mirid (e.g. *Macrolophus pygmaeus*) and anthocorid predatory bugs (e.g. *Orius majusculus*)	
Thrips	Phytoseiid predatory mites	Insect screens
	Anthocorid predatory bugs	Selective insecticides
	Entomopathogenic fungi	Resistant plants (TSWV)
Spider mites	Phytoseiid predatory mites (e.g. *Phytoseiulus persimilis* and *Neoseiulus californicus*)	Selective acaricides
	Predatory midge *Feltiella acarisuga*	
Tarsonemid mites	Phytoseiid predatory mites	
Lepidopterous caterpillars	Egg parasitoids (*Trichogramma* spp.)	Insect screens
	Bacillus thuringiensis	Pheromone traps, mating disruption
		Selective insecticides
Whiteflies	Parasitoids (*Eretmocerus* spp.)	Systemic insecticides
	Phytoseiid predatory mites	Insect screens
	Mirid predatory bugs	
	Entomopathogenic fungi	
Stink and true bugs	Not yet available	Screens, traps, insecticides
Pepper weevil	Not yet available	Screens, traps, insecticides
Powdery mildew	*Bacillus subtilis*, *Streptomyces lydicus*	Sulphur, mineral oil, tea tree oil, sodium bicarbonate, elicitors of plant defense mechanisms (extract of *Reynoutria sachalinensis*)
Grey mould	*Trichoderma harzianum*, *Gliocladium catenulatum*, *Bacillus amyloliquefaciens*, and *Bacillus subtilis*	
Internal fruit rot	Bee vectoring with *Gliocladium catenulatum* or *Bacillus subtilis* (experimental)	
Nematodes	*Purpureocillium lilacinum*, *Beauveria bassiana*, and *Trichoderma* spp.	Solarization

potato aphid *Macrosiphum euphorbiae* (Thomas) which is a generally rare pest of pepper in Europe and in North America, but sometimes occurs when the crop is in close proximity to a tomato crop. All of these species have a global distribution. These can cause severe plant damage by secreting high amounts of honeydew, which are a suitable substrate for sooty mould fungi, and lead to contaminated fruit and leaves. More importantly, the early colonisation of flowers by aphids can result in flower abortion and consequently reduced fruit production. The foxglove aphid is also known to cause growth deformation of leaves and high densities typically result in leaf dropping. In all cases, plants will eventually die when aphid densities are high and this can occur quickly due to their rapid population growth on sweet pepper. Aphids can potentially also transmit non-persistent viruses which infect sweet peppers [*Cucumber mosaic virus* (CMV), *Potato virus Y* (PVY), *Alfalfa mosaic virus* (AMV)], although these rarely occur in greenhouse crops. The use of pesticides is still widely applied to control aphids. Commonly used pesticides often include systemic neonicotinoid, carbamate (pirimicarb) or pyridine azomethine (pymetrozine) class insecticides, which are recommended for use when non-persistent viral infections also occur on a crop, so as to minimize disease transmission. When early detection of infestation is possible, localised insecticide treatment is preferred to minimize non-target effects on established biological control programmes. However, there is also an increasing demand for pepper fruit produced with little to no conventional pesticides, with a preference for management through the application of arthropod natural enemies and entomopathogens.

Biological control of aphids is most effective when applied on a preventative rather than curative basis. It also often requires the concurrent release of several natural enemy species to achieve sustainable levels of control. The main strategies applied for sweet pepper biological control are the frequent releases of specialised aphid parasitoids (*Aphidius* and *Aphelinus* genera) (Fig. 18.1), the predatory midge *Aphidoletes aphidimyza* (Rondani), and occasionally the use of lacewings, as well as of ladybird beetles and syrphids when aphid density is high (Blümel 2004; Messelink et al. 2013). However, the efficacy of parasitoids is often largely restricted by the presence of secondary parasitoids (so-called hyperparasitoids) that parasitize the primary parasitoids. The hyperparasitoids of aphid parasitoids are solitary species from the families Megaspilidae, Pteromalidae, Alloxystidae and Encyrtidae (Sullivan and Völkl 1999). Surveys in greenhouses in the UK, Canada and the Netherlands recorded several species of hyperparasitoids with levels of parasitism up to 100% (Jacobson 2011; Acheampong et al. 2012; Bloemhard et al. 2014). Another concern is the reduced susceptibility of certain phenotypes of *M. persicae* to parasitoids (Gillespie et al. 2009). The predatory midge *A. aphidimyza* can be extremely effective in controlling aphids, but unsuitable climatic conditions or hyperpredation by predatory mites (Messelink et al. 2011a) can also reduce efficacy of this species. A rather new approach in aphid control is the use of generalist predators that can establish in the absence of aphids, and thereby have the ability to rapidly respond to new aphid infestations. Good results have been achieved with the generalist predators *Orius majusculus* (Reuter) and *Macrolophus pygmaeus* (Rambur) (Fig. 18.2) (Messelink et al. 2011b, 2015; Messelink and Janssen 2014).

Fig. 18.1 *Aphidius matricariae* parasitizing the aphid *Myzus persicae* in a sweet pepper flower

Fig. 18.2 *Macrolophus pygmaeus* colonizing sweet pepper flowers

18.2.1.2 Thrips

The most noxious thrips species in sweet pepper worldwide is western flower thrips *Frankliniella occidentalis* (Pergande), which is also an efficient vector of *Tomato spotted wilt virus* (TSWV). Adults and larvae that feed on the fruits cause cosmetic damage and lower the fruit quality. However, this thrips is actually more harmful when transmitting TSWV in a persistent and propagative manner: the virus is acquired by young larvae and, after replication in the vector, it is usually transmitted by adults during their lifetime (Turina et al. 2012). Besides the western flower thrips, many other species can occur and cause damage in different geographic areas including *Thrips tabaci* Lindeman, *Thrips palmi* Karny, *Thrips setosus* Moulton, *Echinothrips americanus* Morgan and *Scirtothrips dorsalis* Hood. The melon thrips *T. palmi* is another efficient vector of tospoviruses, which is expanding its geographical distribution and is a quarantine organism in Europe. Similarly, the geographic range of chili thrips *S. dorsalis* has rapidly expanded from Asia in the 1990s so that today it can also be found in the United States, the Middle East and Central Africa (Dickey et al. 2015). It is therefore seen as a potentially important invasive pest species to Canada and Europe that may threaten the greenhouse pepper industry.

Biological control of thrips is generally effective, and can be carried out with different BCAs, which must be selected in relation to environmental conditions. Biological control of thrips is generally successful when phytoseiid predatory mites are released on greenhouse pepper crops. In the past, *Neoseiulus cucumeris* (Oudemans) was the predominant species used (Ramakers 1980). Since 2005, however other phytoseiids that also control whiteflies have become more popular. The most commonly used species are now *Amblyseius swirskii* Athias-Henriot, *Amblydromalus limonicus* (Garman & McGregor) and *Transeius montdorensis* (Schicha) (Labbé et al. 2019). In addition, some growers release *Iphiseius degenerans* (Berlese), a species that develops very well on sweet pepper pollen and is less vulnerable to low humidity levels. Not all thrips species are controlled well by phytoseiid predatory mites. *Echinothrips americanus* is one of the thrips species that is only suppressed to a certain extent by predatory mites and some species of predatory mites are not effective at all (Ghasemzadeh et al. 2017).

Biological control of thrips is usually more effective when minute pirate bugs of the Anthocoridae family are used, such as the European *Orius laevigatus* (Fieber) or the North American *Orius insidiosus* (Say) (Bosco et al. 2008). These predatory bugs consume predominantly thrips larvae and adults, whereas phytoseiids mainly predate first larval instars; consequently, they together offer strong complementary thrips control. However, most commercialised anthocorid bugs are typical flower bugs that control thrips mainly localized to flowers and are therefore less effective against typical leaf-dwelling thrips such as *E. americanus* or *S. dorsalis*. For the control of such thrips species, leaf-dwelling minute pirate bugs such as *O. majusculus* are more effective. Moreover, these generalist predators are strongly influenced by environmental conditions; therefore, it is important to choose the appropriate predator species accordingly. In southern Europe and in Florida, natural populations of anthocorid species, such as the Palaearctic *O. laevigatus* (Fig. 18.3), *Orius niger* (Wolff), *O. majusculus* or the Nearctic *O. insidiosus*, are abundant and often effective in suppressing thrips infestations in their native distribution (Bosco and Tavella 2013). In certain cases, native predators seem to outcompete non-native agents used for thrips biological control. For instance, non-native anthocorid species may be released when there are delays in crop colonization by native predators. However, later in the season, instead of the released species it is common to find the native species. These in turn seem to establish well and carry on their role of controlling thrips as long as they are not disturbed by pesticide applications (Ghasemzadeh et al. 2017). For example, the exotic *O. insidiosus*, which is very effective against thrips in North America, was rarely or not found following its releases in pepper greenhouses of Italy (Tommasini 2004).

Fig. 18.3 *Orius laevigatus* predating on western flower thrips

18.2.1.3 Mites

Two spotted spider mites *Tetranychus urticae* Koch are important and sometimes challenging pests to control in pepper greenhouses. This mite, native to Eurasia, is now considered a cosmopolitan species. Moreover, it is a polymorphic species, which comprises various races including one first described as a distinct species, the carmine mite *Tetranychus cinnabarinus* Boisduval (Auger et al. 2013). While adults are typically white to light green in colour with two red dorsal spots, mated females produced in the fall appear red in colour. Similar in appearance to these females are the completely red coloured host race of *T. urticae*, described as *T. cinnabarinus* (Raworth et al. 2002).

Biological control of the two spotted spider mite can be successfully achieved through release of the Chilean predatory mites *Phytoseiulus persimilis* Athias-Henriot. This predaceous mite is now considered the most important agent for control of *T. urticae* worldwide. Nonetheless, other predatory mites such as *Neoseiulus californicus* (McGregor), *Neoseiulus fallacis* (Garman), and predatory insects such as the gall midge *Feltiella acarisuga* (Vallot) may also offer spider mite control.

Broad mites *Polyphagotarsonemus latus* (Banks) are a serious pest in pepper in subtropical and tropical areas but, due to increases in global trade and to climate change, they are expanding their global range. These mites are often found on the underside of leaves, and feed primarily on young foliage and flowers. This feeding adversely affects the morphology and/or physiology of attacked plants. Broad mites can be controlled successfully by phytoseiid mites, such as *A. swirskii* (van Maanen et al. 2010), *N. californicus, N. cucumeris* and *Neoseiulus barkeri* (Hughes) (Peña and Osborne 1996; Weintraub et al. 2003), which are commonly used to control other pests (e.g., whiteflies, thrips). In actuality, phytoseiid predators, which are predominately applied to a pepper crop for whitefly and thrips control, inadvertently control broad mite populations meaning that they are seldom a problem pest. Moreover, supplementing pepper plants with pollen, which improves phytoseiid predator establishment, resulted in better control of broad mite populations (Duarte et al. 2015).

18.2.1.4 Caterpillars

Several lepidopteran species can attack pepper causing serious crop losses, by feeding on leaves and/or fruits. Many are polyphagous species with a broad host range that includes crop plants such as pepper. Among these polyphagous species, the most important are noctuids belonging to the genera *Chrysodeixis* [*Chrysodeixis chacites* (Esper), *Chrysodeixis includens* (Walker)], *Helicoverpa* [*Helicoverpa assulta* (Guenée)], *Spodoptera* [e.g., *Spodoptera exigua* (Hübner)], *Trichoplusia* [*Trichoplusia ni* (Hübner)]. Species can vary in relation to their geographical distribution but the damage caused is very similar. Females can lay eggs on pepper plants, and larvae feed on buds, flowers and fruits, and may even destroy young plants.

For instance, the cabbage looper *T. ni* and the soybean looper *C. includens* are known to occur on greenhouse pepper crops in Canada. These generalist insects can migrate readily from one crop type to another as available on a seasonal basis. Control of these pests often depends on the use of *Bacillus thuringiensis* Berliner subspecies *kurstaki* (Btk) or *aizawai*, although resistance of *T. ni* to Btk has limited the effectiveness of such products (Janmaat and Myers 2003). This has to some degree led to the adoption of conventional insecticide usage, particularly for relatively new insecticides such as chlorantraniliprole, which has shown good efficacy in controlling noctuid species in the greenhouse environment. It is however foreseeable that with the widespread use of such insecticides, resistance may ensue. Another management tool that has good potential for control of *T. ni* includes the *Autographa californica* nucleopolyhedrovirus (AcMNPV strain), which is known to effectively infect and kill *T. ni* larvae with minimal effects on non-target BCAs often used in the greenhouse (Erlandson et al. 2007). An important noctuid pest in European greenhouse pepper crops is the tomato looper *C. chacites*. This species is native to southern Europe, the Mediterranean, the Middle East and southern Africa (CABI 2017).

Lepidopteran pests other than noctuids affecting pepper are the European corn borer *Ostrinia nubilalis* (Hübner), the European pepper moth *Duponchelia fovealis* Zeller, which is a regulated species in the United States, and some tortricid moth species (https://www.aphis.usda.gov/aphis/ourfocus/planthealth/import-information/rppl/rppl-table

2017). *Ostrinia nubilalis* is highly attracted by pepper, on which its larvae feed on fruits causing serious crop losses. Besides the application of *B. thuringiensis* products, the use of nets on the openings of greenhouses is strongly recommended to avoid the entry of ovipositing *O. nubilalis* females.

Biological control of many lepidopteran species can include the use of egg parasitoids of the genus *Trichogramma*, and many studies have demonstrated their good potential for control in the greenhouse environment. However, one of the limitations of these species is the need for high densities of hosts, which are not frequent in a greenhouse, and therefore they are often not able to completely eliminate the host species. Larval parasitoids can also be effective (Messelink 2002), but due to the high costs for mass production, they are up to now not used in augmentative biological control programmes.

The sex pheromones of most lepidopteran pest species that occur in pepper crops are known and commercially available. Therefore, such pheromones can be used for monitoring and pest control by mass trapping, attract-and-kill and mating disruption. These control methods are now largely applied to control moths in fruit orchards and vineyards. Recently, a new low-dose pheromone dispenser was assayed on vegetable crops against *Spodoptera littoralis* (Boisduval) successfully (Rama et al. 2011). Similar control measures could be developed to reduce pepper infestation by other moth species (Guerrero et al. 2014).

18.2.1.5 Whiteflies

Sweet pepper is a choice host plant for the tobacco whitefly *Bemisia tabaci* Gennadius (also named silverleaf whitefly or sweet potato whitefly), whereas it is not a suitable host for the commonly occurring greenhouse whitefly *Trialeurodes vaporariorum* (Westwood). The tobacco whitefly is a Mediterranean species, and while it establishes well in greenhouses, it mainly occurs outdoors in sub-tropical areas worldwide, characterised by having fewer than 5 days of frost per winter and an annual mean temperature above 16 °C (Bosco and Caciagli 1998). As with aphids, these phloem feeding insects also cause serious crop damage by the excretion of honeydew, a substrate for sooty mould fungi. These fungi reduce plant photosynthetic capacity, which eventually reduces yield. *Bemisia tabaci* is also feared for its ability to transmit crop destroying viruses to tomato, cucumber and melon plants, but most of *B. tabaci*-vectored viruses are not known to infect sweet pepper. While neonicotinoids are very effective pesticides for whitefly control, consumer demand for pesticide-free produce as well as the high degree of toxicity of these pesticides for pollinating bumblebees has strongly reduced their use.

Biological control of whiteflies in sweet pepper is usually very successful through the use of phytoseiid predatory mites such as *A. swirskii* and *A. limonicus* that, besides thrips, also consume whitefly eggs and crawlers (Nomikou et al. 2001). In addition, whitefly parasitoids *Eretmocerus eremicus* Rose & Zolnerowich and *Eretmocerus mundus* Mercet can be released to parasitize larger larval whitefly stages. Predatory mites combined with parasitoids provide very robust control of whiteflies (Calvo et al. 2009). Several species and strains of entomopathogenic fungi, such as *Beauveria bassiana* (Balsamo) Vuillemin and *Lecanicillium muscarium* (Petch) Zare & Gams, can be used as curative agents when predators and parasitoids are not able to suppress whiteflies sufficiently. However, application of these fungi requires the right climatic conditions, such as a high relative humidity and temperatures that are not too high, which may limit their seasonal usage in some parts of the world (Gonzalez et al. 2016).

18.2.1.6 Plant and Stink Bugs

Among heteropteran species, some plant and stink bugs are reported as noxious pests of pepper crops with problematic species differing geographically. These bug species are generally polyphagous and have a very broad host range. On pepper, feeding and damage of fruits by these piercing-sucking insects can render them unmarketable. Since they are not strictly associated with pepper, they can migrate to this vegetable crop at any time during the growing season, making their control difficult and often not compatible with biological control based integrated pest management (IPM) adopted for other pests.

The tarnished plant bugs *Lygus* spp. cause serious damage through feeding punctures to pepper fruits. In North America, *Lygus lineolaris* (Palisot de Beauvois) is a perennial pest of greenhouse pepper crops, whereas in Europe, *Lygus rugulipennis* Poppius is considered an occasional pest. However, in some years, it has been documented to cause significant damage to pepper crops. In northern Europe, other mirid bugs also occur and cause damage such as the common nettle bug *Liocoris tripustulatus* (F.) and the common green capsid *Lygocoris pabulinus* (L.). The latter one does not establish in pepper crops, but adults that enter a crop cause a typical growth deformation in the young plant parts, which leads to reduced production (Messelink and van Steenpaal 2002).

Sources of these pests are often other weedy and crop host plants that surround greenhouses, from which the mirid bugs migrate inside when field densities are high (Pansa and Tavella 2009). This behaviour makes the control more difficult because of the unpredictability of the infestations, but it could be exploited by selecting more attractive host plants than pepper to be used as trap plants. Therefore, management of mirid bugs often relies on insecticide treatments, which are seen as the most effective means to suppressing pest populations. However, a current issue is arising with the control of these pests on greenhouse pepper crops in many countries. Registration of the systemic neonicotinoid imidacloprid, one of the major insecticides used to control plant bugs, is up for re-evaluation in many countries pending environmental concerns. Without this tool, it is thought that *Lygus* spp. will become more challenging pests to control on pepper crops. Furthermore, biological control is not yet recommended as a viable option for control of these pests. Despite this, some efforts have been made to investigate the potential for microbial control of *L. lineolaris* through bee-vectored *B. bassiana*, which for instance reduced populations of *L. lineolaris* on sweet pepper crops by up to 45% (Al-mazra'awi et al. 2006).

Besides the cosmopolitan green stink bug *Nezara viridula* (L.), which can become a sufficiently noxious pest on pepper to require the use of pesticides in some areas and years, the accidental introduction of the brown marmorated stink bug *Halyomorpha halys* (Stål) in North America and Europe has posed a new serious threat to growers. Pepper fruits are highly susceptible to injury from *H. halys* as well as other stink bugs, because they feed primarily on plant reproductive structures, causing corking or deformed fruits. Bug infestations and their resulting crop injury vary depending on site and year, but they are mainly reduced by the use of chemicals, such as synthetic pyrethroids, organophosphates and neonicotinoids, with negative side-effects on BCAs. As alternatives to the chemical treatments, barrier screens with different mesh sizes were evaluated in relation to pest densities, revealing to be an effective tool to exclude pests, which could be successfully integrated into growing systems (Dobson et al. 2016). Moreover, polyculture trap crops composed of sunflower and sorghum have been tested for organic pepper production in North America: the trap crop was highly attractive for stink bugs, but unable to reduce the damage enough. Therefore, further research is still needed to improve this method and/or integrate it with other management tools (Mathews et al. 2017).

18.2.1.7 Pepper Weevil

The pepper weevil *Anthonomus eugenii* Cano (Fig. 18.4) is one of the most important pests of pepper crops in North America. Native to Mexico, the pepper weevil has a range that extends through Central America and the United States (Bartlett and Clausen 1978). It has also spread to the Caribbean and French Polynesia, with sporadic occurrences in Italy, the Netherlands, Hawaii, and southern Canada (van der Gaag and Loomans 2013; Speranza et al. 2014). The pepper weevil is considered a quarantine pest in Europe, but not in most of North America as it is either considered the native range for this species, or is thought not to overwinter in places such as Canada. In 2016, transient populations of the pepper weevil were detected in field and greenhouse pepper crops in Ontario, Canada, which were subsequently eliminated. This sporadic occurrence could be attributable to a number of factors, with the most important consisting of the frequent importation of peppers into Canada from areas where the pepper weevil is well established. Other factors include the high density of greenhouse and field pepper production in certain localities and the combination of mild winters and hot summers, all of which can represent ongoing challenges for pepper weevil suppression.

At present, the installation of greenhouse vent screens, cultural management, crop scouting and the use of chemical insecticides are the main strategies used to manage pepper weevil populations in and around the greenhouse environment. Of paramount importance is the establishment of preventative clean-up strategies that focus on the careful disposal of infested pepper waste and the elimination of live weevils between crop cycles. Work by Costello and Gillespie (1992) showed that adult pepper weevils have a lethal time (LT_{100}) of 28 days at 10 °C and 7 days at 27 °C in the absence of food. This finding was the basis for the inferred minimum

Fig. 18.4 Adult pepper weevil

critical crop-free condition now used by greenhouse growers of 20 °C for at least 2 weeks to insure that adequate cleanout is achieved. Other preventative practices include establishing virtual hermeticity of greenhouses through screening vents, and doubling doorways, the use and scouting of sentinel trap pepper plants between cropping periods as well as pheromone traps. Once new crops are in the greenhouse, regular scouting of seedlings, flowers and buds are also important. Weekly scouting crops with suspected pepper weevil infestation is intensive, requiring up to two employees per acre for the removal of suspected infested fruit and plant material.

While there are many products registered for treatment of the pepper weevil in the United States and Mexico, few products are currently registered in Canada where those available in 2017 included dibrom, thiamethoxam, novaluron and cyantraniliprole. However, insecticides offer only temporary suppression of adult populations and are unable to target immature life stages of the pepper weevil, which are protected within the pepper fruit. There is also a need to address concerns regarding the negative impacts these products have on non-target BCAs used to manage other important greenhouse pepper pests. For all of these reasons, it is essential to identify new tools, including reduced risk conventional agents, biopesticides and biological control organisms that may contribute to achieving good suppression of the pepper weevil on greenhouse pepper crops.

Recently, surveys of the natural enemies of the pepper weevil in Mexico and Canada have led to renewed interest in biological control of the pest. In Mexico, three wasp species, *Triaspis eugenii* Wharton and Lopez-Martinez, *Urosigalphus* sp., and *Jaliscoa hunteri* (Crawford) account for 96% of all parasitoids that attack the pepper weevil (Rodriguez-Leyva et al. 2007). In Canada, at least seven parasitoid species attack and kill the pepper weevil, including two species, *J. hunteri* and *Pteromalus anthonomi* Ashmead, which are also found in Mexico (Labbé et al. 2017). Some work has investigated the potential for *J. hunteri* to control the pepper weevil in field and greenhouse settings. Field trials performed in Florida have demonstrated that *J. hunteri* can significantly reduce the number of weevil-infested bell pepper fruit (Schuster 2007). Both *J. hunteri* and *P. anthonomi* have the potential to be developed as BCAs of the pepper weevil and require further evaluation.

18.2.2 Diseases

18.2.2.1 Fungal and Oomycetal Diseases

A number of filamentous fungi and oomycetes (fungus-like eukaryotic microorganisms) incite diseases on pepper cultivated in the greenhouse worldwide. They cause (1) soilborne diseases such as damping-off (*Pythium* spp., *Rhizoctonia solani* Kühn, *Fusarium* spp., *Alternaria* spp.), Fusarium wilt [*Fusarium solani* (Mart.) Sacc., *Fusarium oxysporum* Schltdl.], Verticillium wilt (*Verticillium dahliae* Kleb., *Verticillium albo-atrum* Reinke & Berthold), basal rot (*Pythium* spp., *Phytophthora capsici* Leonian); while airborne inoculum causes (2) foliar diseases such as powdery mildew [*Leveillula taurica* (Lév.) G. Arnaud], grey mould (*Botrytis cinerea* Pers.: Fr.), and (3) flower and fruit diseases such as internal fruit rot [*Fusarium lactis* Pirotta & Riboni, *Fusarium subglutinans* (Wollenw. & Reinking) P.E. Nelson].

Soilborne Diseases

Due to their nature, these diseases tend to be an issue for organic pepper production, since plants have to be cultivated in soil to meet organic standards, rather than for conventional production of greenhouse peppers using hydroponic systems. Solarization (Gullino and Garibaldi 2012) and biofumigation (Guerrero et al. 2005) can be used in the greenhouse to disinfest the soil, although care should be taken to ensure that amendments used for biofumigation meet organic standards. Disinfestation of recirculating nutrient solution is essential to prevent the spread of oomycetes like *Pythium* spp. and *P. capsici* in hydroponic systems, since zoospores are motile in water; it is also useful against fungal pathogens like *R. solani*, *Verticillium* spp. and *Fusarium* spp. (Ehret et al. 2001). The current recommendation in North America is that rockwool slabs that are being re-used should also be steam sterilized, although some growers may prefer to take advantage of potential suppressive microbial communities present in re-used rockwool slabs that are not sterilized (Postma et al. 2000). Microbial biopesticides that colonize the soil or growing susbstrate, or can be used as seed treatments, are another useful IPM tool to combat soilborne pathogens in conventional and organic production systems.

Powdery Mildew

Leveillula taurica is the causal agent of powdery mildew on pepper, and this disease has become an important issue worldwide for greenhouse pepper production. This may be at least partly due to increasing production in heated greenhouses. Conidial germination can occur from 10 to 37 °C, although there is evidence that higher daytime and nighttime temperatures may suppress conidial viability. The severity of leaf symptoms has been found highest at 75–85% relative humidity (Elad and Stewart 2007), but the cost required for heating and opening greenhouse vents will have to be weighed against the benefit of higher temperature and lower relative humidity, especially in cold climates. The polycyclic nature of powdery mildew is especially problematic in the greenhouse, where secondary infection cycles can result in the pathogen spreading through the entire crop canopy if left unchecked. The pathogen can survive in leaf debris, even at temperatures as low as −10 °C (Cerkauskas et al. 2011), so proper sanitation measures between crops are important. Commercial varieties with partial resistance to this pathogen are available and should be used as part of an IPM programme. Scouting for early detection is crucial, especially since the pathogen has a latency period of 8–14 days (De Souza and Café-Filho 2003) or longer (Zheng et al. 2013) before signs are visible on the underside of leaves. Biopesticides that induce plant defenses [e.g., extracts of *Reynoutria sachalinensis* (F.Schmidt) Nakai, acibenzolar-S-methyl, harpin (Wiesel et al. 2014)] can also be used as a first line of defense against powdery mildews. However, under conditions favourable for disease development, it is likely that the application of biopesticides with a direct action against *L. taurica* or conventional fungicides will be required to keep infestations at a manageable level and safeguard yield. Biopesticides with a direct action against powdery mildew include products formulated from garlic and other plant extracts, mild chemicals (e.g., mineral oil, sulphur, potassium bicarbonate, tea tree oil), and microbials that can affect the pathogen directly via antibiosis or mycoparasitism (Kiss 2003), such as *Streptomyces lydicus* De Boer et al. (Cerkauskas et al. 2011). Conventional products registered globally against powdery mildew belong to fungicide resistance action committee (FRAC) groups 3 (demethylation inhibitors), 7 (succinate dehydrogenase inhibitors), 9 (anilino-pyrimidines), 11 (quinone outside inhibitors), 12 (phenylpyrroles) and 13 (aza-naphthalenes). Except for group 12 (low risk), the FRAC considers the risk of resistance development to be medium to high for these groups (FRAC 2017), so rotating modes of action and using fungicides as a last resort as part of an IPM programme are important to prevent the development of resistance. Research on UV light has also demonstrated the potential to develop such systems for use in the greenhouse (Suthaparan et al. 2014), but they are only applied yet on a limited scale.

Grey Mould

Botrytis cinerea incites grey mould on greenhouse pepper as well as tomato and eggplant. Proper sanitation between crop cycles, controlling the humidity (below 85%), heat (to avoid condensation on the fruit) and air flow through the crop canopy are key to managing this pathogen. Several biopesticides are also registered globally to use against this pathogen, including products formulated from *Trichoderma harzianum* Rifai, *Gliocladium catenulatum* Gilman & Abbot [recently reclassified as *Clonostachys rosea* f. *catenulata* (Gilman & Abbot) (Schroers 2001)], *Bacillus*

Fig. 18.5 Internal fruit rot caused by *Fusarium* spp.

amyloliquefaciens (Fukumoto) Priest et al. emend. Wang et al., and *Bacillus subtilis* (Ehrenberg) Cohn (Elad and Stewart 2007). Moreover, bee vectoring of a microbial biopesticide has demonstrated the potential to suppress grey mould in greenhouse pepper (Kapongo et al. 2008).

Internal Fruit Rot

While several pathogens (e.g. *B. cinerea*, *F. solani*) cause external rot on pepper fruit, internal rot of pepper fruit has been observed since around 2000 (O'Neill and Mayne 2015) and is believed to be caused by different species of *Fusarium*, including *F. lactis, F. subglutinans* and *F. oxysporum*. The symptoms and signs of internal fruit rot differ from those of blossom-end rot, which is a physiological disorder resulting from lack of calcium in the fruit, and include a whitish mycelium visible on the inside of fruit (Fig. 18.5). Dark green patches on the outside of infected fruit may be visible with severe infections. The pathogens are believed to infect when spores land on the flower stigma (Yang et al. 2010), and the development of the pathogens inside the fruit makes them difficult to target with biopesticides or conventional fungicides, since new flowers bloom daily and only a small percentage of the total spray volume will make contact with the flowers. For this reason, bee vectoring is a promising avenue for control of this pathogen as already demonstrated for the suppression of grey mould caused by *B. cinerea* (Kapongo et al. 2008).

18.2.2.2 Viral Diseases

Viruses causing the most important viral diseases on pepper can be transmitted mechanically, through sap and by seed, and by insect vectors such as aphids and thrips. For example, *Tobacco mosaic virus* (TMV) and *Tomato mosaic virus* (ToMV) belong to the genus *Tobamovirus* and do not rely on an invertebrate vector for plant-to-plant spread. CMV, belonging to the genus *Cucumovirus,* can infect about 100 plant species, both crop and non-crop, including pepper. It is transmitted in a non-persistent way by many aphids, among which *M. persicae* and *A. gossypii*. TSWV (Fig. 18.6) and *Impatiens necrotic spot virus* (INSV) belong to the genus *Tospovirus* and are efficiently transmitted by *F. occidentalis* in a persistent and propagative manner. Tospoviruses replicate in their vectors, and individual thrips are capable of transmitting the virus acquired only during the first two larval stages. These features imply that the vector is also a virus host and that there is a certain time lapse (2–3 weeks) between acquisition and inoculation of the virus (Turina et al. 2012). To contain tospovirus epidemics, an integrated disease management (IDM) approach is needed (Pappu et al. 2009), and all preventive measures (e.g., removal of cultural residues and any other sources of inoculum, use of virus-free and thrips-free seedlings, adoption of a continued vigilance, control of vector thrips) are required. Moreover, commercial pepper varieties carrying the resistance gene *Tsw* (introgressed from *Capsicum chinense* Jacq.) can be used, taking into account the occurrence of resistance-breaking strains (Turina et al. 2012).

To prevent damage from plant viruses, basic sanitation measures aimed at preventing the transmission of viral particles include starting with clean seeds or transplants. These can be certified free of viruses (where appropriate certification programmes exist), tested in-house using commercially available immunological diagnostic kits, or sent out for testing by diagnostic labs. Plants showing symptoms of viral diseases should be removed, along with buffer plants in their immediate vicinity, and disposed of by incineration or burial away from the greenhouse. Greenhouse surfaces can be sanitized using disinfectants, during a viral infestation

Fig. 18.6 Disease symptoms caused by TSWV

or between cropping cycles, although the efficacy of such disinfectants against specific viruses can vary (Li et al. 2015). Weed control in and around greenhouses will remove alternate hosts that can serve as viral reservoirs, especially important when dealing with vector-borne viruses such as CMV, TSWV and INSV. As mentioned earlier, for such vector-borne viruses, an IDM approach will also include control of their insect vectors.

18.2.2.3 Nematodes

Nematodes are microscopic worms that inhabit soil and can cause disease-like symptoms by feeding on the roots of cultivated plants. Like soilborne fungal and oomycetal diseases (discussed in Sect. 18.2.2.1), they have the potential to cause issues when greenhouse crops are cultivated in soil, notably in organic production. The root-knot nematodes *Meloidogyne* spp. cause economically significant losses on vegetable crops worldwide (Giné et al. 2016). Solarization and the application of biofumigants are two possible avenues to combat nematodes in the greenhouse (Butler et al. 2012; Yücel et al. 2007). Genetic resistance exists in pepper (Barbary et al. 2015), and is becoming available in some commercial varieties. Some soils are naturally suppressive to nematodes (Giné et al. 2016), due in part to the microorganisms that they contain. Several biopesticides with claimed efficacy against the root-knot nematodes are available commercially (Tranier et al. 2014), including products based on *Purpureocillium lilacinum* (Thom) Luangsa-ard et al., *B. bassiana*, and *Trichoderma* spp.

18.3 Integrated Pest Management: Problems and Perspectives

IPM is nowadays standard in most European and North American countries, and is increasing in other areas of the world as well. This increase is often strongly driven by consumer and retailer demands for healthy food products with a minimum of pesticide residues, and apparently, the occasional scandal that forces growers to change their management tactics (Pilkington et al. 2010). A major shift towards biocontrol for example occurred in Almeria, in Spain, in 2006–2007 when German retailers started to boycott Spanish pepper fruits after detection of the forbidden pesticide isofenphos-methyl in the majority of Spanish peppers. This fact, together with the availability of *A. swirskii* for biological control of thrips and whiteflies, resulted in a major shift towards biocontrol from 5% in 2005 to almost 100% of a total 6000 ha of protected sweet pepper in Spain within 3 years (Calvo et al. 2015). Similar major shifts can be expected in other parts of the world when, besides food availability, food safety and environmental pollution also become important concerns.

Although biological control based IPM is nowadays widely and successfully applied, there is still a huge need for further developing these systems. First of all, there are still several pest species that cannot be controlled effectively with available BCAs. The control of aphids for example is extremely expensive without the use of insecticides. As a consequence, new strategies for enhancing biological control need to be developed. Secondly, new invasive pest species continue to threaten greenhouse production areas and the absence of suitable control agents can completely disrupt existing biological control programmes targeting established pest species. This is exemplified by areas invaded by pepper weevil or by brown marmorated stink bug for the first time. Such invasions require a tremendous effort by scientists and industry to find new ways of controlling these pest species within an integrated system of multiple pests and natural enemies. Thirdly, the development of an IPM system largely depends on climatic conditions, which determine which pests and diseases occur where, but also which natural enemies are well suited to the crop environment. For instance, some species of predatory mites native to the Mediterranean basin do not perform well at lower temperatures, whereas others are better adapted to temperate climate (Hewitt et al. 2015). The inverse scenario may also arise whereby some species are better adapted to high temperatures and low humidity than others (Ferrero et al. 2010). Hence, IPM and biological control always need to be optimized for local climatic conditions.

Recently, one of the biggest changes in biological based IPM systems has been the change of these consisting of curative control strategies to more preventive strategies with all kinds of new techniques being used to conserve and augment natural enemy populations (Messelink et al. 2014). Sweet pepper is a very successful crop to demonstrate this “standing army” approach, because once flowering, the crop can be inoculated with generalist predatory mites and bugs that survive on sweet pepper pollen as an alternative food source. Nowadays, many more techniques have been developed to establish natural enemies, such as banker plants, nectar-producing plants, and alternative food or prey sprays. For example, sterilized eggs of the flour moth *Ephestia kuehniella* Zeller or eggs of the brine shrimp *Artemia* spp. can be used to support mirid predatory bugs in sweet pepper, to enhance the control of aphids (Messelink et al. 2015). Another relatively old technique is the pest-in-first method, based on intentional releases of spider mites, in order to achieve a stable population of the spider mite predator *P. persimilis* before natural invasions of spider mites occur (Markkula and Tiittanen 1976). This method is often considered risky, but has nevertheless been used successfully for many years by Dutch pepper growers.

The enrichment of sweet pepper crops with a permanent establishment of various species of natural enemies automatically increases food web complexities that can affect the success of biological control. Such interactions include intraguild predation, hyperpredation, hyperparasitism, distraction or predator satiation, which can all reduce the efficacy of biological control (Messelink et al. 2012). However, some interactions can also strengthen the efficacy through complementary or synergistic effects. Parasitoids in sweet pepper can for example facilitate the control by lacewing larvae in the lower plant parts after inducing defense dropping behaviour of foxglove aphids (Rocca and Messelink 2017). These food web complexities emphasize that a thorough understanding of the direct and indirect effects of conservation methods on the total ecosystem in greenhouses is needed in order to avoid potential negative effects on pest control. Interactions that are potentially negative for biological pest control could be avoided by selecting and releasing natural enemy communities that maximise sustainable pest control. Hence, the development of tools that support the establishment of natural enemies should go hand in hand with extending our understanding of species interactions in biological control communities. This all shows that IPM is more than just an integration of several control measures, but it requires an ecosystem approach to maximize the impact on pest and disease control (Fig. 18.6).

18.3.1 Future Challenges

In conclusion, biological based IPM in sweet peppers is one of the best examples of a successful IPM strategy with minimal use of pesticides. However, new challenges need to be addressed on time to avoid disruption of this robust system. New or existing challenges are: (1) invasive pest species, (2) endemic pests for which biocontrol needs improvement. Also, strong efforts are required for those countries where pest and disease control is still based on pesticide use. In areas where the introduction of commercially produced natural enemies is not allowed due to legislation, or problematic because of long transport time or too expensive, new solutions need to be developed. One opportunity can be to start small rearing units of endemic species that are locally produced, combined with the application of food sources that increase natural enemy population densities. Such systems can help to further increase the application of biological control based IPM worldwide and thereby make the production of sweet pepper fruits safer and healthier.

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Chapter 19
Cucurbits

Gerben J. Messelink, F. Javier Calvo, Francisco Marín, and Dirk Janssen

Abstract Several cucurbits species are cultivated in greenhouses worldwide. The most important genera are (1) *Cucurbita*, which includes squash, pumpkin, zucchini and gourds, (2) *Citrullus*, which includes watermelon and (3) *Cucumis*, which includes cucumber and various melons. Pests and diseases affecting cucurbit crops can vary considerably in relation to geographic area and cropping system. Growing in soil or on hydroponics strongly determines the presence of certain soil pathogens or nematodes. Also the way the crop is cultivated, the number of cropping cycles and the transition between cycles strongly affects the performance of pests, diseases and biological control agents. The main pests and diseases detrimental to cucurbits in various parts of the globe are reported here, along with the most effective or sustainable control strategies currently applied to manage them. Many pests can be controlled very successfully with natural enemies, but despite the recent developments on microbiological control agents, integrated pest management (IPM) with a low input of pesticides and, particularly fungicides, remains challenging in cucurbits, mainly because of viruses and diseases that are difficult to manage biologically or with selective control methods. Plant breeding programmes that develop disease tolerant cultivars that can be combined with arthropod natural enemies for pest control are promising to further develop robust IPM systems for cucurbits.

Keywords Biological control · Thrips · Spider mites · Whiteflies · Aphids · Mildew · Grey mould · Hairy root disease · Nematodes · Viruses

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19.1 Introduction

The Cucurbitaceae, also called cucurbits, is a huge plant family consisting of hundreds of plant species. Several cucurbits species are cultivated in greenhouses worldwide. The most important genera are (1) *Cucurbita*, which includes squash, pumpkin, zucchini and gourds, (2) *Citrullus*, which includes watermelon and (3) *Cucumis*, which includes cucumber and various melons. Generally, the protected cultivation of cucurbits represents a fraction of the total cucurbits production including field cultivation, which is worldwide grown on more than 3 million ha (FAOSTAT 2017). Yet, cucurbits are still economically important crops for the greenhouse industry. The most important cucurbit for greenhouse production is cucumber, *Cucumis sativus*. In Europe, the largest producer of cucumber in greenhouses is Spain with a production area of 6.680 ha, followed by Poland (1.630 ha) and Romania (1.220 ha) (EUROSTAT 2017). Curcurbits, and in particular cucumber crops, are very vulnerable for multiple pests and pathogens. Those affecting cucumber crops can vary considerably in relation to geographic area and cropping system (e.g., glasshouses or plastic tunnels, conventional or organic farming, etc.). In modern glasshouses, this crop is usually grown on hydroponics, except in case the crop is cultivated organically. Differently, in plastic greenhouses soil cultivation is more common. Growing in soil or on hydroponics strongly determines the presence of certain soil pathogens or nematodes. Also the way the crop is cultivated, the number of cropping cycles and the transition between cycles strongly affects pest pressure. Cucumber usually has three cropping cycles per year in the temperate greenhouse area, but in the Mediterranean area, production has typically two cycles per year i.e. fall-winter and spring-summer. Most growers replant the whole crop at once, but some choose to interplant in order to maintain some continuity in fruit production. Interplanting usually increases the risk of pest migration from the old to the new crop. The traditional method to cultivate cucumbers in high-tech greenhouses is based on the “umbrella system” where young plants are trained to grow upward to an overhead wire hung at about 2 m height; once these plants reach the wire, every plant is topped and two main laterals are trained to grow along the wire horizontally for about 0.5 m and then hung down from the wire. This is similar to the method used in some low/mid-tech greenhouses, where plants are not topped and the main stem is passed over another overhead wire, which is at the same height as the one used to train the plant but separated ca. 0.5 m, and then hung down directly from this second wire. The results are in either case a dense crop with a specific micro climate and light penetration which also affects the performance of pests, diseases and biological control agents (BCAs). For example, plant architecture of cucumber is known to affect the foraging efficacy of predatory mites (Gontijo et al. 2010). A more modern way of growing cucumber in tall greenhouses is based on the “high-wire system”, in which the plant is trained into a single stem, often in combination with supplemental lighting. In this system, the top of the plant is kept at the same height throughout the season, by laying horizontal the lower part of the stem at the same speed as the plant grows upwards. The productive part of the plant thereby continues to receive maximal benefit from light allowing high yields of quality fruit. Again, also this type of growing system has its typical problems with pests and diseases, influenced by the climatic conditions. For example, the drier climate in the top of the plant can be detrimental for spider mite control with predatory mites. Pests and diseases in cucurbits were for decades mainly controlled by pesticides, which is still the case in many countries. However, pesticides are often environmentally unfriendly, reduce food safety and have negative effects on human health (Pimentel and Burgess 2014). Additionally, its use favours the development of pesticide resistance, which makes chemical control ineffective. Interestingly, customers, retailers, and governments are increasingly limiting chemical control by reducing the list of allowed pesticides and requesting pesticide residue-free products. Under this scenario, interest in other control methods such as integrated pest management (IPM) strategies, which provides additional control options to growers, is increasing. Even so, uptake of biocontrol-based IPM programmes is basically restricted to protected cucurbit crops, which is the focus in this chapter.

19.2 Main Pest and Disease Problems

The above mentioned variety of cultivation methods in different areas makes that control measures adopted to reduce pests and diseases, and consequently crop losses, must be tailored to the environmental conditions, local cultural practices, and final market requirements. They must also observe national regulations on the importation of non-native agents as well as registration requirements. These apply not only to pesticides but also to BCAs. For instance, in some countries, only indigenous or cosmopolitan BCAs can be released for pest control regardless of their effectiveness. With this perspective, the main pests and diseases detrimental to cucurbit crops in various parts of the globe are reported here, along with the most effective or sustainable control strategies currently applied to manage them (Table 19.1).

19.2.1 Pests

19.2.1.1 Spider Mites

The most damaging pest on cucumber is the two-spotted or red spider mite, *Tetranychus urticae* Koch. This mite, native to Eurasia, is now considered a cosmopolitan species. Moreover, it is a polymorphic species, which comprises various races including one first described as a distinct species, the carmine mite, *Tetranychus cinnabarinus* Boisduval (Auger et al. 2013). While adults are typically white to light green in colour with two red dorsal spots, mated females produced in the fall appear red in colour. Similar in appearance to these females are the completely red

Table 19.1 Most important control agents for arthropod pests and fungal diseases in Cucurbitaceae

Pests/disease	Biological control agents	Supplementary measures
Spider mites	Specialist Phytoseiid predatory mites (e.g. *Phytoseiulus persimilis* and *Neoseiulus californicus*)	Selective acaricides Keep RH at levels needed for predators
	Predatory midge *Feltiella acarisuga*	
	Generalist Phytoseiid predatory mites (e.g. *Amblyseius swirskii, Amblydromalus limonicus* or *Transeius montdorensis*)	
Whiteflies	Parasitoids (*Eretmocerus* and *Encarsia* spp.)	Systemic insecticides
	Phytoseiid predatory mites	Insect screens Sticky traps
	Entomopathogenic fungi	
Thrips	Phytoseiid predatory mites	Insect screens
	Anthocorid predatory bugs	Selective insecticides
	Entomopathogenic fungi	Sticky traps
Aphids	Parasitoids (mainly *Aphidius* spp., *Aphelinus* spp.)	Systemic insecticides
	Predatory midge *Aphidoletes aphidimyza*	Soaps
	Lacewings (*Chrysoperla* sp.) and ladybird beetles (e.g. *Adalia bipunctata*)	Neem, natural pyrethrins
	Hoverflies (e.g. *Episyrphus balteatus* and *Sphaerophoria rueppellii*)	
Lepidopterous caterpillars	Egg parasitoids (*Trichogramma* spp.) *Bacillus thuringiensis*	Insect screens Pheromone traps, mating disruption
		Selective insecticides
True bugs	Not yet available	Screens, traps, insecticides
Powdery mildew	*Bacillus subtilis*, *Streptomyces lydicus*	Sulphur, mineral oil, tea tree oil, sodium bicarbonate, elicitors of plant defense mechanisms (extract of *Reynoutria sachalinensis*), fungicides, use of resistant cultivars
Downy mildew	Not available yet	Climate management, fungicides, use of resistant cultivars
Gummy stem blight	*Bacillus subtilis*, *Gliocladium catenulatum*	Climate management (heat and ventilation), seed desinfection
Grey mould	*Trichoderma harzianum*, *Gliocladium catenulatum*, *Bacillus amyloliquefaciens*, and *Bacillus subtilis*	Climate management, fungicides

(continued)

Table 19.1 (continued)

Pests/disease	Biological control agents	Supplementary measures
Pythium root and stembase rot	*Trichoderma* spp. *Pseudomonas fluorescens*	Composts, fungicides
Hairy root disease	Not available yet	Substrate desinfection
Fusarium wilts	*Streptomyces lydicus, Trichoderma* spp.	Use of resistant rootstock or cultivars, solarization, biofumigation
Nematodes	*Purpureocillium lilacinum*, *Beauveria bassiana*, and *Trichoderma* spp.	Solarization, biofumigation

Fig. 19.1 Two-spotted spider mites (left), greenhouse whiteflies (middle) and the predatory mite *Amblyseius swirskii* feeding on greenhouse whitefly eggs (right)

coloured host race of *T. urticae*, described as *T. cinnabarinus* (Raworth et al. 2002). This polyphagous pest causes damage to plants by puncturing the plant cells and feeding on their contents (Helle and Sabelis 1985) (Fig. 19.1). Moreover, it produces protective silk webs, which eventually can completely cover infested plants and if not controlled, it will quickly kill plants. Biological control of the two spotted spider mite can be successfully achieved with the specialist predatory mite *Phytoseiulus persimilis* Athias-Henriot. This predaceous mite is now considered the most important agent for control of *T. urticae* worldwide. Although it can be released preventively, it is a specialist predator of tetranychids, and thus it is normally released when the first spider mites are detected. Early detection of hot spots, in order to release the predator when pest levels are still low, as well as releasing the right initial predator: pest rate, are key issues in order to have success controlling the spider mites (Ferrero et al. 2011). However, this mite is also very drought sensitive. The critical value where 50% of the eggs do not hatch is 70% RH, whereas for most other species of predatory mites, this value is much lower (Ferrero et al. 2010). Hence, biological control can be problematic during prolonged periods of hot and dry weather. The predator tends to abandon the upper regions of the crop canopy then and in such situations, growers need may consider to apply acaricides in order to restore the balance between pest and predator. Increasing greenhouse humidity, e.g. with an overhead fogging system, can increase predator efficacy in such circumstances (Duso et al. 2004). Many other commercially applied phytoseiid predators feed on spider mites, but they are less specialized and feed on other prey as well

(McMurtry and Croft 1997). Highly effective species are *Neoseiulus californicus* (McGregor) and *Neoseiulus fallacis* (Garman). Particularly *N. californicus* has been extensively released for augmentative biocontrol of *T. urticae* and other mites. Because this species can prey on different food sources, including plant producing pollen and several pests, and is available in slow-release sachets (Bolckmans 2012), it can be introduced preventively i.e. before *T. urticae* occurs in the crop. Many generalist predatory mites also contribute to the suppression of spider mites in greenhouse cops, but most of them are hindered by the dense web produced by the spider mites (Sabelis and Bakker 1992). However, in the presence of other alternative food sources or prey, some generalist predatory mites can still effectively suppress spider mites (Messelink et al. 2010). Whether or not combined releases of specialist and generalist predatory mites is better for biological control is still an ongoing discussion, as the generalist predatory mites may disrupt the specialists through intraguild predation (Cakmak et al. 2009). An additional opportunity for biological control of spider mites is the release of the predatory midge *Feltiella acarisuga* (Vallot), which is commercially available in some countries.

19.2.1.2 Whiteflies

In the Mediterranean area, whiteflies are, together with spider mites and thrips, the most economically important pest. The most abundant species is by far the tobacco whitefly *Bemisia tabaci* Gennadius (also named silverleaf whitefly or sweetpotato whitefly). These phloem feeding insects cause serious crop damage by the excretion of honeydew, which subsequently is a food source for sooty mould fungi. These fungi reduce the photosynthesis capacity which eventually can lower yield. *Bemisia tabaci* is also feared for its ability to transmit crop destroying viruses to cucurbits, such as the *Tomato leaf curl New Delhi virus* (ToLCNDV) which infects solanaceous and cucurbitaceous crops, but is especially aggressive in zucchini crops (Juarez et al. 2014; Luigi et al. 2016). In cooler climates, the most commonly occurring species is the greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) (Fig. 19.1). Also this species causes serious damage, but is not involved in transmission of important plant viruses in cucurbits. Biological control of whiteflies in greenhouses started in the UK with the parasitoid *Encarsia formosa* Gahan against *T. vaporariorum* (Speyer 1927) and this wasp is still one of the biggest success stories in greenhouse biological control (van Lenteren 2000). Related wasp species were later on studies and those effective against the tobacco whitefly are *Eretmocerus eremicus* Mercet and *Eretmocerus mundus* Rose & Zolnerowich (Greenberg et al. 2002). A breakthrough in biological control of whiteflies was achieved by the discovery of whitefly feeding predatory mites such as *Amblyseius swirskii* Athias-Henriot (Fig. 19.1) or *Euseius* spp. (Nomikou et al. 2001; Calvo et al. 2015). Interestingly, the control of whiteflies by predatory mites can work better when, besides whiteflies, thrips is also present, as a mixed diet of both pests results in a shorter juvenile developmental time and lower mortality of the predators (Messelink et al. 2008). Enhanced control can also be achieved by adding pollen (Nomikou et al. 2010) or prey mites (Hoogerbrugge et al. 2008) as an alternative food source for the predatory mites. Combined releases of prey and predatory mites gave excellent control of whiteflies and of ToLCNDV in zucchini (Tellez et al. 2017). *Amblydromalus limonicus* is another phytoseiid mite which is capable of providing good whitefly control (Knapp et al. 2013). Other predators, such as the mirid predatory bug *Macrolophus pygmaeus* (Rambur), are successfully applied for whitefly control in tomato crops, but their ability to damage the fruits in cucumbers discourages application in practice. In case preventive releases of predators are not effective, curative treatments with entomopathogenic fungi can be considered. Several strains of entomopathogenic fungi, such as *Beauveria bassiana* (Balsamo) Vuillemin or *Lecanicillium muscarium* Petch can be used, but application of these fungi requires the right ambient conditions to be effective (Gonzalez et al. 2016). In some cases, systemic pesticides, such as neonicotinoids, can be applied, but these persistent pesticides are often not an option because of the strict requirements of the retail industry for pesticide free products or simply because they are not allowed anymore.

19.2.1.3 Thrips

The most problematic thrips species in cucumber worldwide is the western flower thrips, *Frankliniella occidentalis* (Pergande). The adults and larvae that feed on the fruits cause cosmetic damage and lower the fruit quality. Thrips can also transmit tospoviruses, like the Tomato Spotted Wilt Virus (TSWV), but cucurbits are not suitable host plants for these viruses and infection does not cause any disease symptoms. Besides western flower thrips, many more species, such as *Thrips tabaci* Lindeman, *Thrips palmi* Karny, *Thrips setosus* (Moulton)*, Echinothrips americanus* Morgan and *Scirtothrips dorsalis* Hood occur and cause damage. The melon thrips *T. palmi* is expanding its geographical distribution and is a quarantine organism in Europe. Similarly, the geographic range of the chili thrips *S. dorsalis* has rapidly expanded from Asia in the 1990s so that today it can also be found in the United States, the Middle East and Central Africa (Dickey et al. 2015). It is therefore seen as a potentially important invasive pest species to Canada and Europe that may threaten the greenhouse vegetable industry.

Biological control of thrips is generally successful with phytoseiid predatory mites, although it is more difficult in non-heated greenhouses in winter plantations. Nevertheless, provisioning of prey mites or pollen as alternative food improves thrips control in winter plantations by increasing predatory numbers in the crop. In the past, *Neoseiulus cucumeris* (Oudemans) was the predominant species used, but an evaluation of several other species showed that at least 5 species were more effective (Messelink et al. 2006). This, together with the fact that some of those species also control whiteflies, resulted in a shift to the use of more generalist predatory mites like *A. swirskii*, *A. limonicus* and *Transeius montdorensis* (Schicha) (Messelink et al. 2008; Knapp et al. 2013; Calvo et al. 2011; Steiner et al. 2003). Not all thrips species are controlled well by phytoseiid predatory mites. *Echinothrips americanus* is one of the thrips species that is only suppressed to a certain extent and some species of predatory mites are not effective at all (Ghasemzadeh et al. 2017). Other predators like *Orius* spp. or predatory thrips can be used in addition to phytoseiid mites to control this thrips species (Ramakers et al. 2000). However, most *Orius* spp. are typical flower bugs that need pollen to establish their populations, and since most cultivated cucumber plants are parthenogenitic, they do not provide pollen as an alternative food source. Other *Orius* species that are more leaf-dwelling, such as the north European species *Orius majusculus* (Reuter), are more suitable to be used in cucumber. The application of alternative food or prey can be another interesting solution to support establishment and augment predator populations (Messelink et al. 2014).

19.2.1.4 Aphids

The most important aphid species in cucumber is the cotton aphid *Aphis gossypii* Glover. This small black aphid reproduces extremely fast on cucurbits and causes severe plant damage by secreting high amounts of honeydew, which are a suitable substrate for sooty mould fungi and lead to contaminated fruit and leaves. Other aphid species that also occur in cucurbits are the green peach aphid *Myzus persicae* Sulzer (several phenotypes ranging from green to dark red) and the potato aphid *Macrosiphum euphorbiae* (Thomas). Aphids can potentially also transmit non-persistent *Cucumber mosaic virus* (CMV) in cucurbits, although this rarely occurs in greenhouse crops. Biological control of the cotton aphid is very effective with the parasitoid *Aphidius colemani* Viereck, whereas *Aphidius matricariae* Haliday, commonly used against *Myzus persicae* Sulzer, is an unsuitable parasitoid for cotton aphid (Van Steenis 1995). However, the efficacy of parasitoids is often largely restricted by the presence of secondary parasitoids (so-called hyperparasitoids) that parasitize the primary parasitoids. The hyperparasitoids of aphid parasitoids are solitary species from the families Megaspilidae, Pteromalidae, Alloxystidae and Encyrtidae (Sullivan and Völkl 1999). Surveys in greenhouses in the UK, Canada and the Netherlands recorded several species of hyperparasitoids with levels of parasitism up to 100% (Jacobson 2011; Acheampong et al. 2012; Bloemhard et al. 2014). Therefore, additional BCAs are often needed to control aphids. One of the most effective predators is the predatory midge *Aphidoletes aphidimyza* (Rondani), but the efficacy of this predator can also be reduced by unsuitable climatic conditions or hyperpredation by predatory mites (Messelink et al. 2011). Several coccinellid species such as *Adalia bipunctata* Linnaeus or *Scymnus* spp. are also released for curative biocontrol of aphid hot spots. Entomopathogenic fungi could potentially be used to infect and control aphids, but most isolated that are commercially available are not effective (Jandricic et al. 2014). Yet, some selective pesticide treatments might be needed in cases where aphids are not controlled by BCAs. Commonly used pesticides are pymetrozine and pyrethrins.

19.2.1.5 Caterpillars

Several lepidopteran species can attack cucurbits by feeding on leaves and/or fruits, but few species are common pests on cucurbits. Many are polyphagous species with a broad host range that includes crop plants such as cucumber. Among these polyphagous species, the most important are noctuids belonging to the genera *Chrysodeixis* [*Chrysodeixis chacites* (Esper), *Chrysodeixis includens* (Walker)], *Helicoverpa* [*Helicoverpa assulta* (Guenée)], *Spodoptera* [e.g., *Spodoptera exigua* (Hübner)] and *Trichoplusia* [*Trichoplusia ni* (Hübner)]. Species can vary in relation to their geographical distribution, but the damage caused is very similar. Control of caterpillars often depends on the use of *Bacillus thuringiensis* Berliner subspecies *kurstaki* (Btk) or *aizawai, that are more effective against young caterpillars.* Biological control of many lepidopteran species can include the use of egg parasitoids of the genus *Trichogramma*, of which various studies have demonstrated their good potential for caterpillar control in the greenhouse environment (Gonring et al. 2003). However, one of the limitations of these species is the need for high densities of hosts, which are not frequent in a greenhouse, and therefore they are often not able to completely eliminate the host species. Some attempts with larval parasitoids have been conducted, but so far none of them has provided a suitable cost-effective control.

19.2.1.6 Minor Pests

Many other pest species can occur in cucurbits, but they are often considered as minor pests (Shipp 2004). Among them are the tarnished plant bugs, *Lygus* spp.. In North America, *Lygus lineolaris* (Palisot de Beauvois) is the most occurring species in cucurbit crops, whereas in Europe, *Lygus rugulipennis* Poppius is the most abundant plant bug that occasionally enters greenhouse crops. Damage can be particularly severe in cucumber crops with a high-wire cultivation system, because damage to the main shoot has a strong impact on production. Several natural enemies including predators and parasitoids have been tested, but results have been so far disappointing. Consequently, growers have to rely on pesticides, among which neonicotinoids are very effective, but in many cases they are not allowed any more due to consumer demands or regulations. Sources of these pests are often other weedy and crop host plants that surround greenhouses, from which the mirid bugs migrate inside when field densities are high (Pansa and Tavella 2009). This behaviour makes the control more difficult because of the unpredictability of the infestations, but it could be exploited by selecting more favourite host plants than cucumber to be used as trap plants. Leaf miners are often present but rarely a problem. If natural biological control is not sufficient, artificial introduction of larval parasitoids may be considered. Finally, some specific flea beetles (Chrysomelidae) can occur in cucurbits, like the striped cucumber beetle *Acalymma vittatum* (Fabricius) and the spotted cucumber beetle *Diabrotica undecimpunctata* Mannerheim. Both species occur in North America and cause severe crop damage in various cucurbits, although several entomopathogenic nematode species can be an effective choice for their control.

19.2.2 Diseases

19.2.2.1 Powdery Mildew

Two main fungi cause powdery mildew on cucurbits: *Podosphaera xantii* and *Golovinomyces cichoracearum*. *Podosphaera xanthii* (previously known as *Sphaerotheca fusca* or *S. fulginiea*) is frequently reported in warmer climates such as subtropical and tropical regions and under greenhouse conditions (Lebeda et al. 2016). *Podosphaera xanthii* race 3.5 is however the most predominant in Europe on melon, because genetic resistance is currently introduced in melon for *G. cichoracearum* and other races of *P. xanthii*. Symptoms consist of whitish fungal spots that grow on both axial and abaxial (firstly) sides of the leaf as well as on petioles and stems and usually originate on the bottom part of the plant (Fig. 19.2). Heavily infected leaves wither and finally die, and plants show early senescence. Eventually, powdery mildew can decrease the yield by reducing the fruit size and the duration of the harvest period. The primary infection after winter originates from cucurbit crops grown in adjacent greenhouses or wild host plants and an epidemy can spread easily when environmental conditions become favourable (high plant density, low light intensity, more than 50% relative humidity and temperatures between 20 and 28 °C) (Zitter et al. 2004). Currently, disease control is mainly based on the use of genetic resistance, usually used in cucumber and melon, and preventive and systematic chemical applications. Due to pathogen adaptation, the protection provided by resistant cultivars is variable and not always enough to control the disease. In addition, yields are often smaller than those obtained with susceptible cultivars, particularly under suboptimal conditions (Rur et al. 2018). The massive use of fungicides has led to the development of different resistant strains and the need of frequent applications with alternation of different active substances. Consequently, the implementation of additional control methods, such as physical or cultural methods, are strongly recommended to limit the spreading of powdery mildew in cucurbits. Lowering humidity levels through ventilation can reduce conidia germination and initial infection. Luxuriant plant growth will favour pathogen proliferation, which can be reduced by limiting the nitrogen supply and irrigation. Furthermore, weeds can act as alternative hosts and an adequate removal as well as diseased plants at the end of the crop could reduce the reservoir and primary inoculums for the next cycle.

Fig. 19.2 Symptoms of powdery mildew on zuchini (left), downy mildew on cucumber (middle) and grey mould on melon (right)

Other alternative control measures are increasingly applied in practice. Different silicon-based products sprayed on leaves or applied in the nutrient solution (sodium silicate) have been proven effective in protecting cucurbit crops against powdery mildew. Foliar-applied silicon can effectively control infections by mildew only via the physical barrier of silicon deposited on leaf surfaces, and/or osmotic effect of the silicate applied, but cannot enhance systemic acquired resistance induced by inoculation, while root-applied silicon can enhance defence resistance in response to infection by mildew (Liang et al. 2005). The application of Ultraviolet (UV) radiation during the night is another method that shows potential to control powdery mildew in cucumber (Suthaparan et al. 2017).

Biological control of powdery mildew is increasingly applied with commercial BCAs. In most cases, these BCAs have been isolated from the plant phyllosphere, and consequently, selected to be able to colonize this environment. Different species of *Bacillus* spp. show significant suppressive levels under greenhouse conditions. *Bacillus amyloliquefaciens* produces a wide range of antifungal metabolites inhibiting spore germination of *P. xanthii* and inducing plant defence mechanisms (Li et al. 2015), reaching more than 50% disease suppression in cucumber and pumpkin crops under greenhouse conditions (Ji et al. 2013). The *Bacillus* spp. ability to produce spores resistant to UV radiation and unfavourable environmental conditions make these BCAs suitable candidates to formulate commercial products. Yeasts from the *Pseudozyma* genus also inhibit the disease in more than 75% when applied preventively or curatively, through mechanisms such as parasitism, antibiosis, pathogen spore germination and competition for ecological niche (Hammami et al. 2011). Several products are now commercially available for growers based on these and other microorganisms, such as *Bacillus subtilis* (Companion®, Rhapsod® and Serenade®), *B. pumilus* (Sonata®), *Streptomyces spp*. (Actinovate®) or *Ampelomyces quiscalis* (AQ10®) (Gwynn 2014). In addition, other products are being used to control this pathogen by different mechanisms such as plant extracts (*Reynoutria sachalinensis* and *Yuccah schidigera* and substances to stimulate plant protection playing a role of elicitors: potassium bicarbonate, chitosan or mineral oils (Rur et al. 2018). Nevertheless, none of the measures referred above enables the total disease control on its own and a combination of all measures should be taken into account.

19.2.2.2 Downy Mildew

Downy mildew represents one of the most important foliar diseases in producing areas with plastic and non-heated greenhouses. Winter crops in the Mediterranean area suffer from severe losses. The pathogen causing this disease is *Pseudoperonospora cubensis* (Berk. & M.A. Curtis) Rostovzev, a like-fungus classified within the Kingdom Stramenoplia and Phylum Oomycota. The species presents five different pathotypes affecting differentially specific cucurbit hosts. Cucumber and melon are susceptible to all pathotypes, whereas watermelon, zucchini and squash are only to one pathotype. Cucumber is the most susceptible crop in Europe. Sporangia containing zoospores are carried away by wind and constitute the primary inoculum source. Infection occurs with water presence on leaves (rain or dew) during variable periods of time depending on the temperature and photoperiod. Optimal temperatures range 15–20 °C (Palti and Cohen 1980). Released zoospores move towards stomata and initiate infection.

Infection causes small, angular, yellow lesions on the upper side of the leaf. A white to purplish mildew may be observed on the lower side of the leaf during humid weather. When the lesions expand, their centers turn brown. Often the margins of diseased leaves curl upward. Eventually lesions can kill large areas of the leaf surface and in severe cases, the entire plant will die. Sporulation on the underside of leaf lesions provide with the secondary inoculum source (Fig. 19.2). Disease spread quickly across the crop. Total plant defoliation leads to the loss of crop production.

Disease management is currently based on three pillars: (1) cultural practices to decrease humidity on leaves including plant density reduction in unheated greenhouses with severe problems to facilitate aeration, greenhouse ventilation increase and a proper diseased plant material removal to reduce the secondary inoculum; (2) preventive and periodical chemical fungicide applications; and (3) use of tolerant cultivars, especially in cucumber and more recently in melon. Some resistance genes introduced for powdery mildew seem to provide cultivars with crossed tolerance to downy mildew through hypersensitivity reactions; lesions turn necrotic and pathogen cannot continue infection. However, fungicide-resistant pathogen strains are prevailing and the combination of high pathogen pressure and favourable climatic conditions turn the disease management measures insufficient.

Biological control is becoming necessary to complete the integrated disease management programs. Several strains of bacteria, such as *Bacillus* spp. and *Enterobacter* spp., have been tested and show potential as a BCA for the control of downy mildew (Zheng et al. 2018). Some root-colonizing *Trichoderma* strains can also reduce the disease severity by inducing a plant defence, even when applied in an early stage as seed coating (Szczech et al. 2017). Applications of such BCAs in practice need further studies.

19.2.2.3 Grey Mould

Botrytis cinerea Pers.: Fr. (teleomorph *Botryotinia fuckeliana* (De Bary) Whetzel) is a necrotrophic pathogen causing the grey mould, described among the most important diseases of greenhouse-grown vegetable crops in many countries worldwide. It causes problems in different cucurbit crops, such as cucumber, zucchini and melon. Damage usually occurs through yield losses because of fruit infection and rots (Fig. 19.2), but mainly by plant death after stem damage. Infection starts on senescence tissues, the petiole or directly from wounds and evolve surrounding the stem and causing the plant collapse upwards (Dik and Wubben 2007). *Botrytis cinerea* is no-host specific and has the capacity of adaptation to different tissues, crops and conditions. Greenhouses climatic conditions greatly influence epidemics caused by

B. cinerea. Temperatures ranging 15–25 °C and high relative humidity favour the disease development. Thus, unheated greenhouses are more likely to suffer severe damages. The disease control has been based on an integration of several cultural methods and recurrent fungicide applications. Wide plant spacing and de-leafing can reduce *B. cinerea* infection due to improved ventilation. Leaves should be cut just in insertion point with the stem to avoid the presence of senesce petiole remains what constitute the major risk. The effect of nitrogen in the fertilizer is not consistent, but calcium enrichment of the plant tissue generally reduces susceptibility (Dik and Wubben 2007). Timing and method of the irrigation can also affect infection levels. No resistant cultivars exist yet, but cultivars show highly variable susceptibility. Although the control of *B. cinerea* has been traditionally based on the use of fungicides belonging to several groups such as benzimidazoles, dicarboximides, and N-phenylcarbamate, or multi-specific inhibitors such as chlorothalonil, dichlofluanid, iminactodine, and captan, this pathogen represents a classical high risk pathogen for fungicide resistance development due to its high genetic variability, the abundance of sporulation, the short generation time and the wide host range (Leroux et al. 2002). The development of resistant strains has led to alternations with chemicals of different mode of action as a strategy to delay evolution of resistance and to the search of alternative control methods.

Biological control of *B. cinerea* is well developed and several commercial BCAs are available for application in cucurbit crops, such as *B. subtilis* (Cease®, Ecoshot, Rhapsody®, Serenade®), *Bacillus velezensis* (Botryvel), *Streptomyces lydicus* (Actinovate® SP), *Pseudomonas syrigae* (Bio-save® 10/11) and *Burkholderia cepacia* (Botrycid®) (Gwynn 2014). In addition, different studies show the effectiveness of various BCAs applied on leaves and fruits of greenhouse cucumber plants to control *B. cinerea*, such as *Trichoderma hartzianum* T-39 (Trichodex) (Elad 2000) and *Acremonium strictum* BCP (Choi et al. 2009).

19.2.2.4 Gummy Stem Blight

Didymella bryoniae (Auersw.) Rehm (=*Mycosphaerella melonis* (Pass.) Chiu & J.C. Walker) anamorph *Stagonosporopsis cucurbitacearum* (Fr.) Aveskamp,Gruyter & Verkley (synonym = *Phoma curcurbitacearum* (Fr.) causes the gummy stem blight -foliar disease- and the black rot -fruit phase- in different cucurbit species. It is especially destructive as foliar disease in cucumber, melon and watermelon and as black rot in pumpkin and squash, reducing both pre- and postharvest yields (Keinath et al. 1995). The pathogen survives between seasons in diseased adventitious weeds and crop residues. Although the optimal temperature for infection is between 20 °C (melon) and 24–25 °C (cucumber and watermelon), continues foliar humidity results to be more important for disease development than temperature. Infection begins directly through the cuticle, the intercellular spaces around the trichomes in leaves, wounds and by leaf lesion extension in stems, whereas in fruits, wounds or floral scars are the entrance points (Zitter et al. 2004). After infection the pathogen grows rapidly in planta and reproduces readily on all parts of cucurbits, including leaves, petioles, vines, stems, tendrils, pedicels, flowers, peduncles, fruits, seeds, and roots. The most severe damages are found when extended lesions affect the stem base, giving rise to brown and aqueous areas with exudate drops. On them pseudotecia and picnidia are developed and in advanced infections the plant wilts, shows poor development or dies. In cucumber, fruit infection leads to both visible (external) and non-visible (internal) fruit rot, resulting in significant yield losses. In addition, *D. bryoniae* is also a seedborne pathogen and may be present both on and in cucurbit seed. Nevertheless, cucurbits have differential sensibility to *D. bryoniae*. For example, summer squashes (*C. pepo*) are resistant to – or less susceptible to – gummy stem blight relative to other commonly cultivated cucurbits (Keinath 2011).

The control methods against *D. bryoniae* should be based primarily on the use of treated seeds and if possible crop rotation. Although there have been identified resistance genes, currently there are no cultivars with acceptable resistance in any cucurbit. Preventive and regular fungicide applications lead to a proper disease control, though resistant strains to benzimidazole have been detected in greenhouse crops in different European countries and in USA. Greenhouse climatic control can provide a significant decrease in the disease severity by reducing the irrigation and increasing the ventilation in order to minimize the humidity on leaves (Zitter et al. 2004).

Although biological control is not commonly used to manage this disease, several studies show the potential of BCAs. Preventive application of cucumber plants with the antagonist *Gliocladium catenulatum* (Prestop®) reduced the number of plants with gummy stem blight (Utkhede and Koch 2004). Foliar applications of *B. subtilis* can also reduce gummy stem blight severity (Kaewkham et al. 2016). Another interesting and method is the BCA application as seed treatments, including the seed priming with endophytic microorganisms, which allows a prompt seedling colonization after germination and long term protection (Fürnkranz et al. 2012). For this pathogen, special attention should be paid to key moments with a high infection risk, such as during transplanting or during favourable climatic conditions, especially in greenhouses without active climatic control. By integrating cultural measures and BCA application, infection risks can be reduced and thereby also the need for chemical control.

19.2.2.5 Pythium Root and Stem Base Rot

Pythium spp. are like-fungus classified within Kingdom Stramenoplia, Phylum Oomycota and Class Oomycetes. Consequently, they are not true fungus, their cellular wall contains cellulose instead of chitine, and produce sporangia releasing zoospores. They are saprophytic and nonspecialized parasites inhabiting most soils/substrates in producing areas. Pythium proliferation is closely linked to water presence, which is the reason they perform well in hydroponic systems. The most important species affecting cucurbits are *Pythium ultimum* Trow, requiring cool and humid conditions; *P. aphidermatum* (Edson) Fitzp. and *P. myriotylum* Drechs, which need warmer environments (32–37 °C) (Zitter et al. 2004). Inoculum may be introduced through the substrate, the irrigation water or by using non-disinfected tools. Early infections lead to seedling falling (damping off) and death. Once the hypocotyls become mature they acquire some tolerance. Nurseries are specially affected due to conditions prevailing in these facilities: warm temperatures and constant saturated substrates. Once the pathogen appears it spreads quickly through the nursery trays provoking dramatic loses in a few days.

Pythium root rot can also occur in mature plants. This disease is especially severe in hydroponic cultivation. Infected plants show different stress symptoms: delayed growth, chlorotic leaves, necrosis and lesions on fruits and death. Faster symptoms developed in apparently healthy plants include wilts during the warmer hours at midday recovering during the nights, though plant dies in 2–4 days. The combination of fruit setting and a short hydric stress followed by soil/substrate saturation or flooding for 24–48 h seems to make the plant more susceptible to the collapse (Zitter et al. 2004).

The usual control measures have been based on the preventive chemical fungicide applications. An integrated disease management program can include several preventive cultural measures, such as proper tool disinfection, high quality UV-radiated substrate, water disinfection with UV radiation or hydrogen peroxide and a proper irrigation management avoiding a constantly saturated substrate. A common recommendation is that rockwool slabs that are being re-used should also be steam sterilized, but research has proven the advantage of potential suppressive microbial communities present in re-used rockwool slabs that are not sterilized (Postma et al. 2000). Avoiding a biological vacuum is also of major importance in soil cultivation after strong chemical disinfections. Organic applications such as composts to substrate/soil can increase microbial activity and suppress *Pythium spp.* (Scheuerell et al. 2005). There are also several fungal and bacterial BCAs available for preventive control, such as *Trichoderma* spp. and *Pseudomonas fluorescens*, that have proven to be effective in preventing this disease (Roberts et al. 2005; McCullagh et al. 1996).

19.2.2.6 Hairy Root Disease

Most cucumber crops in glasshouses are cultivated out of soil on hydroponics, which is a major advantage to escape from soilborne pests and diseases. However, some new diseases appeared that are typical for hydroponically grown vegetables. Since the early 1990s hydroponically grown cucumber and melon plants, and later also aubergine and tomato crops, have been affected by a root disorder known as 'hairy root disease' (also known as 'hairy roots', 'crazy roots' or 'root mat'). Hairy root disease is characterized by extensive root proliferation within the rockwool cube and across the rockwool slab surface, leading to strong vegetative growth with reduced fruit production. This disease has been found all over Europe, the USA, Japan and New Zealand (Bosmans et al. 2017). The disease on hydroponic crops is generally caused by *Agrobacterium* biovar 1 strains (*Agrobacterium radiobacter*) harbouring a root inducing Ri plasmid (also referred to as 'rhizogenic agrobacteria'). The high genetic diversity present within *Agrobacterium* biovar 1 strains leads to a wide range of conditions where the pathogen can proliferate in hydroponic crops. Optimal temperatures range between 22 and 37 °C and pH 5–9; however, more extreme values could be also tolerated. The root infection begins when pathogenic bacteria are attracted and attached on wounded roots. Substances released by the roots trigger bacterial mechanisms and the Ri plasmid is introduced in the root cell. Once the transferred DNA is integrated into the host plant genome, genes expression leads to different product synthesis and a boosted sensibility to auxins and this in turn to the disease development. Symptoms start 5–8 week after infection (Bosmans et al. 2017).

Once the T-DNA has been integrated into the plant genome, hairy root disease cannot be controlled by curative means. Preventive control can be achieved with chemical disinfection by chlorine-based disinfectants or hydrogen peroxide. However, this will also disrupt beneficial root-colonizing fungi and bacteria that increase plant resilience. Current research is focusing on microbial communities that prevent infection by rhizogenic agrobacteria.

19.2.2.7 Fusarium Wilts

Vascular wilts in cucurbits are among the most devastating plant diseases that occur in all producing areas. *Fusarium oxysporum* Schlechtend.: Fr. Emend. W.C. Snyder & H.N. Hans, the causal agent, present in different formae specialis with specificity for each cucurbit species. Each formae specials is further subdivided into races affecting different cultivars. *Fusarium oxysporum* is a cosmopolite, saprophytic and facultative parasite. It can survive in soils for very long periods of time by growing saprophytically on organic matter or by the production of resting structures. Infection occurs in the roots or by wounds. Once inside, *F. oxysporum* reaches the xylem and proliferates on it causing obstruction by mycelial development and different substances secretion. As a consequence, the water uptake by infected plants is hampered and wilt appears during the warmer hours, often on one side only. In several days, plant develops yellowing, collapses and dies. Plant collapse and death is more probable under stressing situations such as fruit ripening and high water demand.

Three formae speciales and their races are important for cucurbits. The first occurs in melon, which is *F. oxysporum* f.sp. *melonis* (Leach & Currence) W.C. Snyder & H.N. Hans. Specific symptoms are partial wilts and development of longitudinal necrotic lesions along the stem from the crown to 20–50 cm upwards, with emergence of pink sporodochia and eventually gummy exudates. This formae speciales causes not always darkening in vascular tissues. Some resistant cultivars against this formae speciales are available nowadays. Optimal temperatures range 18–25 °C and temperature above 30 °C reduce the severity. The second, *F. oxysporum* f.sp. *niveum* (E.F. Smith) W.C. Snyder & H.N. Hans is also specific for watermelon. It is worldwide distributed and constitutes the most destructive forma speciales. General symptoms are similar to the ones described before. These symptoms can be observed in parts of the plant whereas the rest remain apparently healthy. Recently the use of triploid cultivars has become a usual practice and the majority of triploid watermelon cultivars have little or no resistance to Fusarium wilt (Everts and Himmelstein 2015). Optimal temperatures range 25–27 °C and temperature above 27 °C reduces the disease severity. The third, *F. oxysporum* f.sp. *cucumerinum* J.H. Owen is specific for cucumber and occurs world-wide. This forma speciales has become less important because of resistant cultivars and rootstock.

Fusarium pathogens can also cause root and crown rots, but these are less destructive than vascular wilts. The *F. oxysporum* f.sp. *radicis-cucumerinum* Vakal causes rots in the plant radical system, crown and stem up to 10–12 cm in mature plants. Severely affected plants show orange sporodochia in crown and stem lesions. Infected plants eventually can die. A less aggressive *Fusarium* pathogen in squash, causing necrotic root and crown rot, is *F. solani* f.sp. *cucurbitae* W.C. Snyder &H.N. Hans. Yet, this pathogen has become important because of the fact that it also affects watermelon grafted on squash rootstock. Symptoms include longitudinal necrotic lesions in the crown developing whitish mycelia when the humidity is high.

The most successful method to control *Fusarium* is grafting on resistant rootstocks (Cohen et al. 2002). Soil desinfection is also an opportunity. Successful and environmental friendly methods can be based on solarization, combined with flooding or organic amendments (Yao et al. 2016). An interesting approach is to vaccinate plants with mutant non-pathogenic strains of *F. oxysporum,* which provides cross-protection against pathogenic strains (Freeman et al. 2002; Larkin et al. 1996). However, commercial products based on these strains are currently not available. Other promising BCAs are *Penicillium oxalicum* Currie & Thom, *Paenibacillus* spp., *Streptomyces lydicus* and *Trichoderma* spp. (Everts & Himmelstein 2015; De Cal et al. 2009).

19.2.3 Viruses

To date, more than 70 virus species have been found to affect cucurbits worldwide (Lecoq and Katis 2014). Depending on the species of the virus, they may cause one or more of the following symptoms in cucurbits which are (i) mosaics on leaves, often with discolorations and deformations on fruits, (ii) yellowing of older leaves, (iii) necrotic spots on leaves, fruits or generalized necrosis (wilting) (Fig. 19.3). They may also affect plant growth and yield. Both symptoms on fruits and reduced productions can lead to significant economic losses. In contrast to pests and other diseases such as those produced by nematodes, fungi and bacteria, in the case of viruses in plants, there are no "viricides" that can be used in treatments to protect or to cure the plants. The control of these viruses tends to be tedious and complex, because viral populations are often variable in time and in space, they can easily evolve giving rise to viruses that overcome resistances when such plants are present. Therefore, control of plant viruses is necessarily takes the form of an integrated

Fig. 19.3 Leaf symptoms of viruses in cucurbits: (1) *Squash mosaic virus* (SqMV) in cucumber, (2) C*ucumber green mottle mosaic virus* (CGMMV) in watermelon, (3) *Zucchini yellow mosaic virus* (ZYMV) in zucchini, (4) *Watermelon mosaic virus* (WMV) in melon, (5) *Cucurbit aphid-born yellows virus* (CABYV) in zucchini, (6) *Cucumber vein yellowing virus* (CVYV) in cucumber, (7) *Cucurbit yellow stunting disorder virus* (CYSDV) in cucumber, (8) *Tomato leaf curl New Delhi virus* (ToLCNDV) in zucchini, (9) *Melon necrotic spot virus* (MNSV) in melon

disease management that relies on methods that reduce the amount of primary inoculum. Once a virus is present in a crop, other methods would reduce the secondary spread and the pathological effects on the plants. The nature of the methods and the ways they are adopted depend on the particular features of each viral pathosystem. The application of the different procedures to be used in integrated control requires sufficient knowledge of the biology and ecology of a virus and of the way disease epidemics develop. Essential details of the epidemiology such as infections sources, mechanisms of spread, reservoirs and ways the disease develops, are crucial to take the correct decision on which integrated strategy to follow (Jones 2004). Finally, integrated control of plant viruses also should include procedures that reduce the impact infections in plants may have. The correct management of these elements may help to reduce the effects on the yields of crops.

19.2.3.1 Control of Primary Infections

The control of primary dispersion is of great importance for the management of viral epidemics. Legislative measures to control the movement of plant material are essential to maintain regions or zones free of a virus (Pasquali et al. 2015). In the case of viruses that are dispersed through propagation materials (seeds, vegetative propagules), the establishment of certification systems for the production of virus-free material can be very effective for control. Certification of virus-free seed lots is essential to control *Squash mosaic virus* (SqMV) (Lecoq and Desbiez 2012). This virus belongs to genus *Comovirus*, family *Secoviridae*, and is mainly limited to cucurbits where infections produce mosaic, vein banding and leaf deformation. Seed transmission is the major way for the introduction and long distance dissemination of SqMV. Transmission rates ranging from 0.1% to 10% are commonly observed in infected commercial seed lots (Alvarez and Campbell 1978). Other relevant seed-transmitted virus species in cucurbits are *Cucumber green mottle mosaic virus* (CGMMV), *Cucumber fruit mottle mosaic virus* (CFMMV), *Zucchini green mottle mosaic virus* (ZGMMV) and *Kyuri green mottle mosaic virus* (KGMMV). They belong to genus *Tobamovirus*, family *Virgaviridae*. CGMMV causes systemic mottle and mosaic symptoms on cucurbitaceous plant leaves. In watermelon, the virus causes a pulp deterioration called blood flesh disease and the fruit loses its marketable value. In cucumber, the virus causes deformation and mosaic symptoms. Since it was described in cucumber in England in 1935, its incidence in other countries of the world has increased rapidly during the last decade, possibly through the international seed trade following cucurbit seed crop production in tropical or subtropical countries (Dombrovsky et al. 2017). Contaminated seeds provide a route for the movement of the virus between countries and its introduction into new areas, and several seed treatments currently used, were found insufficient to eliminate the virus from contaminated seed lots (Reingold et al. 2015). CGMMV also constitutes an example of a cucurbit virus that is transmitted by other vegetative propagation material. For these viruses, the use of virus-free propagation material (seed) is essential for the control of epidemics.

This is similar in the case of very stable or transmissible viruses by soil fungi. *Melon necrotic spot virus* (MNSV) belongs to genus *Carmovirus*, family *Tombusviridae*. It causes systemic, necrotic spots on leaves and streaks on stems of melon, watermelon and cucumber and occasionally leads to a plant collapse (“sudden death”). MNSV is seed-borne through an unusual mode: the vector-assisted seed transmission (VAST) (Campbell et al. 1996). For virus transmission to occur, contaminated seeds depend on the presence in the soil of *Olpidium bornovanus*, an obligate, holocarpic, root-inhabiting zoosporic fungus. VAST probably operates through the release of MNSV particles from the contaminated seed coats and their in vitro acquisition by zoospores prior to inoculation by the zoospores when penetrating seedlings roots (Campbell et al. 1996). Another cucurbit infecting viruses that is transmitted in a similar manner is *Cucumber leaf spot virus* (CLSV, genus *Aureusvirus*, family *Tombusviridae*) (Segundo et al. 2001).Chemical soil disinfection or solarization can help reduce the risks of primary infections in these cases where Sources of infection in the soil of culture can also be important foci of primary dispersion.

Most of the cucurbit viruses that are not seed-transmitted are transmitted by insect vectors, predominantly aphids and whiteflies. Control of primary dispersion of these viruses depends on the degree of successful preventing their insect vectors to reach the plants. Relevant viruses can be classified according to their mode of transmission by vectors and based on the persistence or retention capacity of the virus in the vector. Non-persistent transmission viruses are characterized by a retention time in the vector of a few hours and a very fast transmission (from seconds to a few minutes). These viruses do not require a latency time in the vector, being almost exclusively aphids, and they can be transmitted immediately after being acquired. They are viruses that are transmitted in superficial tests in the epidermis or parenchyma and are retained in the cuticle of the buccal apparatus.

Persistently transmitted viruses are characterized by a much longer retention period (days or weeks), periods of acquisition and inoculation of many hours or even days, with a latency period of at least several hours being necessary. These viruses are usually transmitted to the phloem, they can also be transmitted after moulting and their virus-vector specificity is very high. Persistent type transmission is characteristic of several viruses transmitted by aphids, such as *Cucurbit aphid-born yellows virus* (CABYV, genus *Polerovirus*, family *Luteoviridae*). CABYV infects melon, watermelon, squash and cucumber and produces yellowing of the older leaves. Yield reductions can be up to 15% in melon, and 50% in cucumber (Lecoq 1999). Virus species of the genus *Begomovirus* (family *Geminiviridae*) are typically transmitted in a persistent mode by the whitefly *B. tabaci*. They are plant viruses that as a group have a very wide host range, infecting dicotyledonous plants. Worldwide they are responsible for a considerable amount of economic damage to many important crops such as tomatoes, beans, cassava and cotton. To date more than 300 begomovirus species are known and these include several cucurbit-infecting viruses, such as *Cucurbit leaf curl virus* (CuLCV), *Squash leaf curl virus* (SLCV) or *Watermelon chlorotic stunt virus* (WmCSV) (Lecoq & Katis 2014). The general symptoms of begomovirus infections in cucurbits are leaf crumpling and curling, and sometimes growth stunting. Recently, a new strain (called “Spain”) of *Tomato leaf curl New Delhi virus* (ToLCNDV-ES) was found causing significant damage in squash and melon crops in Spain (Juarez et al. 2014).

Semi-persistent transmission combines intermediate characteristics between the types of non-persistent and persistent transmission. This is the case of *Cucurbit yellow stunting disorder virus* (CYSDV, genus *Crinivirus*, family *Closteroviridae*) and *Cucumber vein yellowing virus* (CVYV, genus *Ipomovirus*, family *Potyviridae*) (Lecoq & Katis 2014). Leaves from CYSDV infected cucumber and melon first show mottling of leaves, which evolve to leaves that are completely yellow, with the veins remaining green. Yellowing is predominant in the lower half of the plants.

Cucumber and melon plants infected with CVYV display vein clearing on the youngest leaves. Occasionally, yellow/green mosaic is observed on fruits (Cuadrado et al. 2001). In watermelon, a mild leaf chlorosis is sometimes observed but most often symptoms are inconspicuous or not expressed. However, occasional splitting of fruits has been observed. In zucchini, symptoms range from chlorotic mottling to vein yellowing, or are absent.

Independent of the different modes of transmission and species of insect-vector, most inoculations in plants can occur very fast, so preventing this from happening is a huge challenge. The establishment of barrier cultures that surround susceptible crops or intercropping with a species that is a good host for the vector, but not the virus, can help to limit the primary dispersion rate of viruses transmissible by aerial vectors to the culture from external sources of infection. Several examples exist of successful management of aphid transmitted cucurbit viruses. *Zucchini yellow mosaic virus* (ZYMV, genus *Potyvirus*, family *Potyviridae*) is one of the major pathogens of cucurbits in the world. It causes severe leaf mosaic, yellowing and eventually “shoestring” symptoms in the leaves. The fruits are stunted and deformed by raised protuberances.

Physical barriers that are used to prevent viruliferous (virus-carrying) insects from reaching near to cucurbit crops can be done by enclosing crop plants in permanent or semi-permanent insect-proof housing. In permanent screenhouses, mesh can be used that excludes aphids and whiteflies. Screenhouses improve the growing conditions for vegetables, and offer a physical protection that reduces movement of whiteflies between crops and consequent virus spread. They proved efficient to reduce the incidence of CYSDV and CVYV in cucumber (Janssen et al. 2009).

19.2.3.2 Control of Secondary Spread

The control of the secondary spread of a virus, once introduced into a region or a culture, can be relatively simple if it depends on a vector that would not be present. In this case, legislative, sanitary and quarantine measures are essential to prevent the entry of the vector. Secondary spread of viruses that are easily transmitted from primary foci of infection during handling of plants in crop operations should be minimized by establishing appropriate management measures. There is some experience for CGMMV that is easily transmitted by contact. Timely monitoring for infection in greenhouses, awareness of the movements by staff members as well as proper disinfection of hands and of pruning and harvesting tools, are fundamental (Reingold et al. 2016). Biological control of vectors can also help limit the spread of transmitted viruses. The early installation of the phytoseiid mite *A. swirskii* in zucchini, not only reduces the infestation of *B. tabaci* in that crop species, but also significantly reduces the secondary spread of ToLCNDV (Tellez et al. 2017). Larvae of *Chrysoperla carnea* (Stephens) and adults of *Adalia bipunctata* (L.), managed to reduce the secondary spread of CABYV by *A. gossypii* Glover (Garzon et al. 2016). The elimination of infected plants within a culture can be effective in reducing the rate of secondary dispersion of insect-transmitted viruses in the early stages of an epidemic (Lecoq and

Desbiez 2012). This could be achieved by incineration or deep burial as is suggested in the case of contact-transmitted CGMMV (Dombrovsky et al. 2017).

19.2.3.3 Control of the Effect of the Infection on the Plant

Once the plant is infected, any control strategy must aim to contain the virus and thus limit the damage produced. If effective genetic resistance is available, its incorporation into commercial cultivars is probably the easiest way to control viral diseases at the farmer's level (Gomez et al. 2009). Fortunately, the search for sources of natural resistance for use in improvement programs has been successful in many cases. Intermediate or high level resistances are available against potyviruses ZYMV, *Watermelon mosaic virus* (WMV), and *Papaya ringspot virus* (PRSV), against polerovirus CABYV and also against *Cucumber mosaic virus* (CMV, genus *Cucumovirus*, family *Bromoviridae*) in melon, cucumber, and squash (Lecoq and Katis 2014). Both complete and partial resistances against CGMMV are available in cucumber (Lecoq and Desbiez 2012). Ipomovirus CVYV or crinivirus CYSDV intermediate resistant cucumber varieties provided an efficient virus control especially when combined with the use of insect-proof nets (Janssen et al. 2003). Immunity to MNSV has been associated to one recessive gene (*nsv*) in melon (Coudriet et al. 1981) and is commercially available. Alternatively, grafting on resistant rootstocks are commonly used to prevent soil-borne infection by MNSV or CGMMV. Another way of reducing virus spread and control the virus in plants is based on cross-protection inoculating young plants with mild, attenuated viral strains that induce defence mechanisms, in infected plants without causing disease symptoms. This has been achieved with attenuated ZYMV strains used on a commercial scale to protect cucurbit crops in Europe, Israel, and Hawaii (Lecoq and Katis 2014). With CGMMV, this approach protected infected cucumber and muskmelon plants against later infection with severe strains that would otherwise cause major yield losses and is currently being developed for commercial CGMMV control in Japan and Russia (Slavokhotova et al. 2016).

19.2.4 Nematodes

Nematodes are microscopic worms that inhabit soil and can cause disease-like symptoms by feeding on the roots of cultivated plants. Like soilborne fungi, they have the potential to cause issues when greenhouse crops are cultivated in soil, notably in organic production. *Meloidogyne spp*. are the species provoking damages of economic importance. Nevertheless, nematodes are hardly a problem in cucurbit crops conducted in well disinfected soils, as they normally reach pest levels in crops initiated in previously infested soils. Nematodes are also not a problem in hydroponic cultivation. Biological control of nematodes is currently difficult, which is the reason they are mostly controlled chemically when they appear during the cropping season. Effective nematicides are generally harmful for BCAs, although there are nematostatic pesticides that are more selective with BCAs and can help in maintaining nematode under tolerable levels until the end of the cropping season. At that moment, a disinfection product and/or biofumigation and solarisation techniques can be implemented to reduce or even eradicate the nematodes from the soil. Some soils are naturally suppressive to nematodes (Giné et al. 2016), due in part to the microorganisms that they contain. Several biopesticides with claimed efficacy against the root-knot nematodes are available commercially (Tranier et al. 2014), including products based on *Purpureocillium lilacinum* (Thom) Luangsa-ard et al., *B. bassiana*, and *Trichoderma* spp. (Table 19.2).

Table 19.2 Most important viruses in cucurbits, their mode of transmission and options for management

Virus	Mode of transmission	Options for management
Squash mosaic virus (SqMV)	Seed	Clean plant material
Cucumber green mottle mosaic virus (CGMMV)	Seed and mechanically	Clean plant material
Cucumber fruit mottle mosaic virus (CFMMV)		Avoiding spread through hygiene measures
Zucchini green mottle mosaic virus (ZGMMV)		
Kyuri green mottle mosaic virus (KGMMV)		Cross-protection by attenuated virus strains Use of resistant cultivars
Melon necrotic spot virus (MNSV) *Cucumber leaf spot virus* (CLSV)	Soil fungi *Olpidium sp.*	Soil disinfection grafting on resistant rootstocks
Cucurbit aphid-born yellows virus (CABYV)	Aphids (persistent)	Aphid control, intercropping with non-host plants
Zucchini yellow mosaic virus (ZYMV)	Aphids (non-persistent)	Aphid control, intercropping with non-host plants
Watermelon mosaic virus (WMV)		
Papaya ringspot virus (PRSV)		Cross-protection by attenuated virus strains (ZYMV)
Cucumber mosaic Virus (CMV)		Use of resistant cultivars
Tomato leaf curl New Delhi virus (ToLCNDV-ES)	Tobacco whitefly, *Bemisia tabaci* (persistent)	Whitefly control
Cucurbit leaf curl virus (CuLCV)		
Squash leaf curl virus (SLCV)		
Watermelon chlorotic stunt virus (WmCSV)		
Cucurbit yellow stunting disorder virus (CYSDV)	Tobacco whitefly, *Bemisia tabaci* (semipersistent)	Whitefly control Use of resistant cultivars
Cucumber vein yellowing virus (CVYV)		

19.3 Integrated Pest Management: Problems and Perspectives

19.3.1 Current Challenges

IPM is nowadays standard in most European and North American greenhouses, and is increasing in other areas of the world as well. This increase is often strongly driven by consumer and retailer demands for healthy food products with a minimum of pesticide residues, and apparently, the occasional scandal that forces growers to change their management tactics (Calvo et al. 2015; Pilkington et al. 2010). Although biological control based IPM is nowadays widely and successfully applied, there is still a huge need for further developing these systems (van Lenteren et al. 2018).

First of all, there are still several pest species that cannot be controlled effectively with available BCAs. The control of aphids for example is rather expensive without the use of insecticides. As a consequence, new strategies for enhancing biological control need to be developed. Consequently, the lack of effective BCAs for some pests and disease makes mandatory to combine the biocontrol agents with the right tools in order to get robust and complete programmes that give answer to all growers' pest and disease control needs. For example, some basic rules for chemical control, which is by far the most combined control method with BCAs are: (a) choosing harmless and selective fungicides and pesticides with BCAs for non-well biologically-controlled pests and diseases is crucial and (b) respect the safety period after pesticide applications for the release of the natural enemies. Secondly, new invasive pests and diseases continue to threaten greenhouse production areas and the absence of suitable control agents can completely disrupt existing biological control programmes targeting established pest species. Basic epidemiological knowledge is required for management of new viral diseases, such as host range information, and vector dynamics in the case of vector-transmitted viruses. Also new sources of host plant resistance are necessary that can be combined with other management options.

Thirdly, the development of an IPM system largely depends on climatic conditions, which determine which pests and diseases occur where, but also which natural enemies are well suited to the crop environment. For instance, new predatory mites might be needed to control spider mites at low temperature and humidity levels (Ferrero et al. 2010). Hence, IPM and biological control always need to be optimized for local climatic conditions.

Finally, IPM programmes are based on the implementation of several BCAs, which interactions must be known before they can be recommended.

19.3.2 Future Challenges

In conclusion, biological based IPM in cucurbits is challenging but possible and many examples of robust and successful biological based IPM systems exist. However, new challenges need to be addressed on time to avoid disruption of this robust system. New or existing challenges are; (1) invasive pest species, (2) existing pests where biocontrol needs improvement and (3) the spread of plant viruses and diseases that are difficult to manage biologically or with selective control methods. Finally, we believe that plant breeding offers great opportunities to contribute to robust IPM system for cucurbits. Powdery mildew tolerant cultivars for example largely reduce fungicide applications, which increases the use of arthropod natural enemies for pest control. One step further would be to include plant traits in breeding programmes that enhance the performance of natural enemies (Pappas et al. 2017). Also, strong efforts are required for those countries where pest and disease control is still based on pesticide use. New solutions are needed in case the introduction of commercially produced natural enemies is not allowed due to legislation, or problematic because of long transport time, or too expensive. Such solutions must be adapted to the local situation and legislation and when adopted successfully, they can help to further increase the application of biological control based IPM worldwide and thereby make the production of cucurbit fruits safer and healthier.

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Chapter 20
IPM for Protecting Leafy Vegetables Under Greenhouses

Benjamin Gard and Giovanna Gilardi

Abstract Leafy vegetables are a major production under greenhouses during winter season, grouping different species such as lettuce, chicory and spinach. Leafy vegetable are often consumed fresh, thus presentation quality of the product is of great importance. In this context, crop protection must resolve the challenging equation of a clean, undamaged product with a minimum or no pesticide use at all to preserve environment and human health. IPM strategies for protecting leafy vegetables must meet this challenge.

This chapter presents the main diseases and pests attacking leaf vegetables, with their localization on the plant and the description of the symptoms. This presentation should help the diagnosis. Then, we presented different levers that can be combined in an IPM strategy. These levers are classified in different categories, levers related to cultural practices, to soilborne pests and diseases and to airborne pests and diseases. A short description of each lever is provided, with, where applicable, an illustration of implementation and efficacy of the lever.

This chapter lists non-chemical crop protection techniques, from very well known to more recent and not yet fully adopted by the grower, that should constitute the basis to build efficient IPM strategies for leafy vegetables production.

Keywords Crop protection · Cultural practices · Pests diseases management · Pesticide reduction · Alternative techniques · IPM strategies

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20.1 Introduction

Leafy vegetables are a large category of several edible greens from different botanical species. The main species are lettuce (*Lactuca sativa* L.), chicory (*Cichorium intybus* L.), spinach (*Spinacia oleracea* L.) and the so-called baby-leaves including different types of edible greens such as wild (*Diplotaxis* spp.) and cultivated rocket (*Eruca sativa* Mill.), mustard, Swiss chard (*Beta vulgaris* L. subsp. *cicla*) and lamb's lettuce (*Valerianella olitoria* L.). Leafy vegetables can be produced under greenhouses with or without artificial light, mostly in soil, but soilless crops are increasing across Europe (Alcon et al. 2010). Such products are commercialized fresh, either whole or packaged ready-to-eat. The ready-to-eat vegetable market has undergone very fast growth in recent years; hence, leafy vegetables have become an important economic sector of vegetable production.

Leafy vegetable production is challenging because it involves short seasonal products, subjected to continuous intensification and innovation, and consumer expectation on quality of the final product is very high. Indeed, leafy vegetables must be appealing, that is to say fresh in appearance, without any damage on the leaves, and free from foreign bodies (e.g. insects). Standards of commercialization for ready-to-eat salads are even stricter as regards to the fresh market. Furthermore, concern about health and sanitary risks linked to pesticide residues is rising among consumers. Especially since leafy vegetables are often consumed fresh. On the other hand, leafy vegetables are affected by severe losses due to pests and diseases as a consequence of the dynamism and specialization of such crops, together with the lack of adequate crop rotation, climate conditions under greenhouses that are generally favorable to pest and disease development, and limitations in the use of chemicals for their control (Palumbo and Castle 2009). Additionally, the leafy vegetable sector is characterized by a rapid turn-over of varieties and the introduction of new crop species to adapt to market demands. Consequently, the likely benefits that can be obtained from growing new crop species, also lead to the risk that newly introduced crops will be accompanied by new pathogens.

The current regulatory framework increases the complexity of pest and disease management. European regulation, in particular through the Framework Directive 2009/128/EC (European Commission 2009a, b) promotes the reduction of the use of pesticides and the development of alternative measures by applying the principles of IPM. In addition, new commercialization standards limit the numbers of active substances detected on the final product. These constraints reduce the number of active substances available for crop protection, which may result in the repeated use of chemicals with the same active ingredient, consequently increasing the risk of resistance appearance in pest populations (Leadbeater and Gisi 2010; Lamichhane et al. 2016b). Nonetheless, IPM levers available for leafy vegetables are numerous, and can be combined to improve their efficacy. Attempts to control pest populations include resistance genes, biological control, crop rotations and a variety of cultural practices aimed at reducing pest and disease density in the environment, a factor that directly influences the efficacy of the control measures used (Katan 2017).

Hence, building IPM packages for the leafy vegetable production sector can help to reduce pesticide use and residues, and it is mandatory to guarantee successful long-term pest and disease control.

20.2 Main Diseases and Pests

For good implementation of IPM, correct diagnosis and good knowledge of which pests and diseases can attack leafy vegetables and at which stage of the crop cycle it happens, are essential for the adoption of effective preventive measures. For instance, the multiple mechanisms by which pests and pathogens survive and disseminate (e.g. seed-borne pathogens) represent both opportunities and difficulties in their management. There is a large number of pests and diseases attacking leafy vegetables. In this section, the purpose is not to be exhaustive but to give an overview of the main diseases and pests affecting leafy vegetables causing significant damage and/or economical losses, focusing mainly on fungal and oomycete pathogens and pests. Pests and diseases are further presented according of the main attacked organs and their symptoms. This presentation follows the same logic that one whom wants to realize a diagnostic on leafy vegetable might follow. Main organs to consider for leafy vegetables are leaf, collar and roots.

20.2.1 On the Roots

20.2.1.1 Diseases

Fusarium oxysporum Schlecht. emend. Snyder and Hansen and *Verticillium* sp. are soilborne fungal pathogens that penetrate the root and colonize the vascular system of the plant. The main symptoms are growth reduction, leaf yellowing and plant wilting. Verticillium wilt can be confused with Fusarium wilt; however, in plants affected by Fusarium wilt the vascular discoloration is reddish to brown, while plants affected by Verticillium wilt are generally greenish-brown (Subbarao et al. 2017). Verticillium wilt, incited by *V. dahliae* Kleb., has been observed on lettuce, chicory and spinach and damage is severe when air and soil temperatures are around 20–25 °C. In the case of most of the Fusarium and Verticillium wilt causal agents, seed transmission of the pathogen plays an important role (Gullino et al. 2014).

Different *formae speciales* of *F. oxysporum* have been reported on leafy vegetables. *Fusarium oxysporum* f. sp. *lactucae* J.C. Huber et Gerik, which causes lettuce wilt, has increasingly been observed in lettuce cultivation areas worldwide (Matheron and Gullino 2012; Gullino et al. 2019). It has recently spread to the Netherlands (Gilardi et al. 2017a) and France (Gilardi et al. 2017b), UK, Ireland (Taylor and Clarkson 2018), and Belgium (Claerbout et al. 2018). The presence of four races of this pathogen is known: race 1 is the most widespread, races 2 and 3 have been reported to occur in Taiwan and Japan, while a recent outbreak of race 4 affects the Netherlands, UK, Ireland, Belgium, and Italy (Gilardi et al. 2019). Fusarium wilts also have been observed on other salad crops. Wilt of *E. sativa* and *Diplotaxis* spp. is attributed to *F. oxysporum* ff. spp. *raphani* J.B. Kendr. & W.C. Snyder and *conglutinans* (Wollenw.) W.C. Snyder & H.N. Hansen, the first of which is more frequently detected. It also affects other genera belonging to *Brassicaceae*, such as cabbage, brussel sprouts, broccoli, turnip, and radish (Garibaldi et al. 2006). *F. oxysporum* f. sp. *spinaciae* (Sherb.) W.C. Snyder & H.N. Hansen is a serious constraint to spinach and beet production worldwide. The Fusarium wilt agents from spinach, beet and Swiss chard are classified as race 1 and race 2, respectively (Armstrong and Armstrong 1976).

Pythium wilt (*P. tracheiphilum* Matta) and damping-off pathogens (*P. ultimum* Trow, *P. sylvaticum* W.A. Campb. & F.F. Hendrix, *P. irregulare* Buisman, Mededelingen, *P. aphanidermatum* (Edson) Fitzp., *P. dissotocum* Drechsler) causes pre or post emergence losses in leafy vegetables (Gilardi et al. 2018a, b; Gullino et al. 2019). Generally, they are considered 'minor pathogens', as they act as parasites on root tips or root cortical cells, but may become highly destructive in monoculture, causing growth decline, such as "soil fatigue" and replant diseases (Katan and Gamliel 2012; Katan 2017; Gamliel 2018).

20.2.1.2 Pests

Root knot nematodes (*Meloidogyne* sp., RKNs) are very polyphagous soil pests, attacking leafy vegetables. It is a growing concern for growers, for example in the South of France, where more than 40% of vegetable farms reported attacks due to RKNs (Djian-Caporalino 2012). When it penetrates the root, the female induces the formation of a root-knot gall, inside which it completes its life cycle. Root knots weaken the plant, which is not able to develop until commercial stage, reducing crop yield. Lettuce root aphids are also responsible for root damage. The main species is *Pemphigus bursarius* (L.). Root aphids produce a whitish waxy secretion on the root. The main aerial symptoms are yellowing leaves and plant wilting.

20.2.2 On the Collar

20.2.2.1 Diseases

Gray mold (*Botrytis cinerea* Pers), sclerotinia (*Sclerotinia minor* Jagger, *S. sclerotiorum* (Lib.) de Bary) and *Rhizoctonia solani* (J.G. Kühn) R.T. Moore are pathogens that attack the collar and the basal leaves, and can cause the destruction of the collar and the death of lettuce and chicory plants. *B. cinerea* and *S. minor* are uncommon in greenhouse cultivations of spinach, Swiss chard, lamb's lettuce, wild and cultivated rocket, while, *S. sclerotiorum* is becoming a pathogen that causes serious damage to the production of wild rocket. Symptoms of sclerotinia and gray mold rot are similar: the initial symptom is the wilting of the infected leaves, then the collar rots and the whole plant wilts and decays within the cropping cycle or even in a few days. Under moist conditions, tissues infected by gray mold show brownish sporulation whereas *Sclerotinia* spp. produces a fluffy white mycelium that ultimately develops into sclerotia of different sizes, depending on the species and environmental conditions. Due to the wide host range, *R. solani* can have a strong impact in most leafy vegetable production systems. Rhizoctonia causes seed rot, basal rots, and foliar spots on the midribs of the lower leaves of different leafy vegetable crops. Generally, attacks by *R. solani* on lettuce, rocket, lamb's lettuce, spinach and Swiss chard develop as circular areas of infected plants. The infections of *B. cinerea* on lettuce (Sowley et al. 2010) and *R. solani* on chicory and spinach (Neergaard (1958) may arise also from contaminated seeds.

These pathogens may cause severe losses under conditions of cool weather and high moisture. They are problematic on leafy vegetables because mainly develops at the end of the crop cycle.

20.2.2.2 Pests

Voles can be responsible for important damage in greenhouse crops. By consuming the collar of young lettuce, it destroys the plant which can lead to the destruction of an important part of the crop. Thread caterpillar (*Agrotis* sp.) and wireworms (*Agriotes* sp.) attack the collar, a few centimeters under the soil surface. The larvae of these two pests penetrate the collar and the main root of seedlings and adult plants, causing wilting and plant death.

20.2.3 On the Leaves

20.2.3.1 Diseases

Downy mildews are a group of closely related pathogens that are recognized as some of the most destructive in commercial production, reflected by their highly specialized association with host plants, their specialized spore structures for wind dispersal and long-range transport, and their high "evolutionary potential" for mutation and genetic variation. *Bremia lactucae* Regel is generally considered a major problem for lettuce cultivated in greenhouses. Leaves develop a white powder on the underside, and then they dry out and die. The disease is very rapid and can destroy hundreds of plants in a couple of days. Some other common agents of downy mildew of leafy vegetables include *Peronospora farinosa* f. sp. *spinaciae* Byford (syn. *P. effusa* (Grev.) Rabenh.) on spinach¸ *Hyaloperonospora (Peronospora) parasitica* (Pers.) Constant on rocket salad (wild and cultivated) and other chosen crops from the Brassica family (broccoli, cauliflower, swede, oilseed rape), *Peronospora valerianellae* Fuckel on lamb's lettuce, *P. farinosa* on Swiss chard that are usually minor diseases, but may cause significant damage if environmental conditions are favorable.

Additionally, species in the genus *Alternaria* and *Phoma* represent a potential threat to leafy vegetables in several production areas. In recent years (2010–2016), leafy vegetables have been found to be new hosts for many foliar pathogens. New foliar pathogens of salad crops include *Plecosphaerella cucumerina* (Lindf.) W. Gams on wild rocket, endive and lamb's lettuce, *Fusarium equiseti* (Corda) Sacc. on wild and cultivated rocket and lettuce, *Albifimbria* (syn. *Myrothecium*) *verrucaria* (Albertini & Schweinitz) L. Lombard & Crous on spinach and wild rocket, *Paramyrothecium roridum* (Tode) L. Lombard & Crous on lamb's lettuce, *Allophoma tropica* (R. Schneid. & Boerema) Q. Chen & L. Cai on lettuce, *Alternaria japonica* Yoshii on wild and cultivated rocket (Gilardi et al. 2018a, b; Gullino et al. 2019), *Stemphylium beticola* Woudenb. & Hanse on spinach (Gilardi et al. 2018b; Gullino et al. 2019). Leaf necrosis caused by these pathogens are very similar, and often varies depending on the age and the nutritional status of the plants. Symptoms can also be confused with those caused by other pathogens such as *B. cinerea*.

Some of the new pathogens have been found to be seed transmitted and typical of tropical areas, and are thus favored by the rises in temperature that currently characterize the climate change scenario (Gullino et al. 2014, 2018).

Bacterial leaf spot (*Pseudomonas cichorii* and *Xanthomonas axonopodis* pv. *vitians*) is mainly present on older and basal leaves, toward the margins of the leaves, under cool temperatures (optimal 23 °C). Bacterial soft rot is caused by *Pectobacterium carotovorum* subsp. *carotovorum* (syn. *Erwinia carotovora* subsp. *carotovora*) on different leafy vegetables under favorable temperatures of 25–30 °C. These diseases develop in high humidity conditions, mainly after a stormy episode. Hence, the incidence of these diseases is higher in open-field production compared to greenhouses.

The main viruses attacking lettuces are the lettuce mosaic virus (LMV), the lettuce ring necrosis agent (LRNA), the Mirafiori lettuce virus (MiLV) and lettuce big-vein associated virus (LBVaV). MiLV and LBVaV are transmitted by the soil fungus *Olpidium virulentus* (Woronin) P.A.Dang. These last two viruses are responsible for the lettuce big-vein disease symptoms, which are typical of greenhouse production because symptoms appear only when the temperature is below 10 °C. Other viruses exist, but they are less common in greenhouse production.

20.2.3.2 Pests

Aphids are the main pest on leafy vegetables under greenhouses. They are present during the whole season. Several species are able to develop on leafy vegetables such as *Nasonovia ribisnigri* (specific of lettuce crop), *Myzus persicae, Aphis gossypii, Macrosiphum euphorbiae, Hyporomyzus lactucae* and *Aulacorthum solani* (Blancard 2013). Even if aphids do not cause important damage due to sap feeding, they can transmit several viruses and their presence on leafy vegetable is problematic. Firstly, because foreign bodies are prohibited in commercialized products, and secondly because the honeydew excreted by aphids induces the development of sooty mold which degrades the quality and appearance of the product. This problem is even more important in ready-to-eat salads. Caterpillars (*Autographa gamma*, *Helicoverpa armigera*, *Spodoptera littoralis*) can cause feeding damage to lettuce and depreciate product quality. Thrips (*Thrips tabaci, Frankliniella occidentalis*), and leafminer (*Lyriomiza* spp.) are less problematic. They are occasionally present on the crop but can cause important damage in absence of appropriate control measures. Moreover, *F. occidentalis* is a vector of the tomato spotted wilt virus (TSWV).

20.3 IPM Levers and Available Strategies

For leafy vegetables grown under greenhouses, several IPM levers can be mobilized to control pests and diseases, to avoid or limit, as an ultimate alternative, the use of chemical pesticides. IPM levers can be classified in different categories, which involve several stages of the production system. These levers can have broad or narrow spectrum of action against pests and diseases, and several levers can affect the same target. As some of these techniques can have partial effects, it is necessary to combine levers from different categories to obtain acceptable control of the target.

20.3.1 IPM Lever Categories and Their Targets

20.3.1.1 Cultural Control

Agronomic practices or cultural management methods can be adapted to reduce pest and disease damage. It is important to bare in mind that these techniques aim to reduce the primary inoculum of diseases and to limit the development of pest populations. Cultural control acts directly on the crop environment, firstly to limit pest and disease outbreaks, and secondly, to set the crop in the most favorable conditions to grow, and hence to be well suited to respond to pest and disease attacks. Moreover, it may help to create suitable conditions for the presence pest natural enemies. Cultural control includes several agronomic practices such as crop residue management, climate management and fertigation. By limiting the risk of pest and disease outbreaks, and lowering primary inoculum, cultural control enhances the efficacy of biological control and other alternative techniques.

Optimal soil preparation avoids creating unnecessary stresses to the crop, like root asphyxia due to bad soil structure or an excess of water. The principle is to prepare the soil so that it is as level as possible and well-structured (mid-coarse particles) to create optimal conditions for the crop and its root system to develop. This technique is one of a set of agronomic practices that aim to improve plant functioning and hence its ability to defend itself against biotic and abiotic stresses. For instance, many outbreaks of damping-off may be managed by providing drier conditions for seedling development. Moreover, soil mulching with polyethylene film provides a positive effect against several soilborne and foliar pathogens. For instance, in the early winter, covering the soil surface with polyethylene film diminishes occurrence of gray mold and downy mildew in several vegetable plants, by affecting night-time soil and air temperature, thus reducing the incidence of water condensation on the leaves compared to the unmulched soil (Elad 2000; Cohen et al. 2006).

Intensive land use is common in greenhouse production. In lettuce production, up to 3 cycles of production can be achieved in a year. This intensification increases soil depletion, and the frequency of soilborne and foliar diseases rises (Gamliel and van Bruggen 2016; Gilardi et al. 2018a, b). **Crop rotation** can help reduce soilborne diseases specific to the main crop and then reduce soil infestation. Different possibilities are available for growers to introduce more plant diversity into the crop system, for instance, by diversifying the summer crop, or sowing green manures or replacing one crop of lettuce by another winter crop. For instance, Hao et al. (2003) showed that rotation of lettuce with broccoli can reduce the incidence of lettuce drop caused by *S. minor*. This strategy should be particularly effective against host-specific pathogens, such as *formae speciales* of *F. oxysporum*. However, the ability of the lettuce Fusarium wilt agent to colonize the root system of broccoli, cauliflower and spinach, which are commonly grown in rotation with lettuce, should be taken into account. In order to ensure a minimum risk of economic losses due to lettuce Fusarium wilt, more than 34 months of fallow are needed (Scott et al. 2014). The history of the crop system and the chemical and physical characteristics of soil, favoring the development of Fusarium wilt, could help in the choice of the rotation interval between crops, with the possible use of bioassays to predict Fusarium wilt risk. For instance, because soil pH is generally negatively correlated with Fusarium wilt severity, a 5-year rotation in alkaline soil (7.8–8.0 pH) strongly reduces Fusarium wilt of spinach, while in acid soil (5.8–6.3 pH) *F. oxysporum* f.sp. *spinaciae* is still persistent after 8–15 years of rotation (Gatch and du Toit 2015). The broad host range of *S. sclerotiorum*, *S. minor* and *R. solani* significantly limits the efficacy of crop rotation in different leafy vegetable crop systems. **Controlling humidity** in leafy vegetables production is an important lever against pathogens. With appropriate management of the aeration in the greenhouse, it is possible to reduce the time of wetness of the leaf, and at the same time, create unfavorable conditions for the development of pathogens. This technique is useful against both foliar and soil-borne pathogens such as agents of downy mildew, gray mold, sclerotinia and damping-off (*Pythium* and *Rhizoctonia* spp.). Several actions can be carried out to control plant climate, including: (i) fostering aeration in the greenhouse by opening the ventilation system as much as possible, (ii) irrigating the crop in the morning, during sunny and/or windy days, so that the foliage can dry out quickly, (iii) managing plant density to increase space between plants and foster air circulation. Then, developing new approaches such as replacing spray irrigation by drip irrigation to avoid foliage wetting can also help to reduce airborne diseases.

Nitrogen fertilization has been shown to influence susceptibility of the crop to pests and disease. For instance, nitrogen levels influenced plant sugar contents in

Table 20.1 Method for optimizing management of nitrogen supply in lettuce crop grown under greenhouses

Crop stages	Nitrogen crop needs + buffer stock (kg/ha)	Nitrogen remaining in the soil (kg/ha)	Quantity supplied to the crop
Planting (P)	30	X1	30 – X1
P+4 weeks to P+7 weeks	80–90	X2	80–90 – X2

Adapted from Raynal et al. (2014b)

lettuce, which are linked to plants defense ability against two main pathogens *S. sclerotiorum* and *B. cinerea* (Lecompte et al. 2013). Furthermore, excessive nitrogen fertilization increases the susceptibility of lettuce crops to downy mildew, *B. cinerea*, *S. sclerotiorum*, slugs and aphids (Lecompte et al. 2013; Raynal et al. 2014a). Over-fertilization also induces rapid growth, and thin foliar tissues production, which weakens the foliage and thus facilitates the penetration of the pathogens. Fusarium diseases are generally suppressed by nitrates, through mechanisms mainly related to an increase in pH values in the rhizosphere (Jones et al. 1989). Applying calcium to the root can also have a noticeable effect on suppressing Fusarium wilts; for instance $Ca(NO_3)_2$ was more suppressive than the ammoniacal form (NH_4NO_3) (Woltz and Jones 1981; Jones et al. 1989; Huber and Thompson 2007). Micronutrient availability also affects the incidence of Fusarium wilts; e.g. low iron levels in the growing medium may reduce *F. oxysporum* severity (Woltz and Jones 1981).

Hence, management of fertilization can reduce susceptibility of the crop to several pests and diseases. Based on experimental results, Raynal et al. (2014b) proposed a fertilization plan for lettuce grown under greenhouse. N fertilization is divided into two applications in order to provide timely amounts according to the plant needs and taking into account nitrogen residues in the soil. A first input at planting, with an objective of 30 kg/ha is supplied, taking into account nitrogen reserves present in the soil. The second input is added 3–4 weeks after planting, with an objective of 90 kg/ha, taking into account nitrogen reserves in the soil (Table 20.1).

Finally, **Physical barriers** can be used against airborne pests to reduce their entry into the greenhouse. Insect-proof nets can be installed on the openings of the greenhouse for protection against aphids, and lepidopteran pests. Hence, this technique may help to reduce sprays of insecticide by delaying the first entry of pests, and reducing damage to the crop. However, the use of insect proof-nets could have a negative impact on leafy vegetable production. Indeed, it can reduce ventilation into the greenhouse, creating favorable conditions for pathogens development. Furthermore, insect-proof nets also limit the colonization of the crop by natural enemies from outside.

Plastic covers of greenhouses may be used as a barrier against pests, using ultraviolet-absorbing screens or colored plastic that influence visual stimuli and by consequence pest behavior, and its ability to find its host plants. For instance, Legarrea et al. (2012) demonstrated that UV-absorbing plastic covers reduced the population growth and dispersal of *M. euphorbiae* in lettuce crops. The positive effect of UV-reflective mulch to manage TSWV on cos lettuce in Spain was also demonstrated (Diaz et al. 2006). Hence, it seems possible to reduce primary infestation by manipulating plastic covers of greenhouses.

20.3.1.2 Healthy Seed and Seedlings

Several pests and diseases can be transmitted by seed or seedlings. The fact that several pathogens affecting leafy vegetables are seed-borne is cause for considerable concern (Gullino et al. 2014). Consequently the first preventive strategy that should be considered by growers is the use of healthy seeds and seedlings. In order to further reduce the risk from seed-borne pathogens, it is recommended that stock seeds should undergo precautionary decontamination treatments. Chemical treatments have successfully been applied to vegetable seeds and are in commercial use for leafy vegetables against different seed-borne pathogens (Munkvold 2009; Koch and Roberts 2014). Heat treatments with hot water, aerated steam or dry heat can be very effective, but they need to be optimized due to the differences in temperature and time required for different target pathogens and crops (Nega et al. 2003; Koch and Roberts 2014). For instance, hot water seed treatments reduce or eliminate *Cladosporium variabile* (Cooke) G.A. de Vries (40 °C for 10 min), and *V. dahliae* (55 °C for ≥30 min or 60 °C for ≥10 min) on spinach seed without damaging seed germination, while 55 or 60 °C for ≥10 min are necessary against *Stemphylium botryosum* Wallr., even if the pathogen is not eradicate in highly infected seed lots (du Toit and Hernandez-Perez 2005). Unfortunately, there are only a few examples of commercial use of seed treatments based on microorganisms and essential oils despite the intensive research in this field. In the case of *F. oxysporum* f.sp. *lactucae*, the bacterial (*Pseudomonas* spp.) and fungal strains (non-pathogenic strains of *F. oxysporum* 251/2 and MSA35; *Trichoderma gamsii* + *T. asperellum*) applied as wet or dry powder on lettuce seeds resulted in reducing the pathogen present on the surface of the seed, but did not control internal infection (Lopez-Reyes et al. 2014). Among several microorganisms tested by Cummings et al. (2009), *Streptomyces griseoviridis* reduced the contamination of spinach seeds caused by *S. botryosum*, *Verticillium* and *Alternaria* spp. by 88%, 74% and 84%, respectively, while it was not effective against *F. oxysporum*. Also natural products, such as thyme and savory essential oils, when applied by spraying lettuce seeds at 1%, were effective against *F. oxysporum* f.sp. *lactucae* (Lopez-Reyes et al. 2014).

Aphids and thrips can also infest crops from contaminated seedlings. Early infestation can be very problematic, because it may lead to quick building of high population of these pests, responsible of high damage to the crops, and that will be difficult to control. Furthermore, the risk of virus transmission is increased. Correct inspection of sanitary conditions at the reception of seedlings is essential. Also, choosing seeds and seedlings with phytosanitary passport and insurance on the quality and health of the seed is necessary to avoid contamination.

20.3.1.3 Optimal Choice of the Variety

Plant morphology can play a role in reducing susceptibility of leafy vegetables to collar rot pathogens, because erect basal leaves are less susceptible to rots. Hence, efforts to develop lettuce resistant to drop are in progress; a possible association between horticultural type and resistance to *Sclerotinia* has been observed for lettuce with the highest levels of resistance showed by stem or romaine-type with upright growth habits and early-bolting (Grube and Ryder 2004). However, resistance genes are crucial for the control of several pathogens. For instance, host resistance is the most likely means of controlling the bacterial disease on lettuce, so breeding lines resistant to bacterial leaf spot are intensively screened (Lebeda et al. 2014). In spinach and lettuce, several resistance genes are available from wild species against diseases, especially against downy mildew (Maisonneuve 2003). Strong breeding efforts are made for introgression of these resistance genes into new commercial cultivars (Farrara et al. 1987; Correll et al. 2011). Databases are now available on genetic resources of leafy vegetables, and creating germplasm collections contributes to improving breeding programs (Lebeda et al. 2004). Resistance against downy mildew is very effective, and widely used by growers. Unfortunately, resistance genes are regularly overcome by new virulent phenotypes of the pathogen. In 2018, 20 races (Bl:16-35EU) with significant virulence on lettuce were officially identified by the International Bremia Evaluation Board, in Europe. Indeed, the use of mono or oligogenic resistances that are widely deployed in the field may decrease the durability of the resistance, ever forcing breeders to find and introgress new genes of resistance (Lebeda and Schwinn 1994; Feng et al. 2014). In the end, this could complicate the practical application of plant resistance. This is the case for several cultivated lettuce cultivars belonging to the Batavia and Romaine type that are resistant or at least tolerant to Race 1 of *F. oxysporum* f. sp. *lactucae* (Scott et al. 2010a, b; Matheron and Gullino 2012; Gilardi et al. 2014a; Gullino et al. 2019) and *V. dahliae* (Vallad et.al 2006). Their effective use is complicated by the presence of new races of these pathogens (Fujinaga et al. 2005; Vallad et.al 2006; Gilardi et al. 2017a; Claerbout et al. 2018). Beside the genetic background of the plants, the expression of Fusarium wilt symptoms are strongly influenced by factors such as the aggressiveness of the pathogen isolates, soil temperature and age of the plants. For instance, for several susceptible cos lettuce cultivars, losses ranged from 0% to 1.8% due to lettuce Fusarium wilt when soil temperatures ranged from 11 to 14 °C, whereas the same cultivars suffered disease losses ranging from 51% to 100% in the same field when soil temperatures ranged from 21 to 32 °C (Scott et al. 2010a, b). Thus growing susceptible lettuce cultivars at times when soil temperatures are cooler and less favorable for development of Fusarium wilt could be envisioned. Although the use of resistant cultivars against lettuce fusarium wilt is one of the optimal control measure suggested, there is to consider that some lettuce cultivars with resistance to Fusarium wilt may allow inoculum levels to increase with a significant impact on subsequent plantings of susceptible cultivars (Scott et al. 2010a, b; 2014). Unfortunately, many of the commonly used spinach cultivars have little or no resistance to Fusarium wilt (Correll et al. 1994). While, in the case of rocket, despite intensive research that has been conducted to select resistant cultivars against Fusarium wilt causal agents, it is difficult to adopt this strategy mainly due to the high variability in virulence of the pathogen isolates (Gilardi et al. 2007, 2014a; Gullino et al. 2019).

Concerning pests, a resistance gene against lettuce aphid *N. ribisnigri* has been available in commercial cultivars since 1997 (Sauer-Kesper et al. 2011). This resistance is effective against biotype 0 of *N. ribisnigri*, which shows difficulty in starting colonies on resistant plants. Hence, resistance reduces pest population density. Nonetheless, a biotype 1, able to overcome the resistance was identified in 2007 and has spread widely through Europe. The existence of resistance in wild *Lactuca* has been reported for biotype 1 of *N. ribisnigri* (Thabuis et al. 2011) and for other aphids attacking lettuce crops, such as *P. bursarius*, and *M. euphorbiae* (Lebeda et al. 2014), but the corresponding genes have not been introduced in commercial cultivars yet. Resistance is also available against root knot nematode (Gomes et al. 2000), but, there is no commercial cultivar currently available in Europe. Wild *Lactuca* represent an important reservoir of genes of resistance, with different levels of tolerance, to various pests. Research and breeding efforts must continue to provide growers with more resistant cultivars and create a strong base for building IPM strategies.

20.3.1.4 Alternative Practices for Soil Pests and Diseases Management

Management of soilborne pests, diseases, and weeds can be achieved through various physical and biological techniques, to replace the use of chemical fumigation or herbicides. These technics have been described in detail in a previous chapter (Gamliel 2018). In this chapter, we focus on their use in IPM strategies for leafy vegetable production.

Most of these techniques have a broad spectrum of action. **Soil solarization** has shown interesting results to control pests, diseases and weeds in crop systems involving lettuce (Hasing et al. 2004; Patricio et al. 2006; Katan and Gamliel 2012). Solarization is effective against *O. virulentus*, which transmits viruses to lettuce, and against root knot nematodes (*Meloidoigyne* spp.) which attacks lettuce roots. Solarization for 30 days reduced the incidence of lettuce fusarium wilt by up to 91% (Matheron and Porchas 2010). In field studies by Fernández-Bayo et al. (2018), its combination with digestate-organic soil amendments further improve the soil inoculum density inactivation of *F. oxysporum* f. sp. *lactucae*. Despite the lack of information for leafy vegetables, there is evidence for the capacity of solarization and *Trichoderma harzianum* to systemically induce resistance to foliar diseases such as gray mold and powdery mildew in various plants (Okon Levy et al. 2014). Indeed, the involvement of induced plant defence mechanisms by *T. harzianum* in control of *B. cinerea* on lettuce was previously reported by De Meyer et al. (1998). For instance, *T. harzianum* T39 soil treatment provided 25–100% reduction of grey mold symptoms on lettuce, causing a delay or suppression of lesion formation.

Another technique consists in **applying a massive amount of organic matter** (compost, animal manure, vegetable crop residues, and organic amendments) to the soil, to improve soil disease suppression against different soilborne pathogens with a variable degree of success (Blok et al. 2000; Bonanomi et al. 2007; Janvier et al. 2007; Gamliel 2018). Currently, most of the studies about the effect of organic matter against soilborne pathogens of lettuce and other leafy vegetables are from microcosm in controlled environment. Thus, extra evaluations in field, under more realistic conditions, are needed. For instance, Smolińska et al. (2016) provided the evidence of the beneficial effect of the incorporation into the soil of organic agro-industrial wastes based on dry onion rind, apples, strawberry pomaces and rapeseed meal overgrown with selected strains of *Trichoderma* sp. on the incidence of lettuce drop and survival rate of sclerotia of *S. sclerotiorum*. Gilardi et al. (2016b) applied *B. carinata* (pellets and flour) and compost 30 days before planting lettuce which led to promising results in Fusarium wilt control. Finally, in microcosm simulation, Kotsou et al. (2004) demonstrated that soil treatment with olive oil mill wastewater induced a significant disease suppressiveness effect against *R. solani* on lettuce, for a prolonged period of time. Among organic amendments, the use of **compost** is a partially established commercial practice, even if there is scientific evidence of improved crop production, soil health, nutrient levels, organic matter, plant growth and suppression of disease caused by soilborne plant pathogens (Noble and Coventry 2005; Termorshuizen et al. 2006; Bonanomi et al. 2007, 2010; Mehta et al. 2014). The raw material for composting is generally a waste material of agricultural or municipal source; the compost replaces fertilizers and improves soil structure in the case of field applications or may replace peat, in the case of container media (Blok 2016). There are several reports on compost-based suppression ranging from 20% to 70% against Fusarium wilts of basil, lettuce, rocket and spinach (Reuveni et al. 2002; Escuadra and Amemiya 2008; Ferrocino et al. 2014; Gilardi et al. 2014b; 2016b), Pythium damping off (Scheuerell et al. 2005) and *S. sclerotiorum* on lettuce (Lumsden et al. 1983), while *R. solani* is considered to be the most difficult soilborne pathogen to control with composts (Scheuerell et al. 2005; Bonanomi et al. 2007). Inconsistent levels of plant disease suppression, due to the nature of the raw materials from which the compost is prepared, of the composting process used, of the maturity and quality of the compost, of different methods of application (rate and frequency), complicate its practical use. For instance, the frequency of compost application should be taken into account considering its possible short-time effect (Escuadra and Amemiya 2008; Gilardi et al. 2016b). Moreover, on spinach grown in a continuous cropping system, the soil amended with composts became suppressive to *F. oxysporum* f.sp. *spinaciae* on the second and third crop cycle (Escuadra and Amemiya 2008). Thus, repeated addition to soil of low to moderate amounts of compost is recommended (10–20 $t.ha^{-1}year^{-1}$). Moreover, the use of compost is suggested under IPM, for example after a soil disinfestation treatment to avoid possible re-infestation of soil by plant pathogens. To improve the consistency of disease control using composts, biocontrol agents have been added to compost amendments. Moreover, mixtures of bacterial and fungal BCAs are generally more effective than single BCAs in inducing suppression, as reported against *Rhizoctonia* and *Pythium* (Ryckeboer et al. 2003; Noble and Coventry 2005; Termorshuizen et al. 2006).

Despite the important role of organic amendments in maintaining plant health within an IPM framework, there is an issue for the potential food safety risks associated with the use of animal manure and compost, related to the potential microbial and chemical contamination and the internalization of human pathogens on lettuce plants (Chitarra et al. 2014; Alsanius et al. 2016). The need for extra management is required especially for leafy vegetable crops. B**iochar** that is a heterogeneous material generated through pyrolysis from a wide range of organic materials has received increased interest for possible use under IPM. Indeed, it has been shown to induce resistance in plants against a variety of foliar as well as soilborne pathogens and bacteria, with a beneficial impact for example on lettuce yield (Graber et al. 2014; Nieto et al. 2016; Frenkel et al. 2017).

The introduction of **green manures in crop rotation** could be another possibility to improve soil health (Gamliel 2018). Green manures can act with different modes of actions against soilborne pests and diseases. Firstly, species with a strong root system such as sorghum have positive effects on soil structure. Then, the aboveground biomass produced, when it returns to the soil stimulates microbial activity and biomass which may benefit to beneficial microbial communities and participate to build up of soil suppressiveness (Gamliel 2018). Secondly, some species used as green manure have a biocidal effect, when buried into the soil. This technique is called biofumigation (Matthiessen and Kirkegaard 2006). Species containing glucosinolate (Brassiceae and Allioidaee), and species containing cyanoglucosides (sorghum) have been identified as interesting green manure to grow for biofumigation purposes (Collange et al. 2011). After hydrolysis; glucosinolate and cyanoglucoside release biocidal compounds, respectively isothiocyanates and hydrogen cyanide, which act as a biofumigant against soilborne diseases and nematodes attacking leafy vegetables. Then, green manures can also act as a trap cover crop to reduce nematode populations in the soil (Navarrete et al. 2016). The nematodes are able to penetrate the root of the plant but the reproduction is prevented due to resistance mechanisms or the green manure is destroyed before the life cycle of the nematode is completed. Recent work has shown that, sorghum is a host plant for root knot nematodes and can be used as a trap cover crop (Goillon et al. 2016).

In the case of intensive agricultural systems, biofumigation can also be achieved by incorporating seed meals (i.e. *Brassica carinata* seed meal) or dried plant material treated to preserve isothiocyanate activity, hence allowing to save time and space. However, Lu et al. (2010) and Mazzola et al. (2012) reported a possible negative effect of their use due to an increase of pathogen inoculum potential when the substrate serves to sustain saprophytic growth of pathogens such as *Pythium* or when brassicas, used as an intercrop, are susceptible hosts of the target Fusarium wilt agent of rocket.

In order to obtain greater effectiveness in controlling soilborne pests and diseases, soil solarization and biofumigation can be combined. Positive effect of such a combination has been demonstrated to control soilborne diseases of lettuce (Pane et al. 2012; Garibaldi et al. 2010; Klein et al. 2011; Gilardi et al. 2014b). The combination of amendments with solarization can also be effective to reduce the length of soil solarization in order to encourage more growers to adopt this technique. Some examples of the positive effect of chicken compost and green compost, alone or combined with soil solarization, have been reported against *Meloidogyne incognita* and *Pythium ultimum* on lettuce and against Fusarium wilts of rocket and basil, respectively (Gamliel and Stapleton 1993; Gilardi et al. 2014b). Moreover, there is potential to optimize digestate amendment combined with soil solarization in the presence of sub-lethal soil temperatures to improve lettuce fusarium wilt control, *Brassica nigra* weeds inactivation and soil quality (Fernández-Bayo et al. 2018).

Furthermore, the adoption of alternative crop systems may have contrasting effects on different pests and diseases. For instance, a positive effect of sorghum green manure observed against *Sclerotinia* on lettuce depended mostly on a shortened sorghum cropping period and by limited irrigation (Collange et al. 2014). Moreover, the combination of two lettuce cycles, an annual crop of melon, and the combination of sorghum green manure and solarization alternatively, allowed the control of *Sclerotinia* but was associated with a high level of nematode attacks (Collange et al. 2014).

Another cultural measure that is increasingly investigated to reduce inoculum of soilborne diseases is **anaerobic soil disinfestation** (ASD) (Blok et al. 2000; Shennan et al. 2014; Gamliel and van Bruggen 2016; Shrestha et al. 2016). The ASD process is based on the addition of labile carbon sources to the soil in order to stimulate microbial growth and respiration, followed by irrigation, and the covering of soil with plastic films, thus permitting a reduction in the soil oxygen levels for 3–10 weeks of treatment (Blok et al. 2000; Shennan et al. 2014). This technique has also shown potential to control plant parasitic nematodes (effect ranging from 15% to 56%) (Shrestha et al. 2016). ASD is effective against bacterial, oomycete or fungal pathogens and pests through different mechanisms, probably due to the release of various volatiles in the ASD treated soil and to microbiological changes. The choice of effective, cheap and easily available C-sources is of particular importance (Shennan et al. 2014; Shrestha et al. 2016). Among pathogens suppressed by ASD, interesting results have been observed against *Fusarium* spp., *Rhizoctonia*, *Verticillium*, *Phytophthora* and *Pythium*, while ASD is generally less effective against *S. sclerotiorum* (Shrestha et al. 2016) and its application would be useful for leafy vegetable crop systems. For instance, ASD provided 87% reduction of *F. oxysporum* f.sp. *spinaciae* using *Brassica juncea* as C-sources (Mowlick et al. 2013). However, ASD needs to be further evaluated under realistic conditions for protected leafy vegetables crops, considering that the period of treatment should be reduced to less than 3 weeks when temperatures range from 16 to 30 °C (Shrestha et al. 2016). ASD has also been found to be effective against weeds, providing a reduction of 32–81% (Shrestha et al. 2016). Other specific techniques against weeds can be used. For instance, false seedbed combined with mechanical weeding can control weeds without using herbicides. Plastic mulch can be used to cover the soil to prevent weeds from germinating, hence reducing the need to spray herbicides.

20.3.1.5 Biological Control

Biological control using microorganisms has been intensively investigated for leafy vegetables. Microorganisms can be used to control pests because they produce different types of toxins that, once ingested by the pests lead to their death. One common biopesticide is *Bacillus thuringiensis*, which is widely used in fruit and vegetables crops, and in leafy vegetables particularly to control lepidopteran caterpillars. Nuclear polyhedrosis viruses have been registered as biopesticides to control caterpillars in leafy vegetables. Nonetheless, viruses are very specific compared to bacterial toxins. For instance, two nuclear polyhedrosis viruses are registered in Europe against lepidopteran larvae for use in leafy vegetables but each virus is specific to a single species, either *Spodoptera littoralis* or *Helicoverpa armigera*.

Fungi and bacteria have also been identified for their efficacy in controlling plant diseases, and isolated to be used as natural biofungicides. *Coniothyrium minitans* is a mycoparasite that is able to infect and destroy sclerotia of *S. sclerotiorum*, hence reducing the incidence of lettuce drop (Jones and Whipps 2002). Other mycoparasites, with an efficacy against *Botrytis*, *Rhizoctonia* and *Pythium* have been found from different genera such as *Trichoderma* and *Gliocladium*. In their review, Vos et al. (2015) gave a comprehensive description of the role of *Trichoderma* to control disease due to *B. cinerea* affecting vegetables, and in enhancing plant growth and inducing plant defenses. Some *Trichoderma*, such as *T. hamatum*, show a good control of lettuce drop (Rabeendran et al. 2006). Several *Trichoderma* species are commercially available, for use on the leafy vegetables, showing different host specificity, different environmental requirements for their development, and different mechanisms to control the disease (among them: mycoparasitism, toxins, spatial and resource competition) (Howell 2003), which increases the range of use of this BCA.

The formulation, rate and application method are certainly among the most critical parameters that determine the efficiency of biocontrol products (Bashan et al. 2014). For instance, Lynch et al. (1991) illustrated that a threshold level of *Trichoderma* was needed to give effective control of *R. solani* and *P. ultimum* causes damping-off in lettuce. Generally, applying BCA as a soil drench is among the most widely used strategy; for instance soil drench with *Gliocladium catenulatum* effectively suppressed Fusarium wilt on spinach (Cummings et al. 2009).

The use of preventive treatments in the nursery will lead to a more efficient use of biocontrol agents. For instance, *Bacillus subtilis* QST713 has been shown to reduce Fusarium wilts in lettuce and rocket by up to 50% when applied as a preventive treatment starting from the nursery, using three to four treatments in a short interval (Gilardi et al. 2016a). Unfortunately, such a level of protection and the positive effect on yield are not sufficient for growers, in part due to the lack of consistency. Their use in practice should be integrated with other control strategies, involving for example host plant resistance and pesticides. Furthermore, the application of beneficial microorganisms to seeds is an effective mechanism that optimizes their functionality, providing for example a better colonization of seedling roots and resulting in an efficient delivery method for plant growth-promoting rhizobacteria (O'Callaghan 2016). Unfortunately, several *Trichoderma* strains can have inhibitory effects on seedling emergence and growth of lettuce (Ousley et al. 1993).

Macroorganisms have been widely used in biological control to protect crops against pests. Many efficient species of natural enemies have been discovered and over 200 species are commercially available today (van Lenteren 2012). Besides, in greenhouses, biological control using macroorganisms could be more efficient because natural enemies are not diluted in wide, open environments. Lacewing (*Chrysoperla carnea*) is a generalist predator which feeds on aphids and can be used for aphid regulation in leafy vegetable production (Smith et al. 2007). Several parasitoids are also commercialized to protect lettuce crops against aphids such as *Aphidius colemani*, *A. ervi*, *Aphelinus abdominalis*. But due to their host specificity, it is important to correctly identify the species of aphid causing the damage, before selecting the parasitoids to be released. Hoverflies (Diptera: Syrphidae) are also interesting natural predators able to control aphids. Syrphid larvae consume aphids and are able to suppress aphid populations (Smith et al. 2007; Hopper et al. 2011).

Habitat manipulation has also been investigated in open field lettuce production to increase the population of natural predators and parasitoids of lettuce aphids. Introduction of wildflower strips into the field or banker plants between lettuce plants allowed an increase of the populations of natural enemies of lettuce aphids and improved their biological control (Skirvin et al. 2011). New research is now needed to transfer this methodology to greenhouse production.

20.3.1.6 Alternative Substances to Pesticides Against Pests and Diseases

Chemical mediators and plant, animal or mineral substances can be used to protect leafy vegetable crops. Stimulating plant defenses to prevent pests and pathogens from attacking the crop is a promising approach (Walters and Fountaine 2009). Stimulators of plant defenses (SPD) are intensively investigated for use on lettuce, mainly to control downy mildew. The main active ingredients are acibenzolar-S-methyl, laminarine and DL-3-amino-butyric acid (BABA) (Cohen et al. 2010). Control of diseases should be achieved with preventive applications of SPD, in order to anticipate the pathogen attack. However, cultivars may not respond with the same intensity to treatments. Thus, efficacy partly relies on the choice of the cultivar (Maisonneuve et al. 2013). Some SPD such as acibenzolar-S-methyl can stimulate a wide range of cultivars, against foliar or soilborne pathogens. For instance, acibenzolar-S-methyl has been found to be effective in controlling Fusarium wilt of both lettuce and rocket at 0.0125 mg/l, with a positive effect on yield (Gilardi et al. 2016a). The same product enhanced the efficacy of trifloxystrobin against the white rust fungus (*Albugo occidentalis*) on spinach (Leskovar and Kolenda 2002), and induced resistance in several crops against downy mildew causal agents (Godard et al. 1999), bacterial pathogens, insects and viruses (Walters and Fountaine 2009).

Among mineral substances, inorganic salts with biocidal effects have shown interesting efficacy for the control of plant diseases, including leafy vegetables

(Deliopoulos et al. 2010). These substances can have a direct effect on pathogens or can act as a SPD. For instance, phosphite (phosphorous acid) is used to control *B. lactucae* on lettuce (Coffey and Ouimette 1989; Thao and Yamakawa 2009), and *P. cucumerina* on wild rocket (Gilardi et al. 2015). When applied in the nursery on seedlings, phosphite-based products have been shown to provide consistent control of *F. oxysporum* f. sp. *lactucae* on lettuce (from 61% to 69% disease reduction), and of *F. oxysporum* f. sp. *raphani* on rocket (54–65% disease reduction), with a significant effect on the yield (Gilardi et al. 2016a). Moreover iron phosphate is used to protect leafy vegetables against slugs and snails. Speiser and Kistler (2002) have demonstrated that the application of iron phosphate reduced the number of slugs and increased the number of marketable lettuce compared to an untreated plot. Finally, in hydroponic crops, the addition of salts (silicates in particular) to the nutrient solution is also widely popular for disease management. Potassium silicate supplied via nutrient solution, at 100 $mg.l^{-1}$, to hydroponically grown lettuce reduced downy mildew severity from 33% to 78% showing its positive effect on lettuce quality grown in saline conditions (Garibaldi et al. 2011). Silicates were also effective against *A. japonica* on rocket and *Colletotrichum gloeosporioides* on basil grown in soilless system (Gullino et al. 2015).

Among natural products, essential oils represent an interesting option against plant pathogens (Isman 2000; Koul et al. 2008), generally due to their proven antibacterial and antifungal activities. For instance, seed treatments with essential oils should also be integrated with other strategies for enhancing pathogen control, such as with biocontrol agents or with a physical seed treatment (Lopez-Reyes et al. 2016). The efficacy of basil oil compounds have also been tested against insects within the IPM framework, and were shown to be effective (Kim et al. 2015).

20.3.1.7 Decision Making Tools

Pesticides are often used in a preventive strategy, with regular applications rather than occasional curative treatments to control pests and diseases. Nonetheless, IPM aims to reduce the negative impact crop protection has on the environment, by reducing the use of pesticides to the strict minimum. Hence, the use of decision making tools to spray accurately, deliver the right dose at the right time at the most susceptible stage of pest or disease is determining to get the best efficacy from pesticide application. Furthermore, accurate pesticides application contributes to delaying the risk of resistance development, while reducing their unnecessary use.

Population sampling and scouting are a cornerstone of IPM to determine when and how to apply chemical control solutions for an identified pest or disease. Detection of airborne inoculum of *P. effusa, Botrytis squamosa, S. sclerotiorum, Erysiphe necator, Leptosphaeria maculans* using spore trapping systems, in combination with DNA amplification using conventional or real-time quantitative polymerase chain reaction (qPCR)-based methods, have been deployed successfully (Correll et al. 2011; Gent et al. 2013) in different crop-system and can help manage disease epidemics. The availability of rapid and reliable detection methods is essential to identify the causal agents of the disease, offering growers and extension services many practical and effective tools to adopt preventative control measures. This is the case of the loop-mediated-isothermal amplification (LAMP) that has recently been developed for the rapid detection of *F.* oxysporum f.sp. *lactucae* from seeds, soil and plant material (Franco-Ortega et al. 2018).

Monitoring for insects can help to foresee insect outbreaks. Most of the main pest cycles are well known for leafy vegetables, and the period of damage during crop cycles are identified. This can help to know which pest is present in the crop and when to adapt monitoring and avoid wasting time (Flint 1987). Pheromone trapping is widely used in agriculture to detect insects, and can be used in IPM strategies for early detection of pests and population monitoring. Pheromones are available for several lepidopteran pests attacking leafy vegetables: *Spodoptera littoralis, Autographa gamma, Helicoverpa armiger*a (Reddy and Manjunatha 2000). However, as most of these species are ubiquitous of many parts of the world, it is important to check that the pheromones sold by companies are effective for local populations. Early detection is essential so that management of low populations can be effective.

Finally, economic and action thresholds are necessary for pest management. Determining thresholds to decide on intervention provides support to help growers decide. For instance in Spain, Morales et al. (2013) proposed a threshold for the control of *N. ribisnigri* in lettuce. The authors demonstrated that very low thresholds are necessary to avoid visual damage on lettuce due to aphids. A combination of pheromone trapping and intervention thresholds may be a good decision support tool to trigger treatment.

20.3.1.8 Chemical Control/Spray Application

In conventional lettuce crops in the Mediterranean region, eight to ten chemical pesticides are applied on average to manage pests and pathogens during the 60- to 90-day-long crop cycle (Barrière et al. 2015). The main pesticides used in leafy vegetables production under greenhouses are fungicides against collar rot agents, and downy mildew and insecticides against aphids and in less extend caterpillars.

The choice of the mode of action of the active substances is crucial for the efficacy of pesticides application. The control of aphids in lettuce is highly concerned. Indeed, when the crop starts to form a head, aphid outbreaks located at the leaf base, in the lettuce head, are protected from insecticide droplets resulting in poor control with contact insecticides. In this case, the choice of a systemic insecticide (*i.e.* spirotetramat) is more suitable for control. Furthermore, the compatibility with biocontrol agents (micro and macroorganisms) must be taken into account when choosing an active substance to apply. Because some released natural enemies may be susceptible to the toxicity of pesticides, which can alter the efficacy of biological control.

With the reinforcement of the EU regulation on pesticides (Regulations (EC) 1107/2009 and 2015/408), some of the active substances authorized for leafy vegetables protection may no longer be available soon. Indeed, the most dangerous actives substances will be excluded according to cut-off criteria, or substituted by less dangerous active substances (candidates for substitution). For leafy vegetables protection, fungicides and insecticides are the most actives substances concerned. At least, eight active substances could be removed soon because of their toxicity (substances classified as carcinogenic, mutagenic, or toxic for reproduction) or endocrine disrupting properties: lambda-cyalothrine, pyrimicarbe, copper, cyprodinil, fluidioxonil, fluopicolide, mancozebe, metam sodium. These reductions in the pesticides available for leafy vegetable protection increase the need to develop, to experiment and to incorporate alternatives technics to chemical pesticides in the IPM strategies.

20.4 IPM Strategies, Taking into Account Levers Complementarity and Interactions

Because IPM is an integrative approach, interactions between different pests and different management practices must be taken into account to get the best control. Avoiding negative interactions and favoring synergies between management practices may help to reinforce the efficacy of the IPM global strategy for crop protection (Sanyal and Shrestha 2008). Indirect non-target effect of pesticides on beneficial arthropods introduced or naturally present is one of the most important negative interactions to take into account (Walker et al. 2007). The choice of selective rather than broad spectrum insecticides may reduce the non-target effect on beneficials and on the environment. Besides, indirect non-target effects may also exist between two biocontrol agents. Shrestha et al. 2017 reported in their study that the larvae of the parasitoid *A. abdominalis,* used to control aphids (*N. ribisnigri*) on lettuce, are highly susceptible to the entomopathogenic fungus *Beauveria bassiana* also used to control aphids in IPM strategies. On the other hand, synergy also exists in the control of aphids on lettuce (Fagan et al. 2010).

20.5 Perspectives for Development of IPM in Leafy Vegetable Production

As shown previously, several levers are available for building IPM strategies in leafy vegetable production. These levers must be combined to get most effective control of pests, diseases and weeds. Nonetheless, the efficacy of IPM is linked to pest and disease pressure. In order to get the best results, it is essential to implement control techniques against low populations of pests and diseases. Hence, prevention is essential. New techniques have been developed in the past few years to control soilborne diseases and pests, including biofumigation and anaerobic soil disinfestation. These techniques may be used as an alternative to chemical disinfection of soil. Although they have shown interesting results in controlling soilborne disease and pest, their use by growers is still limited. An important work of transfer and valorization of these methods to the growers is now needed.

Solutions found in these highly specialized and intensive systems will be very helpful for outdoor or less intensive systems. Exchange of knowledge and experience among stakeholders (researchers, policy makers, growers and processors), countries and cropping systems is very valuable and requires attention to make any IPM strategy fruitful (Lamichhane et al. 2016a). However, the supply of knowledge and technologies alone is not enough for the adoption of IPM innovations by growers. Indeed, motivation plays an important role. To gain access to wider market segments with higher product prices and in so doing increase profitability could be a good incentive for growers to implement IPM strategy. This aspect is very important especially for the leafy vegetable crop sector that allow continuous innovation of their production systems (i.e. leafy vegetables for the ready-to-eat market).

With increasing research in biotechnology, biochemistry and related fields, new biopesticides might be available for control of airborne and soilborne diseases and pests in the next coming years (Seiber et al. 2014). Essential oils are studied on leafy vegetables. Currently, results concerned post-harvest treatments for increasing shelf-life (Ponce et al. 2004) or as biopreservative against microbial contaminants (Ponce et al. 2011) but research are conducted in Europe to develop essential oils as biopesticides against aphids or downy mildew in lettuce, for instance. Furthermore, incentives for developing biopesticides exist in Europe and United States through different research programs funding and fast track registration. Research on bioherbicides is equally strongly needed because of the increasing problem of resistance, and the lack of new modes of action in conventional herbicides in lettuce crop, that has existed for the last 20 years. Furthermore, weed control is very problematic for organic farmers due to the poor efficacy of current weeding techniques. Finally, new tools, like RNA interference (RNAi), for pest control provides a very specific and effective control method that reduces or eradicates side effects (Spadaro et al. 2018).

Ecological services also play a key role in the agroecosystem and precisely in the regulation of pests and diseases (Moonen and Barberi 2008). Taking into account the whole cropping system helps to reduce primary inoculum for all crops, and to consider crop rotation in order to improve the sanitary state of fields. It is now essential to replace agricultural practices and inputs, especially pesticides, by ecosystem services. Designing new cropping systems for leafy vegetables, including alternative techniques to pesticides and promoting ecosystem services such as natural regulation is a new challenging perspective. Recent studies have shown the possibility of setting up such cropping systems for lettuce production. In their review Barrière et al. (2013) suggested that alternative techniques should be selected to promote ecosystem diversity and to enhance associated services. Finally, the implementation of a set of decision rules to manage those alternative techniques would allow a better adaptation to each local context. This work must now be extended to other leafy vegetable crops.

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Chapter 21
Implementation of IPDM in Strawberries and Other Berries

Surendra K. Dara

Abstract Several high value small fruit crops are grown under greenhouse conditions around the world. Integrated pest and disease management (IPDM) in greenhouse production of small fruits can take advantage of a number of practices for maintaining optimal crop health while ensuring good yields and sustainability. These practices include the use of resistant cultivars and clean plant material free of pests and diseases, effective substrate, irrigation, and nutrient management, regular monitoring and good sanitation practices, substrate disinfestation and sterilization with fumigation alternatives, modifying the environmental conditions to reduce pest and disease pressure, chemical and non-chemical control options, along with biostimulants and beneficial microbes. Several examples of successful use of these tactics are discussed and general IPDM guidelines are presented in this chapter.

Keywords Small fruits · Strawberry · Cultural practices · Non-chemical alternatives · Beneficial microbes · Induced resistance · Substrate disinfestation · Fumigation alternatives · Microbial control · Entomovectoring

21.1 Introduction

Strawberries, raspberries, blackberries, and blueberries are high value crops. Although they are primarily grown in open fields or under high tunnels in major producing regions in the world, considerable amounts of greenhouse production also take place, especially in Europe and other areas. Greenhouses offer a unique opportunity to regulate the environment or administer specific production practices that are required for these specialty crops. However, the same conditions that promote plant growth can also be ideal for arthropod pests and diseases, which warrant

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aggressive management tactics that include pesticide applications. Greenhouses used for producing nursery plants need to maintain a higher standard of crop protection to produce pest and disease free berry transplants. Many a time, pest-infested or disease-infected transplants lead to major problems in the fruit production. While the basic IPDM principles for greenhouse berry production are same as those employed under field conditions, some approaches can be different.

Compared to the pest and disease management in the fields, pesticide applications can be higher in greenhouses, and IPDM is necessary to reduce their use and residue levels. A comparison made among greenhouse, conventional, and organic cucumber production systems in Egypt revealed highest levels of pesticide residues in greenhouse cucumbers (Mansour et al. 2009). Similarly, a study in Colombia showed that greenhouse tomatoes had a higher number of pesticide residues per sample compared to those produced in open fields (Bojacá et al. 2013). A Norwegian greenhouse study recommended 7–14 days of preharvest interval for certain fungicides, which is a challenge because strawberries are harvested more frequently (Stensvand 2000; Baker et al. 2002). On the other hand, pesticide residues are reported to be generally higher in strawberry (Safi et al. 2002) warranting a need for non-chemical pest management strategies.

Although several biocontrol options are available for pest management in greenhouses, chemical pesticides are still important tools and IPDM practices are also necessary for resistance management. While there are several mechanisms for the development of pesticide resistance, in general, there is an increased risk of breeding resistant pest populations or pathogen propagules in greenhouses due to a high selection pressure as well as the lack of unexposed, wild alleles dilute the frequency of resistant mutants. Pesticide resistance is frequent around the world in twospotted spider mite, *Tetranychus urticae*, greenhouse whitefly, *Trialeurodes vaporariorum*, and western flower thrips, *Frankliniella occidentalis*, which are some of the common greenhouse pests of strawberry and other small berries (Gorman et al. 2001; Bi et al. 2002; Herron and James 2005; Van Leeuwen et al. 2010). Fungicide resistance is also an issue in disease management. For example, there are several reports of fungicide resistance in *Botrytis cinerea*, an important pathogen of strawberry, blackberry, raspberry and blueberry causing gray mold or blight (Elad et al. 1992; Raposo et al. 1996; Yourman and Jeffers 1999).

This chapter will cover the key aspects of IPDM for strawberry and other berries with examples from both field and greenhouse studies. Some examples of from other crops will also be included as those management practices are applicable to berries or similar pests or diseases affect berries.

21.2 Resistant Cultivars

Cultivar choice usually depends on the berry quality, yield potential, shelf life, and consumer preference, among other factors. Selection of appropriate cultivars suited for the local conditions based on the risk of a particular pest or disease in the region can be one of the key steps in IPDM. In general, berry cultivars are bred more for disease resistance than for pest resistance. An earlier review of strawberry breeding programs around the world identified fruiting season, fruit size, firmness, quality, and disease resistance as the main objectives in developing new cultivars (Faedi et al. 2002). Resistance in strawberry cultivars Aromas, Camino Real, Festival, Portola, San Andreas, Ventana to *Fusarium oxysporum* f. sp. *fragariae* (Fang et al. 2012; Koike and Gordon 2015), cultivars Bounty, Cabot, and Cavendish to black root rot caused by *Rhozoctonia fragariae*, *Pythium*, an *Patylenchus penetrans* (Particka and Hancock 2005), and cultivars Camino Real, Marquis, Pataluma, San Andreas to *Verticillum dahliae* (Ivors, personal communication) were reported in multiple studies in Australia and United States. However, some cultivars that were highly resistant in some studies were susceptible in others and it is important to verify the performance of each cultivar under local conditions. Averre et al. (2002) reported relative resistance of several strawberry cultivars to anthracnose, leaf spot, leaf blight, powdery mildew, and red stele where most of the cultivars recommended for North Carolina were resistant to powdery mildew, but had varying levels of resistance to other diseases. Such information helps the growers to choose an appropriate cultivar for the local conditions.

While a few strawberry cultivars possess pest resistance to some extent, breeding for arthropod resistance does not seem to be a focus even today for a major berry crop, like strawberry, that has several pest problems (Ferrer et al. 1993; Hancock et al. 2008). Although the development of aphid resistant raspberry cultivars has been practiced for several decades, the primary focus is to manage different viruses that aphids transmit (Keep and Knight 1967; Birch and Jones 1988).

In blackberry, varying levels of resistance to various diseases, such as anthracnose (*Elsinoe veneta*), botrytis fruit rot (*Botrytis cinerea*), and double blossom/rosette (*Cercosporella rubi*) is seen among cultivars and some thornless ones are more resistant to certain diseases (Bruzzese and Hasan 1987; Ellis et al. 1991; Gupton 1999; Kidd et al. 2003). An older study also reported that cultivars having the germplasm of North American species are more resistant that those with European blackberry species to European blackberry rust (*Phragmidium violaceum*). However, blackberry breeding centered around improving fruit quality, thornlessness, environmental adaptation, and primocane fruiting especially in cultivars released between 1985 and 2005 (Clark and Finn 2008).

In blueberries, lowbush varieties or others that have a higher level of lowbush blueberry germplasm are resistant to *Monilinia vaccinia-corymbosi* that causes blight in emerging shoots and leaves and mummy berry in fruits (Ehlenfeldt et al. 2010). Susceptibility of highbush blueberry to *M. vaccinia-corymbosi* also varies among cultivars and there are several resistant or moderately resistant cultivars to be considered (Schilder et al. 2008). The incidence of another important blueberry disease, anthracnose, caused by *Colletotrichum acutatum* is less in cultivars that grow vigorously and produce higher yields (Polashock et al. 2005). Half-high blueberry cultivars appear to be more resistant than lowbush, highbush, southern highbush, and rabbiteye cultivars to botryosphaeria stem blight caused by *Botryosphaeria dothidea* and phomopsis twig blight caused by *Phomopsis vaccinia* (Polashock and Kramer 2006).

21.3 Cultural Practices

Cultural practices such as choosing a clean source of transplants, appropriate type of soil/substrate, spacing, irrigation, nutrient management, sanitation, and pest and disease monitoring play a significant role in reducing pest and disease occurrence and spread.

In general, plants that receive optimum irrigation and nutrient inputs maintain good health and withstand pests and diseases better than those under water stress and excessive or insufficient nutrient inputs. For example, excessive nitrogen fertilizers, water stress, high temperatures, or dust on foliage can increase infestations of the twospotted spider mite, *Tetranychus urticae* in strawberry, raspberry, and other crops (Alston 2017; Garcia 2017; Ruckert 2017). On the other hand, soil amendment with poultry litter in greenhouse strawberry effectively reduced the viability of microsclerotia of *Macrophomina phaseolina*, causal organism of charcoal rot or crown and root rot (Pratt 2006) and poultry manure and compost suppressed root-lesion nematode, *Pratylenchus penetrans* in raspberry (Forge et al. 2015). While high irrigation reduced western flower thrips (*Frankliniella occidentalis*) adult numbers, high nitrogen and phosphorus promoted thrips populations (Schuch et al. 1998; Chow et al. 2012; Chen et al. 2014). Very low soil moisture (0 or 25% water holding capacity) or flooded conditions (125% moisture) reduced the viability of *M. phaseolina* microsclerotia (Pratt 2006). Other studies had also indicated that high soil moisture content affects their viability (Short et al. 1980; Zveibil et al. 2012). Maintaining good soil fertility, particularly optimal levels of phosphorus, along with avoiding water and heat stress are recommended for mitigating *M. phaseolina* severity in strawberry (de los Santos et al. 2016). Manipulating irrigation and nutrient management practices can be an effective tool in pest and disease management.

Several pests and diseases can be introduced into greenhouses through infested or infected transplants and multiply when the soil or substrate or contaminated. Obtaining clean transplants from a reputable source and using a substrate free of pests and disease propagules is a critical a step in IPDM. If the substrate is used multiple times or there is a risk of pests or diseases, there are multiple ways to disinfest using non-chemical alternatives, which are discussed later in this chapter.

Regular monitoring for early identification of problem areas and timely administration of corrective actions will reduce potential yield losses and pest and disease problems. Sanitation practices, such as the removal of infected fruit or plant material, play a big role in reducing pathogen inocula or pest infestations in the environment. Removal of discarded or fallen berries is a recommended management practice for anthracnose (*C. acutatum*), Rhizopus fruit rot (*Rhizopus* spp.) and Mucor fruit rot (*Mucor* spp.) in strawberry (Dara 2015a), mummy berry in blueberry (Schilder et al. 2008), and spotted-wing drosophila (*Drosophila suzukii*) in different berries (Leach et al. 2016).

21.4 Substrate Disinfestation with Fumigation Alternatives

Compared to the field production of berries, where chemical fumigation is frequently practiced for managing several soilborne pests, pathogens, nematodes, and weeds, using a clean substrate in greenhouses eliminates the need for fumigation and reduces the risk of those problems. However, techniques such as solarization, steam sterilization, anaerobic soil disinfestation (ASD), or biofumigation can be used when there is a risk of contamination (Stapleton 2000; Tanaka et al. 2003; Bañuelos and Hanson 2010; Shennan et al. 2017).

Solarization can be done in multiple ways depending on the greenhouse conditions, but passive solar energy is employed for heating moist substrate usually covered by transparent plastic mulch. In addition to killing parasitic and pathogenic organisms, solarization increases the availability of soluble mineral nutrients and the activity of beneficial microorganisms (Stapleton 2000; Candido et al. 2008). In a field study in Turkey, several weeds and pathogens (*Rhizoctonia* spp. and *Phytophthora cactorum*) were effectively controlled and strawberry fruit yield was maintained from soil solarization at a level comparable to the methyl bromide treatment (Benlioğlu et al. 2005). Compared to metam sodium fumigation, soil solarization resulted in a higher strawberry yield in another study conducted in Spain (Campruí et al. 2007). It also appeared that arbuscular mycorrhizal fungi were not affected by both solarization and fumigation in this study.

Steam sterilization is another non-chemical soil disinfestation process where soil or substrate are exposed to steam. This technique is especially useful in temperate regions where solarization is not possible. In a field study conducted in California strawberries, weed control from steam or steam+solarization was similar to that achieved by methyl bromide+chloropicrin fumigation (Samtani et al. 2012). Some stream treatments were also as effective as chemical fumigation in reducing *Verticillium dahliae* microsclerotia at a depth of 15 cm. Steam sterilization decreased soil fungi and bacteria (including those that oxidize ammonia and nitrite) to a greater extent and for a longer duration than methyl bromide fumigation in a Japanese study while increasing the ammonical nitrogen content in the soil (Tanaka et al. 2003).

Biofumigation generally refers to pest, disease, or weed suppression through soil incorporation of Brassica plant material or seed meal as green manure that releases phytochemicals. Use of microbes, manure or other organic waste that produce volatile compounds or gases is also considered as biofumigation. Glucosinolates in Brassica plants produce allyl isothiocyanate, nitriles, and other compounds that have antimicrobial and insecticidal properties (Fenwick et al. 1983; Mattner et al. 2008). These plant-based isothiocynates or sulfur-containing compounds are similar to methyl isothiocyanate, a byproduct of chemical fumigants metam sodium, metam potassium and dazomet. The combination of steam sterilization with mustard seed meal resulted in good weed and pathogen (*M. phaseolina*, *Pythium ultimum*) suppression along with improved strawberry yields comparable to chemical fumigation in a California study (Fennimore et al. 2014). In Spain, the combination of solarization and biofumigation with chicken manure was superior to solarization alone in weed control and improving strawberry growth and yield (Medina-Mínguez 2002). Bañuelos and Hanson (2010) reported improved weed suppression and strawberry yield in a California study with selenium-enriched mustard and canola seed meals that served as both bioherbicides and green fertilizers. Some degree of weed and pathogen (*P. cactorum*) suppression was seen from soil incorporation of *B. rapa/B. napus* crop in a field evaluation, but a higher degree of suppression in six soilborne pathogens of strawberry was seen from isothiocyanates of these plants in laboratory assays (Mattner et al. 2008). It also appeared the roots of *B. rapa/B. napus* plants have higher quantities of isothiocyanates than the shoots. A combination of techniques that included summer irrigation, solarization, mulching, and biofumigation with cruciferous residues caused a significant reduction in *M. phaseolina* populations and viability (Lodha et al. 1997). Similarly, biofumigation with mustard seed meal followed by solarization, mustard seed meal supplemented with steaming, and steaming followed by solarization resulted in significant yield improvement compared to untreated control (Daugovish and Fennimore 2011) and incorporation of mustard pod residues followed by solarization nearly eradicated *M. phaseolina* and *F. oxysporum* f.sp. *cumini* propagules in soil (Israel et al. 2005).

Preliminary studies in California strawberries with a new commercial formulation of the fungus *Muscodor albus* showed its potential as a biofumigant (Melissa O'Neal, personal communication). Isobutyric acid and 2-methyl-1-butanol from *M. albus* have antifugal properties against a variety of pathogens including *Botrytis* spp., *Colletotrichum* spp., and *Rhizopus* spp. (Mercier and Jiménez 2004).

Antagonism by beneficial bacteria, fungi, and yeasts is another strategy for managing soilborne pathogens. Several species of *Azorhizobium*, *Azospirellum*, *Azotobacter*, *Bacillus*, *Comamonas*, *Citrobacter*, *Enterobacter*, *Glomus*, *Paecilomyces*, *Pseudomonas*, *Rhizobium*, *Rhizophagus*, *Streptomyces*, *Saccharomyces*, and *Trichoderma* are sold as biopesticides (fungicides and nematicides), biostimulants, or soil builders which are expected to improve crop health and yields through antibiosis, antagonism, competitive displacement, or induced systemic resistance (Table 21.1). Although some of these microorganisms are independently sold as biopesticide formulations, various combinations of multiple species are currently marketed as biostimulants or soil amendments. Field studies conducted in California strawberry suggested that beneficial microbes could play a positive role in improving crop yield or health especially when there is a disease pressure (Dara and Peck 2016, 2017). Beneficial microbes were applied as transplant dip at the time of planting and/or through drip irrigation at periodical intervals. Preplanting dip allows inoculation of transplants with beneficial microbes before they are exposed to plant pathogens. Greenhouse and field studies conducted in Germany demonstrated that rhizobacteria, *Raoultella terrigena*, *B. amyloliquefaciens*, and *P. fluorescens* were very effective in antagonizing *Phytophthora fragariae* var. *fragariae*, causal agent of red stele, and *P. cactorum*, causal agent of crown rot, sometimes equal to the chemical fungicide aluminum tris (O-ethyl phosphonate) in strawberry (Anandhakumar and Zeller 2008). In another German field study, transplant dip in the chitinolytic rhizobacterium, *Serratia plymuthica* strain

Table 21.1 Examples of commonly used beneficial microbes formulated as biostimulants and biopesticides

Microorganism		Intended purpose or target pests/pathogens
Biostimulants or soil conditioners – promote plant and root growth, health, soil structure, and yields		
Bacteria	*Azorhizobium* spp.	Crop and soil health
	Azospirillum spp.	Crop and soil health
	Azotobacter spp.	Crop and soil health
	Bacillus spp.	Crop and soil health
	Citrobacter spp.	Crop and soil health
	Enterobacter spp.	Crop and soil health
	Pseudomonas spp.	Crop and soil health
	Rhizobium spp.	Crop and soil health
	Rhizophagus irregularis	Crop and soil health
	Streptomyces spp.	Crop and soil health
Fungi	*Glomus* spp.	Crop and soil health
	Rhizophagus spp.	Crop and soil health
	Trichoderma spp.	Crop and soil health
Yeast	*Saccharomyces cerevisiae*	Crop and soil health
Biopesticides – pest, disease, and nematode management		
Bacteria	*Agrobacterium agrobacter*	Plant pathogens
	Bacillus amyloliquefaciens	Plant pathogens
	B. firmus	Plant parasitic nematodes
	B. thuringiensis	Insect pests
	B. subtilis	Plant pathogens
	Burkholderia rinojensis[a]	Arthropod pests
	Chromobacterium subtsugae	Arthropod pests
	Panibacillus popilliae	Lepidopteran pests
	Streptomyces lydicus	Plant pathogens
Fungi	*Beauveria bassiana*	Arthropod pests
	Coniothyrium minitans	Plant pathogenic fungi
	Gliocladium spp.	Plant pathogens
	Glomus spp.	Plant pathogens
	Hirsutella thompsonii	Insect pests
	Isaria fumosorosea	Arthropod pests
	Lecanicillium giganteum	Mites
	L. lecanii	Scale insects
	L. longisporum	Aphids
	L. muscarium	Thrips and hemipteran pests
	Metarhizium anisopliae	Arthropod pests
	M. brunneum	Arthropod pests
	Paecilomyces lilacinus	Plant parasitic nematodes
	Pseudomonas spp.	Plant pathogenic fungi
	Pseudozyma flocculosa	Plant pathogenic fungi
	Trichoderma spp.	Plant pathogens

(continued)

Table 21.1 (continued)

Microorganism		Intended purpose or target pests/pathogens
Nematodes	*Heterorhabditis* spp.	Insect pests
	Steinernema spp.	Insect pests
Viruses	Granuloviruses	Lepidopteran pests
	Nucleopolyhedroviruses	Lepidopteran pests
Yeast	*Aureobasidium pullulans*	Plant pathogenic fungi
	Candida spp.	Plant pathogenic fungi

Sources: Product labels and Dara et al. (2017)

[a]No live microbes are present

HRO-C48 reduced Verticillum wil (caused by *V. dahliae*) and crown rot (*P. cactorum*) and improved strawberry yields (Kurze et al. 2001).

Entomopathogenic fungi also appear to have an impact on strawberry health and yield through their direct interaction with plants and potentially pathogenic organisms (Dara and Peck 2016). In a greenhouse study conducted in California, commercial formulations of *B. bassiana* (BotaniGard ES), *I. fumosorosea* (PFR-97), and *M. brunneum* (Met52) effectively antagonized *F. oxysporum* f. sp. *vasinfectum* and improved the health of cotton seedlings as effectively, or superior, to botanical (Regalia, based on the giant knotweed extract) and microbial (Actinovate AG, based on *Streptomyces lydicus* strain WYEC108 and Stargus, *B. amyloliquefaciens* strain F727) fungicides (Dara et al. 2017a). Lozano-Tovar et al. (2013) showed antagonism of *B. bassiana* and *M. brunneum* in a laboratory study in Spain. Compared to *Trichoderma atroviride* which resulted in a 64–79% reduction in the mycelial growth of *Phytophthora* spp. and *V. dahliae*, entomopathogenic fungi caused a 42–62% reduction in *Phytophthora* spp. and 40–57% reduction in *V. dahliae* growth. Another recent study also demonstrated that culture filtrates of two Korean isolates of *B. bassiana* and *M. anisopliae* had antifungal activity against *B. cinerea* (Yun et al. 2017). These studies shed light on the potential of entomopathogenic fungi in managing plant pathogens in addition to arthropod pests.

ASD technique involves adding a carbon source such as rice bran or molasses to the soil followed by irrigation and covering with plastic mulch to create anaerobic conditions. Anaerobic decomposition of the carbon source results in the production of organic acids and volatile compounds that are toxic to pathogens and other soil pests. In a recent report based on multiple California studies, varying levels of suppression of *Fusarium* spp., *Rhizoctonia* spp., *Pythium* spp., and *V. dahliae* resulted from ASD, but it was dependent on soil temperature, the type of carbon source used, the extent of anaerobic conditions, and the location of the experiment (Shennan et al. 2017). ASD did not provide weed control in these studies. Inoculating the substrate with beneficial microbes following the disinfestation process can be a good strategy to promote microbial activity for additional protection.

While several studies demonstrated the potential of nonfumigation alternatives in reducing disease or weed pressure, it is important for the suppression to translate into increase fruit yields.

21.5 Manipulating Environmental Conditions

Environmental conditions that promote plant growth and reproductive development also influence pests and diseases. A thorough understanding of optimal conditions that are ideal for good yields while limiting the pest and disease proliferation help manipulate the greenhouse environment as an IPDM strategy.

Adequate chilling of strawberry plants is critical for plant vigor, which indirectly impacts the ability of plants to withstand pests and diseases (Husaini and Xu 2016). Additionally, cooler temperatures favor root rot causing pathogen *Pythium* spp. and botrytis fruit rot/gray mold causing pathogen *B. cinerea*, while warmer conditions favor *Fusarium* spp. that cause wilt and *M. phaseolina* (Bulger et al. 1988; Olaya and Abawi 1996; Maas 1998; Husaini and Xu 2016). On the other hand, the powdery mildew causing *Podosphaera macularis* (=*Sphaerotheca macularis* f. sp. *fragariae*) favored relative humidity above 75% and temperatures between 15 and 30 °C for conidial germination (Amsalem et al. 2006). However, disease severity was the lowest at 10 and 30 °C, a relative humidity of 95%, and light intensity of 7000 lux in growth chambers. In a different study, the efficacy of microbial control of *B. cinerea* with beneficial fungi appeared to increase when temperatures increased from 10 to 25 °C (Sutton and Peng 1993).

High relative humidity above 80% favored the development of second instar larvae and promoted pupation of *F. occidentalis* on plants rather than in the soil (Steiner et al. 2011). However, increasing relative humidity by 15% increased *B. bassiana* infections by 17–25% and helped reduce *F. occidentalis* and the greenhouse whitefly, *Trialeurodes vaporariorum* populations in greenhouse (Shipp et al. 2003). Relative humidity and temperature will also influence the natural enemies and their biocontrol efficacy. Predation of *T. urticae* by the predatory gall midge, *Feltiella acarisuga* increased with increasing greenhouse temperatures from 15 to 27 °C and with increasing relative humidity at 27 °C (Gillespie et al. 2000). Predation was affected by extended periods of low relative humidity below 60%.

Moisture on the flower or fruit surface favors *B. cinerea*, which is a major pathogen of strawberry, raspberry, blackberry and other hosts (Jarvis 1962; Ellis 2008). Good air circulation and plant spacing that allows a quick drying of wet plant surfaces helps reduce gray mold development. Early morning heating in the greenhouse can help dry the plant surface and reduce *B. cinerea* incidence (Dik and Wubben 2004). Williamson et al. (2007) discussed manipulating ventilation, UV light, and temperature among other control options for managing *B. cinerea* in blackberry, raspberry, strawberry and other crops. Disease forecasting models have been developed based on ambient temperature and leaf wetness to predict the time for fungicide applications for *B. cinerea* (MacKenzie and Peres 2012; Rasiukevièiûtë et al. 2013). Under greenhouse conditions, such models are not only useful for curative actions, but may also help manipulate the environment to avoid or delay disease onset.

Anthracnose infections in blueberry increased with increasing May temperatures (Polashock et al. 2005). On the other hand, class II chitinases that accumulate in stems at low temperatures and important in cold hardiness imparted resistance to anthracnose (Miles et al. 2011). Cold acclimation or exposure to sublethal cold temperatures increase the accumulation of pathogenesis-related proteins, abscisic acid, total phenolics, and other compounds that aid plants in fighting diseases (Meyer and Kirkpatrick 2011). Cold tolerant strawberry species, for example, possessed resistance to a wide variety of diseases, nematodes, and environmental stress factors (Sjulin and Dale 1987). Zveibil et al. (2012) reported that the viability of microsclerotia of *M. phaseolina* reduced when the soil temperatures were kept at 25 °C or fluctuated between 18 and 32 °C under greenhouse conditions compared to a constant temperature at 30 °C. Dara et al. (2017) discussed manipulation of relative humidity, temperature, soil moisture and other environmental conditions to improve microbial control of arthropod pests including greenhouse pests.

Since CO_2 levels are elevated in the greenhouses for improved plant growth and yields, it is important to determine optimal levels that do not interfere with pest and disease management efforts. Increasing atmospheric CO_2 is reported to have an impact on pests and diseases and also affect the resistance of some crops (Ziska and Runion 2007; Zavala et al. 2008; Gregory et al. 2009). While elevated CO_2 promoted the growth and development of some pests, it negatively impacted the others (Ziska and Runion 2007). *Tetranychus urticae*, a significantpest of many berry crops, is one of those pests that benefits from increased nonstructural carbohydrate content as a result of elevated CO_2 level (Heagle et al. 2002). However, the negative impact of elevated CO_2 on resistant alleles on rendering some resistant cultivars susceptible is a significant one to consider. For example, aphid resistance of a red raspberry cultivar broke down by elevated CO_2 levels (Martin and Johnson 2010). The European large raspberry aphid, *Amphorophora idaei* grew faster and larger at 700 μmol/mol of CO_2 compared to plants grown at 375 μmol/mol on of the two resistant cultivars. It is necessary to understand such interactions with different cultivars and either use the ones whose resistance is not altered or use appropriate CO_2 levels.

Positive pressure ventilation system can also be used a means of pest management in greenhouses. In addition to the screening that prevents the entry of pests, maintaining air velocity higher than the flying speed of insects through positive internal greenhouse pressure and adjusting the ventilation windows is recommended by Mears and Both (2002) to exclude pests in tropical and subtropical regions.

UV light transmission has an impact on greenhouse production and pest management practices. For example, photodegradation of insecticides such as bifenthrin, esfenvalerate, imidacloprid, thiamethoxam, and spinosad was significantly reduced in raspberry under tunnels with UV-reducing plastic compared to uncovered or tunnels with transparent plastic (Leach et al. 2017). Residual activity of the insecticides and their efficacy against *D. suzukii* also improved under UV-reducing plastic. However, UV-protection did not have such a positive impact on insecticides acetamiprid, cyantraniliprole, cypermethrin, and malathion in this study. Preliminary studies conducted by Janisiewicz et al. (2015) suggested UV-C irradiation of strawberry plants followed by a dark period and application of beneficial microbes as a strategy for managing *B. cinerea*, *C. acutatum*, and *P. aphanis*.

21.6 Biological Control

Biological control is an integral part of greenhouse pest management and predators and parasitoids have been successfully used against insect and mite pests for several decades (Van Lenteren and Woets 1988). With the increase in greenhouse acreage, the use of predatory phytoseiid mite *Phytoseiulus persimilis* against *T. urticae*, prasitoid *Encarsia formosa* against *T. vaporariorum* significantly increased in 1970s and 80s in Europe. Commercial production and use of other natural enemies also proliferated during this period. Currently, several species of natural enemies are produced on a commercial scale for greenhouse and field pest management around the world (Table 21.2). Releasing predatory mites is a popular practice for managing spider mites in strawberry, blackberry, and raspberry in California (Godfrey 2011; Zalom et al. 2016). Several species of predators and parasitoids are recommended and released for augmentative biological control for managing various greenhouse pests (Van Lenteren 2000; Smith 2015; Van Lenteren et al. 2017). Selection of the right natural enemy, releasing at appropriate times and numbers, maintaining ideal environmental conditions to promote their activity, providing refuge, and avoiding pesticide sprays that are harmful to natural enemies are among some of the tactics to enhance biocontrol efficacy.

21.7 Botanical Control

Azadirachtin, essential oils, giant knotweed extract, and pyrethrum are some of the plant extracts that are used as antifeedants, repellents, acaricides, insecticides, fungicides or insect growth regulators. Azadirachtin, extracted from the seeds of neem (*Azadirachta indica*), has insecticidal and antifeedant properties and also acts as an insect growth regulator. Neem oil, also extracted from neem seeds, is used as a fungicide, acaricide, and insecticide. Studies conducted in California strawberry showed its potential for managing *L. hesperus* and other insect pests (Dara et al. 2013; Dara 2016). Extract of the giant knotweed (*Reynoutria sachalinensis*) effectively antagonized *Fusarium oxysporum* f.sp. *vasinfectum* (Dara et al. 2017a). Pyrethrum, extracted from *Chrysanthemum cinerariaefolium* flowers, is an effective pesticide, but it is also very toxic to natural enemies. Simmonds et al. (2002) reported that azadirachtin and pyrethrum to be very effective against *T. vaporariorum*, but found pyrethrum to be very harmful to the parasitoid *Encarsia formosa*. Similarly, Contreras et al. (2006) reported very effective control of *F. occidentalis* by spinosad and pyrethrum, but the latter was highly toxic to the predator *Orius* spp. Essential oils extracted from aromatic plants are used for pest management in stored grains, agriculture, and urban enviroments (Isman 2000). The green peach aphid, *Myzus persicae* and *T. urticae* are among the pests that can be effectively controlled by essential oils (Isman 2000; Miresmailli and Isman 2006; Dara 2015b). Neem and essential oils can also be effective against plant pathogens. Essential oils of rose-

Table 21.2 Examples of commercially available natural enemies and their target pests

Natural enemy		Target pests
Parasitoids		
Hymenoptera	*Aphidius* spp.	Aphids
	Cotesia spp.	Lepidopterans
	Dacnusa spp.	Leafminers
	Encarsia spp.	Whiteflies
	Trichogramma spp.	Lepidopterans
Predators		
Acari	*Amblyseius* spp.	Mites and thrips
	Euseius spp.	Thrips, whiteflies
	Galendromus spp.	Mites
	Hypoapsis spp.	Fungus gnats and thrips
	Mesoseiulus spp.	Mites
	Neoseiulus spp.	Mites
	Phytoseiulus spp.	Mites
Coleoptera	*Adalia* spp.	Aphids, other small insects and mites
	Atheta spp.	Fungus gnats
	Coccinella spp.	Aphids, other small insects and mites
	Cryptolaemus spp.	Mealybug
	Harmonia spp.	Aphids, other small insects and mites
	Hippodamia spp.	Aphids, other small insects and mites
	Stethorus spp.	Mites
Diptera	*Aphidoletes* spp.	Aphids
	Feltiella spp.	Mites and thrips
Hemiptera	*Diaeretiella* spp.	Aphids
	Geocoris spp.	Aphids, hemipterans, mites, thrips, and whiteflies
	Macrolophus spp.	Whiteflies
	Orius spp.	Aphids, hemipterans, mites, thrips, and whiteflies
	Pediobius spp.	Coleopterans
	Tamarixia spp.	Psyllids
	Thripobius spp.	Thrips
	Trissolcus spp.	Hemipeterans
	Xylocoris spp.	Aphids, hemipterans, mites, thrips, whiteflies
Neuroptera	*Chrysoperla* spp.	Aphids, mites, thrips, and whiteflies
	Micromus spp.	Aphids
Thysanoptera	*Scolothrips* spp.	Mites and thrips

Sources: Hale and Hensley (2010) and Van Lanteren et al. (2017); several commercial insectary listings

mary, lavender, and origanum were very inhibitory to *B. cinerea* in both in vivo and in vitro (Soylu et al. 2010). In an in vitro study, essential oils of dictamnus, oregano, and thyme completely inhibited the growth of *B. cinerea*, *Fusarium solani* var. *coe-*

ruleum, and *Clavibacter michiganensis* subsp. *michiganensis* (Deferera et al. 2003). Koul et al. (2008) discussed various insecticidal, ovicidal, larvicidal, oviposition inhibitory, antifeedant, repellent, attractant, antifungal, antiviral, and fumigant of cinnamon, clove, eucalyptus, holy basil, lavender, lemongrass, mint, orange, rosemary, thyme, turmeric, and other essential oils against a variety of arthropod pests and plant pathogens suggesting their potential as green pesticides.

21.8 Chemical Control

Chemical pesticides are widely used for managing pests and diseases around the world and are generally considered as an affordable and effective control option. While insecticides and acaricides are typically applied when pest populations are present and reach damaging levels, prophylactic fungicide treatments are not uncommon to protect crops from common diseases. For example, some protectant fungicides are applied to control *M. vaccinia-corymbosi* in blueberry before environmental conditions become conducive for fungal infections (Schilder et al. 2008). Since *B. cinerea* can multiply in plant debris and be present in the crop environment throughout the production season, frequent fungicide applications are made starting before flowering in blackberry, raspberry, and strawberry to manage grey mold (Eckert and Ogawa 1988). In California strawberries, chemical fungicides are routinely used for controlling *B. cinerea*, *Podosphaera aphanis*, *Rhizopus* spp., and other foliar and fruit diseases and fumigation continues to be the main choice for managing soilborne pathogens *C. acutatum*, *Fusarium oxysporum* f. sp. *fragariae*, *M. phaseolina*, *Phytophthora* spp., and *Xanthomonas fragariae* which cause crown or root rot and foliar diseases (Dara 2015a). Chemical fungicides are also commonly used or recommended for controlling several diseases in blueberry (Scherm and Stanaland 2001; Cline et al. 2006), blackberry (Ivey et al. 2016), raspberry (Heidenreich 2006) and other berries. Since the efficacy of fungicides varies depending on the crop, disease, and other factors, treatment decisions based on the crop needs and efficacy data from local or regional data would be useful. For example, in a study was conducted in North Carolina blueberries against leaf spot fungi, *Septoria albopunctata* and *Gloeosporium minus* (Cline 2002) fungicide efficacy varied among various parameters evaluated. Fenbuconazole (Indar®) was very effective in reducing defoliation and improving bud set and fruit yield. While fenhexamid (Elevate®) and cyprodinil + fludioxonil (Switch®) were not effective, captan (Captan®) + bonomyl (Benlate®) combination was moderately effective in improving bud set and berry yields. In a recent Serbian study, tebuconazole, fluopiram, and boscalid provided 95–100% control of the spur blight (*Didymella applanata*) of raspberry (Stević et al. 2017). Chlorothalonil, copper-hiroxide, dithianone, and mancozeb resulted in a 64–82% disease suppression while the efficacy of azoxystrobin, fluazinam, and pyraclostrobin was low and varied from 14% to 38% suppression.

Although chemical pesticides play an important role in pest and disease suppression, preventing yield losses, and ensuring returns, excessive reliance on chemical control led to several resistance problems around the world. For example, high levels of resistance to both an older (carbendazim) and a newer (cyprodinil) fungicide among others was seen in *B. cinerea* from greenhouse strawberry in China (Fan et al. 2017). Similarly, high levels of neonicotinoid, pyrethroid, and ketoenol resistance to *T. vaporaiorum* in Greece (Kapantaidaki et al. 2017) and pyrethroid and avermictin resistance in *T. urticae* in Cypress and Greece (Ilias et al. 2017), and resistance to several groups of insecticides in *F. occidentalis* (Gao et al. 2012). Considering the high risk of pesticide resistance, non-chemical control options should be fully exploited before chemical insecticides, acaricides, and fungicides are used. When necessary, chemical pesticides should be used at the recommended rates when treatment thresholds have reached. It is also important to avoid the repeated use of same pesticide and rotating those among different mode of action groups.

21.9 Mechanical or Physical Control

Pest exclusion through proper screening of doors and ventilation windows is a common practice in greenhouse production. Yellow sticky cards/tapes or traps equipped with attractants or pheromones, reflective materials, barriers, footbaths, and other such mechanical and physical control tactics are also frequently used for managing several arthropod pests, disease vectors, or diseases. Bug vacuums can also be used to aspirate larger insects and for spot treatments. Yellow sticky cards are also useful for monitoring pests and help with treatment decisions.

21.10 Microbial Control

Microbial control refers to the use of beneficial microorganisms for controlling pests and diseases. Several bacterial and fungal formulations are commercially available as fungicides for controlling a variety of diseases. Bacteria such as *Bacillu* spp., *Pseudomonas* spp. *Streptomyces* spp., and fungi such as *Gliocladium* spp., *Penicillium* spp., *Trichoderma* spp. have been used for disease control.

Sutton and Peng (1993) reported a very high level of *B. cinerea* control in strawberry using *Gliocladium roseum*, a *Penicillium* sp., and *Trichoderma viridae*. Efficacy of the three mycofungicides was as effective as chlorothalonil in several field and greenhouse studies. Three applications of the commercial formulations of *Gliocladium catenulatum* (Prestop) and *T. harzianum* (PlantShield) resulted in up to 45% of reduction in anthracnose by *C. acutatum* in blueberry (Verma et al. 2006). Similarly, inhibition of *M. vaccinia-corymbosi*, which causes mummy berry disease in blueberries, was reported by commercial formulations of *B. subtilis* (Serenade) and *Pseudomonas fluorescens* (BlightBan) in a laboratory study (Scherm et al. 2004). Scherm and Krewer (2008) discussed mummy berry and foliar disease management in organic rabbiteye blueberries using *B. subtilis* and fish oil-based products among others with varying levels of disease control.

Several studies demonstrated the efficacy of *Trichoderma* spp. against multiple strawberry diseases. Ahmed and El-Fiki (2017) reported that root rot causing fungi *Fusarium oxysporum*, *F. solani*, *M. phaseolina*, and *Rhizoctonia solani* were effectively controlled by *Trichoderma album*, *T. harzianum*, *T. hamatum*, and *T. viridae* in a strawberry field study in Egypt. Plant growth, fruit yield, and total chlorophyll, nitrogen, and phenol content was also improved from these treatments that included both commercial and local isolates of *Trichoderma* spp. Barakat and Al-Masri (2017) reported a complete control of *B. cinerea* in greenhouse strawberry with the combination of *T. harzianum* (at 10^9 spores/ml) and pyrimethanil or cyprodinila+flydioxonil. Compared to the stand-alone treatments of fungicide and *T. harzianum* or their combination with 10^8 spores/ml rate of *T. harzianum* that provided 38–70% of control, the higher rate of fungus made a significant difference in providing 100% control. Good control of damping off (*R. solani*) of multiple greenhouse crops was also achieved with a formulation of *Trichoderma* spp. and *Gliocladium* spp. growing on vermiculite-bran mixture (Lewis and Lumsden 2001).

Studies with yeasts also showed promising results in post-harvest control of *B. cinerea* in strawberry. *Sporidiobolus pararoseus* suppressed natural infections of *B. cinerea*, *Mucor* spp., *Penicillium* spp., and *Rhizopus* spp. in strawberry (Huang et al. 2012). Volatile organic compounds produced by *S. pararoseus* also suppressed mycelial growth and conidial germination of *B. cinerea* in vitro. Another yeast *Rhodotorula mucilaginosa* was also found to be effective in post-harvest protection of strawberry from *B. cinerea* (Zhang et al. 2013). Combining phytic acid, with *R. mucilaginosa* enhanced the efficacy of post-harvest protection in this study. Phytic acid is the primary storage form of phosphorus mainly found in cereal grains, legumes, and nuts and used as a food preservative.

Several entomopathogenic bacteria, fungi, nematodes, and viruses are also commercially available for managing a variety of arthropod pests on small fruits and greenhouse crops (Dara 2017; Wraight et al. 2017). Since bacteria (e.g., *B. thuringiensis* subsp. *kurstaki* against lepidoptera and *B. thuringiensis* subsp. *tenebrionis* against coleoptera) and viruses (e.g., Spodoptera exigua multiple nucleopolyhedrovirus) need to be ingested by the host insect to be infective, they are more suited for insects such as lepidopteran larvae that have chewing mouthparts. However, formulations based on metabolites of bacteria such as *Chromobacterium subtsugae* and *Burkholderia rinojensis* are also available as insecticides and acaricides. Entomopathogenic fungi (e.g., *Beauveria bassiana*, *Isaria fumosorosea*, *Lecanicillium lecanii*, and *Metarhizium brunneum*) infect hosts through contact and are popular in greenhouse management of thrips, whiteflies, aphids, mealybugs, scales, and other sucking pests and mites. The fungus, *Paecilomyces lilacinus* is available as a myconematicide for controlling plant parasitic nematodes. Entomopathogenic nematodes (e.g., *Heterorhabditis* spp. and *Steinernema* spp.), on the other hand, are ideal for soil pests or pests that have soil inhabiting life stages.

In general, entomopathogenic bacteria are used for lepidopteran and coleopteran pests, viruses for lepidopteran pests, nematodes for soil inhabiting stages, and fungi for mites, thrips, and sucking pests. Because of their contact mode of infection, entomopathogenic fungi can be used against almost all kinds of arthropod pests for soil and foliar treatments.

Multiple studies conducted in field or greenhouse strawberries in California showed that *B. bassiana*, *I. fumosorosea*, and *M. brunneum* can be potential control options for managing various arthropod pests (Dara et al. 2013; Dara 2015b, 2016). These studies suggested that combining or rotating entomopathogenic fungi with botanical or chemical pesticides is a better strategy for pest management. Synergism between *M. anisopliae* and entomopathogenic nematodes, *Heterorhabditis bacteriophora*, *Steinernema feltiae*, and *S. kraussei* was also seen against the black vine weevil, *Otiorhynchus sulcatus* under greenhouse conditions (Ansari et al. 2008, 2010).

Rhizosphere bacteria, mycorrhizae, and even entomopathogenic fungi that endophytically colonize plants are reported induce systemic resistance in plants to pests and diseases (Van Loon et al. 1998; Van Wees et al. 2008; Lopez et al. 2014; Mauch-Mani et al. 2017; When plants are treated or primed with these beneficial microbes, certain defensive genes are upregulated in a manner similar to pathogen-induced immune response helping them withstand pests and diseases. These beneficial microbes directly and indirectly contribute to improving crop health and yields and managing pests and diseases.

21.11 Entomovectoring or Beevectoring of Beneficial Microbes

Honey bees and bumble bees, which are used to enhance pollination in greenhouse berries can also be used to dispense the inocula of mycopesticides. This technology is referred to as beevectoring or entomovectoring and is now commercialized by companies such as Biobest (Flying Doctors®) and Bee Vectoring Technologies, which equip bee hives/boxes with trays that hold microbial pesticides. Since bees are employed to improve pollination in greenhouse berries, using them to deliver the inocula of beneficial microbes is an added advantage. Bees pick up the microbial pesticide formulations as they exit their hives and disperse them as they visit different flowers. *Gliocladium roseum* and *T. harzianum* have been successfully used for managing *B. cinerea* in strawberry for a long time (Peng et al. 1992; Kovach et al. 2000; Bilu et al. 2003). Bumble bee (*Bombus terrestris*) dissemination of *Gliocladium catenulatum* over 3 years resulted in a significant decrease in *B. cinerea* infections in field strawberry (Karise et al. 2016). Field study in lowbush blueberry reported a 10–20% decline in *B. cinerea* infections by *Clonostachys rosea* vectored by *B. impatiens* (Reeh et al. 2014).

Beevectoring can also be used for delivering entomopathogens for insect and mite control. In a caged field study in UK, Butt et al. (1998) demonstrated effective control of the pollen beetle, *Meligethes aeneus* with *Metarhizium anisopliae* delivered by honey bee, *Apis mellifera*. In a different study, *A. mellifera* carried and dispersed *Heliothis* nucleopolyhedrovirus in crimson clover fields causing significant infections in corn earworm (*Helicoverpa zea*) populations (Gross et al. 1994). They had observed 100% of beetle mortality in spring rape especially when the beetle and bee activity was the highest. Jyoti and Brewer (1999) reported that *Bacillus thuringiensis* delivered by *A. mellifera* was equal or superior to manual application in controlling the banded sunflower moth, *Cochylis hospes* and resulted in higher sunflower yields. In a greenhouse, *B. bassiana* (BotaniGard 22WP) was effectively delivered by *Bombus impatiens* without affecting their mortality (Shipp et al. 2012). Although survival of the minute pirate bug, *Orius insidiosus* was negatively impacted by *B. bassiana*, the level of parasitism by multiple parasitoids (against *T. vaporariorum* and *M. persicae*) and predation by *O. insidiosus* or the predatory mite *Amblyseius swirskii* (against *F. occidenatalis*) were not affected. Honey bee-vectored *B. bassiana* caused significant levels of infection in tarnished plant bug, *Lygus lineolaris*, in caged canola (Al Mazra'awi et al. 2006). Based on these studies, beevectoring can be a very effective tool especially in an enclosed greenhouse environment and could save on pesticides and their application costs.

21.12 Non-conventional Chemicals and Induced Resistance

In addition to the conventional pest and disease management practices, treating plants with certain minerals and chemicals can be a prophylactic strategy to induce systemic resistance and improve plant performance under biotic and abiotic stress factors. Abscisic acid, jasmonic acid, silicates, salicylate-based compounds, chitosan, beneficial bacteria, mycorrhizae and other treatments have a positive impact on crop growth, yield, and disease and pest resisting abilities (Archbold et al. 1997; Reddy et al. 2000; Dihazi et al. 2003; Holopainen et al. 2009; Meyer and Kirkpatrick 2011; Pieterse et al. 2014). Application of such materials is a good preventive and curative strategy in IPDM.

Methyl jasmonate, salicylic acid, methyl salicylate, and benzothiadiazole are some of the elicitors or compounds that stimulate plant defenses through the production of phenolic compounds (Holopainen et al. 2009). A significant reduction in crown rot caused by *Phytophthora cactorum* and *P. fragariae* var. *fragariae* was observed when strawberry plants were treated with putative disease resistance elicitors, acibenzolar-*S*-methyl and chitosan, a polysaccharide compound (Eikemo et al. 2003). Treating strawberry plants with chitosan, 5 or 10 days before harvest, significantly reduced postharvest *B. cinerea* incidence in storage (Reddy et al. 2000). Chitosan also improved strawberry quality in terms of fruit firmness and slower ripening. Similarly, natural volatile compounds like hexanal, methyl salicylate, and methyl benzoate inhibited *B. cinerea* in postharvest storage of strawberry, blackberry, and grape (Archbold et al. 1997). A laboratory study in Italy demonstrated that treating harvested strawberries with chitosan, benzothiadiazole, and a commercial formulation of calcium and organic acids up-regulated several defense genes (Landi et al. 2014). In table grapes, preharvest application of chitosan alone or in combination with postharvest irradiation with UV light improved protection from *B. cinerea* (Romanazzi et al. 2006). Carlen et al. (2004) reported the results of multiple greenhouse and field studies in Europe where commercial formulations of the synthetic elicitor, acibenzolar-S-methyl and the extract of giant knotweed, *Reynoutria sachalinensis* provided a good control of *P. aphanis* on strawberry. The extract of *R. sachalinensis* was as effective as fungicide treatments in controlling *B. cinerea*. Soil amendment with silicon, considered as a beneficial nutrient, resulted in a significant reduction of *P. aphanis* in high tunnel strawberry in Canada (Ouellette et al. 2017). Foliar application of silicon, on the other hand, had conflicting effects in reducing *P. aphanis* (Wang and Galletta 1998; Palmer et al. 2006). Silicon is thought to interfere with biotrophic or parasitic pathogens such as *P. aphanis* in finding target sites in the host plant (Vivancos et al. 2015).

21.13 General Guidelines for IPDM

General guidelines that prevent and control pests and diseases are listed below (Fig. 21.1):

- Choose cultivars that are resistant to pests and diseases especially in areas are prone to these problems.
- Obtain healthy and certified transplants, free of pests and diseases, from reputed nurseries.
- Inoculate transplants with beneficial microbes for a healthy start and to induce systemic resistance against potential pests and diseases. Continue periodical inoculation to maintain crop health.
- Use clean substrate or consider non-chemical fumigation alternatives to disinfest if substrate has to be used multiple times.
- Secure the greenhouse with proper screening, positive pressure ventilation, footbaths/sticky mats, double-doors, restricted accesses, and other measures that minimize the entry of pests.
- Maintain optimal temperature, relative humidity, ventilation, plant density that are ideal for healthy crop growth without promoting pest and disease populations.
- Regularly monitor crop health, pest and disease levels, and employ appropriate control measures as warranted by treatment thresholds.
- Maintain proper sanitation by removing dead, diseased, or infested plant material.

- Adopt ideal fertility and irrigation management practices as healthy plants can withstand pest and disease pressure and reduce the need for corrective treatments.
- Release predators and parasitoids to promote biological control.
- Make use of yellow sticky cards, pheromones, attractants, vacuums and other such mechanical or physical control options.
- Take advantage of botanical and microbial pesticides, biostimulants, and materials that induce systemic resistance and use chemical control options only when necessary.
- Use pollinators for delivering beneficial microbes that control pests and diseases.
- When chemical pesticides and fungicides are applied, be judicious in their use and rotate among different mode of action groups to reduce the risk of resistance development.

Fig. 21.1 Preventive, curative, maintenance, and regulatory approaches in IPDM

- Enforce regulatory control to prevent the spread of pests and diseases from nurseries and between greenhouse operations, to ensure application of recommended rates and amounts of pesticides, and to encourage IPDM practices.
- Implement good outreach efforts to disseminate information to the growers and pest management experts, and encourage grower collaboration and exchange of ideas for area-wide management of pests and diseases.
- Increase public awareness of invasive pests and diseases to prevent their accidental introduction, and of IPDM practices to promote their preference and thus sustainable management practices.

21.14 Conclusion

IPDM, by adopting a variety of management techniques, maintains high productivity while ensuring environmental sustainability and affordability. Sustainable practices such as IPDM may also improve the quality of the fruits as seen in the Asami et al. (2003) study where marionberry and strawberry had significantly higher antioxidant (total phenolic and ascorbic acid) content compared to conventionally produced berries. Such antioxidants are also important in plant defense against pests and diseases. As new crop protection technologies emerge, they need to be continuously evaluated and adopted as appropriate for pest and disease management in greenhouse berries. Outreach of IPDM practices, new research developments, and emerging threats, and regulatory changes is also important to enable growers for taking appropriate actions. While some pest management techniques might be guarded as proprietary information by some growers, exchanging best management practices and new ideas among the grower community helps address area wide issues. Increasing consumer awareness about IPDM practices and their contribution to healthy and sustainable food systems also promotes the adoption of IPDM.

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Chapter 22
Integrated Pest and Disease Management in Greenhouse Ornamentals

Margery Daughtrey and Rose Buitenhuis

Abstract Greenhouse ornamentals are part of a 55 billion USD global ornamentals industry. They present one of the greatest challenges to integrated pest and disease (IPDM) management because the crops are so diverse and often the entire plant must be aesthetically pleasing. Crop propagules are exchanged between continents, and new species and genera of host plants, pests and pathogens are being introduced constantly. This chapter notes the new or re-emerging insect, mite and disease problems that have been problematic in greenhouse ornamentals since the turn of the century. Public preference for ornamentals free from chemical residues is driving constant refinement of sustainable pest management methods. Production systems are unique for bedding plants, foliage plants, flowering potted plants, and cut flowers and foliage plants; these difference affect the key pests and diseases and IPDM approaches. The second section of the chapter covers tools and techniques for IPDM: monitoring, the systems approach, plant-based solutions; environmental solutions and control agents. A detailed thought process on how to manage western flower thrips is offered as an example of the integrated strategy needed to successfully manage a pest (and the viruses it vectors). Methods for extending information to growers are highlighted.

Keywords Greenhouse · Floriculture · Pests · Diseases · Systems approach · Biological control · Monitoring · Integrated pest management · Invasive species · Western flower thrips

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22.1 Overall Introduction

Greenhouse ornamentals are an important part of a large and valuable global ornamentals industry with an estimated value of 55 billion USD covering 650,000 ha (van Rijswick 2015). These crops are unique in their diversity and in the diversity of their production systems (Fig. 22.1). They include cut flowers and foliage, flowering potted plants, potted foliage plants, and bedding plants. Some are seasonal (poinsettia, Easter lily, annual bedding plants) and some have year-round demand

Fig. 22.1 Ornamental production systems often feature a multiplicity of crops in the same greenhouse: here coleus and New Guinea impatiens are grown adjacent to foliage plants

(cut flowers, foliage house plants). They are used for interior or exterior decoration for homes, businesses, or places of worship; they play a role in social interactions from dates to weddings to funerals to parades.

Ornamental crops have high value and are subject to rapidly fluctuating market trends. Consumers of ornamentals have a profound interest in what is new and different: crops may fall in or out of fashion. Purchasing behavior is subject to changes in lifestyle and trends in how people use their discretionary income.

Greenhouse growers of ornamental crops may specialize in certain stages of plant production, e.g. producing tissue culture plantlets, clean stock for cutting production, seedlings or rooted cuttings in small plugs used for transplanting, or plants for final sale to the consumer. Other businesses grow ornamentals from start to finish.

In order to keep crops more profitable and affordable, ornamentals production has become highly globalized, with the more labor intensive or energy-requiring aspects often being conducted in parts of the world with optimal environmental conditions and lower labor costs. Cut flowers, in particular, have become a crop of warmer climates in developing countries, shipped by airfreight to consumers in parts of the world where production costs would now be largely prohibitive. Similarly, the stock plants used to provide propagative material are often located in countries thousands of miles away from where greenhouse growers will root cuttings and finish crops for sale.

Because of their aesthetic *raison d'*ê*tre*, ornamentals must be essentially blemish-free, and this creates the highest of standards for ornamental pest and disease management programs. Historically the need for maintaining attractive foliage as well as flowers has been met by heavy pesticide use, but the paradigm has shifted to an integrated pest and disease management (IPDM) approach. This is beneficial for many reasons: it addresses the practical problems of a chemically-based approach, such as phytotoxicity and ineffectiveness of treatments due to the development of resistance, high cost, potential effects on worker health, and potential effects on the environment. In addition, modern consumers are increasingly unwilling to bring pesticide residues into their homes and gardens on either foodstuffs or ornamentals. Retailers and consumers are now interested in sustainable growing practices for ornamentals, with a particular interest in the health of pollinators. The observed increase in use of biological control in greenhouse ornamental crops, including beneficial microbes, is one indicator of this change having occurred in Europe and North America (van Lenteren et al. 2018). In Canada in 2001, for example, 26% of growers were using biocontrol for management of pests (Murphy 2002), and this grew to 69% by 2014 (Summerfield et al. 2015) and 92% in 2018 (Summerfield 2019). In the United States, change is slower than in Canada and Europe, but there has been considerable progress in the US from programs using no biocontrol to those that use biocontrol for at least one pest, and in some cases for multiple pest species.

Greenhouse ornamental growers are cognizant of the benefits of using a multifaceted (IPDM) strategy to manage their arthropod pests and diseases, utilizing careful sanitation practices, cultural techniques, and the best crop genetics in addition to biological and chemical management tools. Each production system and each crop has some unique features that require that their IPDM model be flexible, but the basic principles of IPDM are highly regarded and widely practiced by the greenhouse industry. Not only do IPDM practices allow reduction in the use of insecticides and fungicides, but in many instances they actually improve pest management by increasing prevention efforts and decreasing (often ineffective) reactive applications to insect epidemics and disease epiphytotics. The environmental stewardship and human safety considerations inherent in an IPDM plan are appreciated by growers, workers and neighbors of ornamental production businesses. These new approaches will help to keep these businesses viable even as horticultural production is increasingly conducted in highly populated areas. The development and refinement of reliable IPDM methods is critical for the greenhouse ornamentals industry. They are needed for the established crops and the all-too-familiar problems, but they are also needed for the new challenges ahead. New crops and new pest and disease problems are everyday features for those concerned with producing greenhouse ornamentals. Table 22.1 shows some of the new or re-emerging disease and insect problems in greenhouse ornamentals documented since 2000.

In this chapter we will first discuss characteristics of the **different greenhouse ornamental crop sectors and some of the major pest and disease management concerns/problems associated with these factors**.

A second section will describe the **techniques and tools for arthropod and disease management** available to the greenhouse ornamentals producer, with more detail provided on how these are deployed and how they perform (in research & practice), and how they may be integrated along with other activities in the greenhouse. Where there has been experience in application of IPDM methods, we will tell the story of successes in research or practice.

22.2 Important Disease and Arthropod Problems in Different Ornamental Crop Sectors

22.2.1 Bedding Plants

Bedding plants are fast-growing annual or herbaceous perennial plants for use outdoors in flowerbeds or planters in gardens or around buildings. Plants are started in greenhouses during late winter and early spring, and are sold and planted after the risk of frost outside has passed. Bedding plants are grown in a variety of formats and sizes, mainly in flats, pots, hanging baskets or even hanging plastic bags. It is quite common to grow several species of bedding plants in the same container to sell as mixed planters. The bedding plant business is mainly a local industry with limited exports and plants are sold in garden centers or big box stores. Pest and disease problems are found sporadically on many bedding plant crops (Chase et al. 2018) and their occurrence may be directly related to characteristics of greenhouse bedding plant production:

Table 22.1 Some new or re-emerging diseases and pests in greenhouse ornamental production reported since 2000

Disease or pest common name	Pathogen/pest	Some crops infected/infested	Selected reports
Alternanthera mosaic	*Alternanthera mosaic virus* (AltMV)	Angelonia, crossandra, portulaca, helichrysum, phlox, salvia, scutellaria, torenia	On portulaca: Eshenaur et al. (1995); On angelonia: Lockhart and Daughtrey (2008) On torenia: Duarte et al. (2008); On crossandra: portulaca and scutellaria, Baker et al. (2006)
Angelonia flower break	*Angelonia flower break virus* (AnFBV)	Angelonia, nemesia, phlox, verbena	Adkins et al. (2006) and Winter et al. (2006)
Bemisia tabaci biotype Q	*Bemisia tabaci* biotype Q	Many, including anthurium, begonia, chrysanthemum, fuchsia, gerbera, heather, hibiscus, hypoestes, lantana, pentas, poinsettia, sage, thyme, verbena	Dennehy et al. (2005) and MacKenzie et al. (2012)
Calibrachoa mottle	*Calibrachoa mottle virus* (CbMV)	Calibrachoa, petunia	Liu et al. (2003)
Calibrachoa powdery mildew	*Podosphaera xanthii*	Calibrachoa and other previously recorded hosts including verbena and petunia	Brielmaier-Liebetanz et al. (2015)
Calla lily chlorotic spot	Calla lily chlorotic spot virus (tentative tospovirus)	Calla lily	Chen et al. (2005a, b)
Chilli thrips	*Scirtothrips dorsalis*	South Asia 1: Rose, hedera, gardenia, gerbera, and others; East Asia 1: Hydrangea, azalea)	Silagyi and Dixon (2006), Dickey et al. (2015) and Scott-Brown et al. (2017)
Chrysanthemum white rust (CWR)	*Puccinia horiana*	Chrysanthemum and certain relatives	Bonde et al. (2015)
Coleus vein necrosis	*Coleus veinal necrosis virus* (CVNV)	Coleus and verbena	Mollov et al. (2007)
Coleus downy mildew	*Peronospora* sp.	Coleus, agastache	Daughtrey et al. (2006)
Echinothrips/ poinsettia thrips	*Echinothrips americanus*	Chrysanthemum, dieffenbachia, impatiens, Irish shamrock, poinsettia and others	Rosetta (2014) and Vierbergen et al. (2006)

(continued)

Table 22.1 (continued)

Disease or pest common name	Pathogen/pest	Some crops infected/infested	Selected reports
European pepper moth	*Duponchelia fovealis*	Azalea, begonia, chrysanthemum, coleus, croton, geranium gerbera, impatiens, kalanchoe, poinsettia, and others	Brambila and Stocks (2010)
Foxglove aphid	*Aulacorthum solani*	Calibrachoa, chrysanthemum, dianthus, pansy, petunia, salvia and others	Jandricic and Sanderson (2010)
Freesia sneak	*Freesia sneak virus* (FreSV)	Freesia, *Lachenalia* sp.	Verbeek et al. (2004)
Fusarium wilt	*Fusarium oxysporum* f. sp. *chrysanthemi*	Chrysanthemum, gerbera, osteospermum, and argyranthemum	Garibaldi et al. (2004) and Minuto et al. (2007)
Fusarium wilt	*Fusarium oxysporum* f. sp. *tracheiphilum*	Gerbera	Troisi et al. (2009)
Impatiens downy mildew	*Plasmopara obducens*	*Impatiens walleriana*, *I. balsamina* and other *Impatiens* species	Wegulo et al. (2004)
Japanese flower thrips	*Thrips setosus*	Hydrangea	Vierbergen and Loomans (2016)
Light brown apple moth	*Epiphyas postvittana*	Camellia, chrysanthemum, lupine, rose and others (over 250 associated genera)	California Dept. of Food and Agriculture (2018)
Melon thrips	*Thrips palmi*	Chrysanthemum, cyclamen, sunflower and others	CABI (2017)
Petunia chlorotic mottle	Petunia chlorotic mottle virus (PCMoV) (provisional name)	Petunia	Bratsch et al. (2017)
Petunia powdery mildew	*Oidium longipes*	Petunia and other previously reported hosts	Kiss et al. (2008)
Phytophthora root and crown rot	*Phytophthora capsici*	Calibrachoa, lupine and everlasting sweet pea; pothos (*Epipremnum aureum*)	Enzenbackeret al. (2015) and Wick and Dicklow (2002)
Phytophthora root and crown rot	*Phytophthora tropicalis*	Calibrachoa; cyclamen; vinca (*Catharanthus roseus*); pothos and English ivy (*Hedera helix*)	Enzenbacker et al. (2015), Gerlacher and Shubert (2001), Hong et al. 2008, and Orlikowski et al. (2006)
Phytophthora root rot	*Phytophthora chrysanthemi*	Chrysanthemum	Naher et al. (2011)
Plantago asiatica mosaic of lily	*Plantago asiatica mosaic virus*	Lily	Anonymous (2010)

(continued)

Table 22.1 (continued)

Disease or pest common name	Pathogen/pest	Some crops infected/infested	Selected reports
Sansevieria anthracnose	*Colletotrichum sansevieriae*	Sansevieria	Nakamura et al. (2006)
Southern wilt	*Ralstonia solanacearum* (phylotype 1, sequevar 14)	*Dipladenia, Osteospermum*, *Mandevilla*, *Sutera* and *Vinca major*	Bocsanczy et al. (2014) and Weibel et al. (2016)
Verbena virus Y	Verbena virus Y	Verbena	Kraus et al. (2010)

22.2.1.1 Seeds and Other Propagative Starter Material

Bedding plants are started from seed or from cuttings. Starting from seed may avoid many pest and disease concerns, although seed can still be a source of pathogens such as *Xanthomonas* spp., *Rhizoctonia solani* and *Alternaria* spp.—or even certain viruses. Many growers do not include the seeding step on their own premises, but instead bring in plants as well established "plug" seedlings, in trays, ready for transplanting to pots.

Although traditionally most bedding plants were grown from seed, there has been an increasing trend towards vegetative propagation in recent years. For example, today—over 25 years after the vegetatively propagated petunia was introduced—at least 10% of petunias produced in the U.S. are likely to be propagated from cuttings (Marvin Miller, Ball Horticultural Co., personal communication). Other crops such as verbena and calibrachoa are primarily grown from cuttings.

In vegetative propagation, stock plants are grown and encouraged to branch so that cuttings can be harvested regularly over a period of several months (Faust et al. 2017). Vegetative propagated material is shipped to growers directly as unrooted cuttings, or is rooted at specialized rooting stations and re-sold to growers as rooted cuttings. The health and pest status of these crops is generally determined by the quality of the IPDM at the propagator, rooting station or plug production greenhouse that passes the young plants (seedlings or unrooted/rooted cuttings) on to the finisher.

Pests or inoculum of pathogens may be introduced on the seedlings or cuttings of spring bedding plant crops. For example, starting from cuttings increases the likelihood that powdery mildew inoculum will arrive at a greenhouse along with the starter plants, and pests such as thrips, whiteflies (especially *Bemisia*), aphids, spider mites and broad mites may also be present on cuttings, causing problems right from the beginning of the crop. For example, broad mite can be a significant problem in New Guinea impatiens, as well as other crops. Presumably, it is commonly shipped on cuttings not yet showing symptoms. An additional concern is that propagation facilities for unrooted cuttings are often located abroad, which increases the potential for movement of new invasive pests and pathogens from country of origin to new countries. New technology for the offshore production of bare-root cuttings of bedding plants has just been introduced (Fig. 22.2).

Fig. 22.2 New technology announced at the California Spring Trials in April, 2018 will allow global shipment of rooted cuttings, as shown on these dahlias. (Photo courtesy P. Allen Hammer)

To comply with phytosanitary requirements at the border, stock plants for cuttings are often heavily treated with insecticides and fungicides, so any remaining pests (such as thrips, *Bemisia* and spider mites) and pathogens on cuttings are likely to be resistant to some pesticides (Frewin et al. 2014). To further complicate matters, pesticide residues on the cuttings may also affect the efficacy of biocontrol agents and jeopardize the success of biocontrol programs that are needed to manage pesticide-resistant pests or diseases at the finishing greenhouse.

22.2.1.2 Growing Medium

Bedding plant production has been the growth sector for the ornamentals industry since the development of soilless mixes in the early 1960s. The necessity to steam soil for use in a growing mix has now been all but eliminated because growers have adopted mixes based largely on peat, perlite and vermiculite, with occasional additional components such as peanut hulls, rice hulls, coconut coir or foam pellets. Peat-based mixes predominate at this time. High quality peat provides a consistent medium component with good cation exchange capacity and good drainage but without the rich microflora and nutrient components of mineral soil. Growers continue to experiment with alternative media because peat is a limited resource and an expensive media component. Using a soil-free growing medium helps to avoid fungi that cause damping-off of seedlings and subsequent root rot of older plants. Most nematode problems are also reduced in a soilless system. Pathogens, including *Globisporangium*/*Pythium, Thielaviopsis* and *Fusarium* spp., have been occasionally found in commercial bales of peat moss (Favrin et al. 1988; Kim et al. 1975; Graham and Timmer 1991), but contamination of growing media from reuse of trays and pots is a more important concern.

Certain insect pests are associated with peat-based growing media: fungus gnats, shore flies and moth flies all thrive in wet organic media. Bedding plant crops (especially geranium and vinca) may be plagued by fungus gnats, which may originate from contaminated growing media, from incoming plugs or be resident in the greenhouse. Fungus gnats may be injurious in their own right, by interfering with callusing or root development, or may be harmful because of vectoring or adding to injury of pathogens. They have been shown to spread *Thielaviopsis basicola* (Harris 1995), *Verticillium dahliae* (El-Hamalawi 2008a) and *V. albo-atrum* (Kalb and Millar 1986), and *Fusarium avenaceum* (El-Hamalawi and Stanghellini 2005); in some cases they have been reported as Pythium vectors (Goldberg and Stanghellini 1990). Other researchers have found, however, that fungus gnats did not vector *P. aphanidermatum* and even reduced infection by that pathogen, possibly through effects on the host (Braun et al. 2009). Fungus gnat larvae exhibited a preference for *Pythium*-infected over healthy geranium seedlings in laboratory tests, and adults also preferred to oviposit in media containing *Pythium* spp. or certain other tested microbes (Braun et al. 2012). Shore flies are known to vector bacteria, *V. dahliae*, *Fusarium oxysporum* f. sp. *basilicum* and *Thielaviopsis basicola* (El-Hamalawi 2008b), although they do not feed on roots or shoots directly. Moth flies have been shown to spread *Verticillium*, *Fusarium* and *Thielaviopsis* spp. experimentally (El-Hamalawi 2008a).

22.2.1.3 Production Time and Season

Bedding plant production is generally faster than that of other floriculture crops, which is advantageous as pests and pathogens have less time to reach damaging levels. Often production of bedding plants in temperate climates (as in northern North America or Europe) begins in the winter months, when pests and pathogens will not move in through open vents the way they may during the warmer season. Crawling pests such as mealybugs, spider mites and broad mites will be of minor importance, provided plant material is clean on arrival and the greenhouse has been sanitized between crops. Thrips, especially western flower thrips, and aphids are the main insect problems during the bedding plant season.

Due to their fast development time, thrips populations can increase rapidly to damaging levels. The thrips problem intensifies as temperatures increase and flowers with pollen become more abundant in the later months of bedding crop production. Some plants, e.g. ivy geraniums, are injured outright by thrips feeding, showing leaf distortion and silvery feeding scars. Other crops are injured primarily because of the thrips' vectoring capacity, as they spread both *Impatiens necrotic spot virus* (INSV) and *Tomato spotted wilt virus* (TSWV). Crops including zinnia, verbena, impatiens, New Guinea impatiens, and certain begonias are all highly susceptible to INSV and TSWV vectored by thrips.

Aphids, especially foxglove aphids, thrive under spring conditions (Jandricic et al. 2010) and their toxic saliva causes deformations of growing plant tissue. A few spring bedding crops (e.g. calibrachoa, pansy) are particularly vulnerable to aphids. Some of the broad host range viruses such as *Cucumber mosaic virus* (CMV), *Lettuce mosaic virus* (LMV) and *Potato Virus Y* (PVY) are aphid-vectored, but these are fortunately not frequently seen in bedding plant crops. Cool temperatures, low light conditions and short daylength during early spring hamper the efficacy of aphid predators such as *Aphidoletes aphidimyza* that diapause under these conditions, making biological control challenging. In addition, the potential loss of neonicotinoid pesticides, due to concerns about their negative impact on pollinator health, would take away an important aphid management tool—one that is relatively compatible with established biological control programs against other pests in bedding plants.

Whiteflies are more rarely encountered, but may trouble lantana, verbena and Regal geraniums, among others. Greenhouse whitefly (*Trialeurodes vaporariorum*) can fly in from weeds or other plants grown in the same greenhouse. In temperate climates, *Bemisia tabaci* primarily is introduced on cuttings, as it does not survive outside in winter.

Pests not managed well during bedding plant production may linger in the greenhouse into the summer and continue to cause problems on fall crops.

22.2.1.4 Variety of Bedding Plant Species Grown in the Same Greenhouse

Bedding plants include many familiar annuals and, increasingly, herbaceous perennial species (see Table 22.2). New cultivars, as well as new species, are introduced each year. Usually, a wide variety of species and cultivars from different propagators are grown in the same greenhouse structure or compartment at the same time. This multiplies the risk of introduction of pests and pathogens, which can spread quickly throughout the greenhouse. It also makes the design of pest and disease management programs more complicated, because different crops have different needs.

Sometimes even the diversity of container shapes and sizes can cause difficulties. Hanging baskets, suspended a few meters above greenhouse benches or hung high above walkways, are difficult to scout and to treat if a problem occurs. Once the foliage expands, problems with thrips, powdery mildew or tospoviruses easily go unnoticed in a hanging basket. If hanging baskets are not carefully managed, they can be a breeding ground for many problems. This is unfortunate because hanging baskets stay in the greenhouse for the longest period of time, often contain many of the most thrips-attractive crops, and are grown at higher temps than floor or bench crops (promoting more rapid pest development). Thrips pupae can drop to crops below, allowing for easy spread. Pathogens may drip down onto bench or floor level crops as well. Other types of multi-level growing similarly increase pest management challenges. Some bedding plant growers utilize rolling benches above floor-level crops, sending the benches outdoors on railings in good weather. Again, this complicates both scouting and treatment for pests and diseases.

In addition to ornamentals, an increasing portion of bedding plant business is devoted to the production of vegetable and herb transplants. The juxtaposition of edible with ornamental crops has an important impact on pest management actions, as the fungicides and insecticides labeled for use on ornamentals are often not

Table 22.2 Key pests and diseases of common bedding plants

Crop	Key pests	Key diseases
Ageratum	Whiteflies, thrips, aphids, two-spotted spider mite	TSWV, INSV
Alyssum	Whiteflies, thrips, aphids	Rhizoctonia, downy mildew
Basil	Whiteflies, thrips	Fusarium wilt, INSV/TSWV, downy mildew
Begonia	Fungus gnats, broad mites	Damping off (*Rhizoctonia solani*; *Globisporangium*/*Pythium* spp.), Botrytis blight, *Fusarium foetens*, INSV, TSWV
Calibrachoa	Thrips, aphids	Calibrachoa mottle, powdery mildew, Thielaviopsis root rot
Celosia	Thrips, aphids	Rhizoctonia damping off
Cyclamen	Thrips, aphids, two-spotted spider mite, cyclamen mite, fungus gnats	INSV/TSWV, Fusarium wilt, Botrytis blight, bacterial soft rot, anthracnose (*Cryptocline* and *Glomerella*)
Dahlia	Aphids, thrips	Botrytis blight, INSV, TSWV, Powdery mildew, Pythium root rot
Dianthus	Thrips	Botrytis blight, bacterial leaf spot (*Burkholderia andropogonis*)
Gazania	Thrips	Rhizoctonia stem and root rot
Geranium, zonal (cutting grown)	Fungus gnats, whiteflies, foxglove aphid, two-spotted spider mite	Botrytis blight, bacterial blight (*Xanthomonas hortorum* pv. *pelargonii*), root rot (*Pythium* and *Globisporangium* spp.), rust, Fe/Mn toxicity at low pH, Southern wilt (*Ralstonia solanacearum*)
Geranium, ivy (cutting grown)	Thrips, two-spotted spider mite, whiteflies, fungus gnats, broad mites	Bacterial blight (*Xanthomonas hortorum* pv. *pelargonii*), oedema
Geraniums, hybrid (seed-grown)	Whiteflies, fungus gnats	Botrytis blight, Pythium root rot, bacterial blight (*Xanthomonas campestris* pv. *pelargonii*), Pseudomonas leaf spot, Acidovorax leaf spot
Gerbera daisy	Thrips, aphids, whiteflies, two-spotted spider mite, leafminer, broad mites	INSV, TSWV, Pythium root rot, Pseudomonas leaf spot, powdery mildew
Herbs, esp. vegetatively propagated	Whiteflies, aphids, thrips, two-spotted spider mite, mealybugs,	On various species: *Rhizoctonia*, *Pythium/ Globisporangium,* powdery mildew, downy mildew, rust
Impatiens walleriana and hybrids	Thrips, aphids, broad mites, two-spotted spider mite	TSWV, INSV, Pseudomonas leaf spot, Alternaria leaf spot, crown rot (*Rhizoctonia solani*), Pythium root rot, Botrytis stem & leaf blight, downy mildew

(continued)

Table 22.2 (continued)

Crop	Key pests	Key diseases
Kale and cabbage, ornamental	Imported cabbage worm, diamondback moth	*Xanthomonas campestris* pv. *campestris*
Lantana	Whiteflies	Rhizoctonia root/stem rot
Marigold	Thrips, aphids, leafminer, two-spotted spider mite	Botrytis blight, Alternaria leaf spot, micronutrient toxicity (Hi Fe or Mn), aster yellows
New Guinea impatiens	Thrips, broad mites	INSV, TSWV, crown rot (*Rhizoctonia solani)*, crown rot (*Globisporangium cryptoirregulare*), Botrytis stem and leaf blight, Myrothecium and Phyllosticta leaf spots
Pansy	Aphids, thrips	Black root rot (*Thielaviopsis basicola*), downy mildew, crown rot (*Phytophthora nicotianae*), Cercospora leaf spot, anthracnose, powdery mildew, Myrothecium stem rot
Petunia	Thrips, aphids	Powdery mildew, *Tobacco mosaic virus* (TMV), Thielaviopsis root rot, *Sclerotinia sclerotiorum*
Pepper, ornamental	Thrips, aphids	TSWV, INSV, Xanthomonas leaf spot
Portulaca	Thrips	INSV, *Alternanthera mosaic virus* (AltMV)
Primula	Aphids, thrips, whiteflies	Botrytis, INSV, TSWV, Pythium root rot
Ranunculus	Aphids, thrips	INSV, TSWV, powdery mildew, Xanthomonas leaf spot
Rosemary		Botrytis; Pythium and Fusarium root rot, Rhizoctonia blight; powdery mildew
Salvia	Aphids, whiteflies	Downy mildew, Rhizoctonia stem rot, *Sclerotinia sclerotiorum*
Snapdragon	Thrips, aphids	Pythium root rot, downy mildew, Botrytis blight
Torenia	Aphids, whiteflies, thrips	Powdery mildew, INSV
Verbena	Thrips, aphids, two-spotted spider mite	Verbena virus Y (provisional name), TSWV, INSV, Phytophthora crown rot, powdery mildew
Vinca vine (*Vinca major*)	Two-spotted spider mite, aphids	Rhizoctonia crown rot, Thielaviopsis root rot, Phoma canker
Vinca (Madagascar periwinkle, *Catharanthus roseus*)	Thrips, broad mites, fungus gnats, aphids	Rhizoctonia damping off and crown rot, *Phytophthora nicotianae*, Rhizoctonia stem rot
Zinnia	Whiteflies, thrips, melon and green peach aphids	TSWV, INSV, bacterial leaf spot (*Xanthomonas campestris* pv. *zinniae*), Alternaria leaf spot, Botrytis blight

INSV impatiens necrotic spot virus, *TSWV* tomato spotted wilt virus labeled for use on edibles as well. Growers can produce these two crop sectors in different areas, or can elect to have an organic program or one using least-toxic, broadly labeled materials, with an emphasis on biological and biorational materials.

In many areas with a temperate climate, production of bedding plants is limited to spring and early summer. If no other crops are grown, facilities will be empty of crops by mid-summer or mid-fall, allowing for a thorough clean-up and fallow period before the next bedding plant season in late winter/early spring, when plugs or pre-finished material is brought into the greenhouse again. Removing the host plants for a prolonged period allows a break in the pest management continuum, although it should be noted that at cool temperatures, pests and pathogens can persist for long times without a host.

22.2.2 Potted Foliage Plants

The foliage industry is concentrated largely in tropical and subtropical parts of the world (Chen et al. 2005a, b). Foliage plants typically include many genera in the Agavaceae, Araceae, Araliaceae and Arecaceae as well as some notable crops outside those genera, including *Aphelandra*, *Maranta* and *Sedum*. Sedums and other succulents are seeing new importance today as principal components of green roof plantings. Stock plants for propagation are frequently located in countries where labor is less expensive, and then cuttings or cane sections received from such “off-shore” locations may be rooted and finished by greenhouse operations in temperate climates. Both Florida and California have significant foliage plant production in the United States, while foliage plant production is a continuing, but less important sector of glasshouse production in colder climates. Sales in Florida’s foliage industry alone were over $21 billion in 2015 (FNGLA 2018). The benefits to indoor air quality from houseplant use and interior green walls are inspiring a continuing market for foliage plants.

22.2.2.1 Seeds and Other Propagative Starter Material

Material for foliage plant propagation includes seed, cuttings and cane sections, as well as tissue culture. Cultivars of many of the most popular foliage plants, including dieffenbachia, philodendron, spathiphyllum, cordyline and ficus, are often micropropagated through tissue culture (Chen and Henny 2006). Tissue culture production supports fast introduction of improved plant types, which make it a good system for multiplying new cultivars less prone to insect pests and diseases. See Table 22.3 for a listing of some important foliage plants and their key pest and disease problems. The cleanliness of foliage plant starter material has been improving over time, but sources vary in this respect, so growers finishing these crops should seek out a reliable supplier.

Table 22.3 Key pests and diseases of common foliage crops

Crop	Key pests	Key diseases
Aglaonema	None	Bacterial soft rot (*Dickeya* and *Pectobacterium* spp.), nematodes, Fusarium stem rot
Aphelandra	Aphids, mites, scales, thrips	Corynespora and Myrothecium leaf spots, Phytophthora stem rot, and Pythium root rot
Caladium	Aphids, thrips, mealybugs two-spotted spider mite	Bacterial soft rot (*Pectobacterium carotovorum*), Bacterial leaf spot (*Xanthomonas axonopodis* pv. *dieffenbachiae)*, *Dasheen mosaic virus* (DMV), Fusarium tuber rot, Pythium root rot (*Pythium myriotylum*), Rhizoctonia root rot and blight, *Sclerotium rolfsii*
Cordyline (Ti plant)	Mealybugs, scale	Bacterial blight (*Pectobacterium* and *Dickeya* spp.), Fusarium leaf spot and stem rot, Phytophthora and Phyllosticta leaf spots, Southern blight (*Sclerotium rolfsii*)
Dieffenbachia	Aphids, mealybugs, scale, two-spotted spider mite and thrips	Bacterial blight (*Dickeya* and *Pectobacterium* spp.), *Xanthomonas axonopodis* pv. *dieffenbachiae*, *Dasheen mosaic virus* (DMV)
Dracaena	Mealybugs, scale, thrips, two-spotted spider mite	Fusarium leaf spot, Pythium root rot, bacterial soft rot, Rhizoctonia stem rot
English ivy (*Hedera helix*)	Fungus gnats, two-spotted spider mite	*Xanthomonas hortorum* pv. *hederae*, anthracnose, Rhizoctonia stem rot, *Phytophthora palmivora* stem rot
Ferns (*Nephrolepsis exaltata* and others)	False spider mites, Florida fern caterpillar (*Callopistria floridensis*), mealybugs, scale, and thrips	Rhizoctonia aerial blight
Ficus (F. *benjamina*, *F. elastica*, etc.)	Mealybugs, scale, thrips, two-spotted spider mite	Phomopsis twig canker, Pythium root rot, Fusarium root rot, Rhizoctonia stem and root rot, bacterial leaf spot (*Xanthomonas campestris* pv. *fici*), *Xanthomonas axonopodis* on rubber tree
Maranta	Mites, scales, root mealybugs	*Cucumber mosaic virus* (CMV), Drechslera leaf spot
Palms (Parlor, Majesty and Lady Palms, and others)	Two-spotted spider mite, aphids, scale, mealybugs, thrips	Damping off (*Globisporangium*/*Pythium, Phytophthora, Fusarium, Rhizoctonia* spp.); little foliar disease in covered cultivation
Philodendron	Aphids, mealybugs and scale	*Xanthomonas axonododis* pv. *dieffenbachiae*, bacterial soft rot (*Dickeya* sp.)
Pothos (*Epipremnum aureum*)	Two-spotted spider mite, scale, mealybugs	Pythium root and stem rot
Sedum spp.	Aphids, thrips, mealybugs	Fusarium and Pythium root rots, Rhizoctonia stem and root rot, Powdery mildew, INSV

(continued)

Table 22.3 (continued)

Crop	Key pests	Key diseases
Schefflera	Mealybugs, two-spotted spider mites, aphids, scale	Alternaria leaf spot, bacterial leaf spot (*Xanthomonas hortorum* pv. *hederae*)
Spathiphyllum	Aphids, caterpillars, mealybugs, scale, thrips and whiteflies.	*Cylindrocladium spathiphylli,* Phytophthora and Pythium root rots, Myrothecium leaf spot
Nephthytis (*Syngonium podophyllum*)	Mealybugs, scale and spider mites	Bacterial leaf spots (*Pectobacterium* and *Dickeya* spp.), bacterial leaf blight (*Xanthomonas campestris* pv. *syngonii),* Cephalosporium leaf spot, black cane rot (*Ceratocystis fimbriata*), Myrothecium leaf spot and Rhizoctonia aerial blight

INSV impatiens necrotic spot virus, *TSWV* tomato spotted wilt virus

22.2.2.2 Growing Media and Irrigation

Similar growing media are used for foliage plants as for bedding plants and flowering potted plants: they are primarily coir- or peat-based. Maintaining good drainage in organic substrates is important for good root health. In production areas specialized for foliage plants, irrigation is commonly either subirrigation (for smaller plants) or drip irrigation (for larger plants). Subirrigation reduces water usage as well as reducing certain foliar disease problems whose spread is promoted by overhead watering. Foliage plants are especially prone to diseases caused by bacteria, which are easily splashed from one plant to another. Subirrigation is not always the solution to disease management, however: *Ralstonia solanacearum* is one example of a dangerous pathogen that is easily spread by water to infect root systems of other plants sharing a common water reservoir.

22.2.2.3 Production Time, Season and Location

Foliage plant production is a year-round business, generally not tied to holidays or time of year. A trend in the early twenty-first century towards tropicals as bedding plants has led to some foliage plants being used in northern gardens during the growing season. The majority of foliage plants, however, are used to create plantings in interior settings, both public and private, in the north and outdoor plantings in frost-free areas. The salient feature of foliage plant production systems is that the plants are usually propagated in warm, humid climates to minimize heating costs. Many foliage plants for the European market are propagated in developing countries in Africa, for example, where the climate is ideal. For the United States, foliage plant propagative material often comes from Central America. In the tropical and subtropical areas where foliage plants are propagated, population growth of both pests and diseases is often greatly fostered by the prevailing warmth and humidity—thus businesses receiving foliage plants for growing-on may regularly find themselves needing to curb already-established populations of (often pesticide-resistant) insects, mites and pathogens.

22.2.3 Flowering Potted Plants

Flowering potted plants are grown in the greenhouse until they reach the flowering stage, at which point they are sold for use indoors. Some species (such as poinsettias, Easter lilies or daffodils) are grown for a specific season or holiday, while others such as chrysanthemums and mini-roses are grown year-round. However, even year-round cropping programs such as the above will be expanded and intensified for occasions such as Valentine's Day, Easter and Mother's Day. Crops must be carefully scheduled: short days are sometimes required to induce flowering (as for poinsettia and chrysanthemum) or black-out curtains are used to create the right conditions. After they are sold, potted flowering plants may last longer than a bouquet of cut flowers, but usually they are discarded when the flowering period is over. However, with a bit of care, these plants can be maintained as a houseplant for longer periods and even be made to flower again.

The production of flowering potted plants is mainly a local industry with limited exports due to restrictions for moving soil or substrate over international borders, as this is regulated as a high-risk pathway for the introduction of quarantine plant pests and diseases. However, soil-free propagative starter material, in the form of unrooted cuttings, travels globally. New technology will also allow the international shipment of substrate-free, rooted cuttings. Finished plants are sold in garden centers, florist shops, big box stores and supermarkets. The variety of flowering potted plant species grown in the same greenhouse is typically less than that seen in bedding plant production. In larger operations, growers of flowering potted plants only grow one plant species per greenhouse compartment, yet there will be several different cultivars to provide consumers with a range of colors and flower shapes, and plants may be grown at different levels to more efficiently utilize greenhouse space (Fig. 22.3). Growing practices are generally very similar among cultivars, but susceptibility to pests and diseases can vary greatly. For example, considerable variation exists among chrysanthemum cultivars in susceptibility to damage by thrips, leafminers and spider mites (Kos et al. 2014). Major potted flowering crops include poinsettia, gerbera, chrysanthemum, cyclamen, holiday cactus, mini-roses, kalanchoe, phalaenopsis orchids, hydrangea and various bulb crops. See Table 22.4 for a more extensive list of potted flowering crops, along with their commonly associated pest and disease problems.

22.2.3.1 Seeds/Propagative Starter Material/Tissue Culture/Bulbs

Flowering potted plants can be started from seed, vegetative cuttings, tissue culture plantlets or bulbs. Similar to bedding plants, seeds of flowering potted plants can carry pathogens such as *Globisporangium* or *Pythium* spp. or *Rhizoctonia solani*. Many crops are started from vegetative cuttings to ensure the stability of desired traits and high success rate in propagation (Faust et al. 2017). However, vegetative cuttings can arrive from the propagator's facility already infested with cosmopolitan

Fig. 22.3 Ornamental crops grown at multiple levels present challenges for scouting, deploying biocontrols and treating with pesticides

or exotic pests or pathogens that may or may not be pesticide resistant. For example, the whitefly *Bemisia tabaci* is regularly found on poinsettia cuttings (Cuthbertson et al. 2011; Frewin et al. 2014) and mandevilla, while chrysanthemum cuttings may arrive infested with western flower thrips (Romero 2011) and spider mites (Buitenhuis, unpublished data). All three pests are known to be commonly resistant to multiple chemical pesticides (Arthropod Pesticide Resistance Database, IRAC), and pesticide residues on the cuttings may negatively affect the efficacy of biological control agents, limiting growers' control options.

Similarly, low levels of powdery mildew fungi or leaf spot pathogens may unwittingly be introduced on plugs or cuttings, and these may likewise have pesticide resistance issues. Rooting of cuttings is often done under mist, or under plastic to maintain high humidity. Many root rot and leaf spot problems start to spread in the wetter conditions of propagation, only to become obvious later in production when infected plants show more conspicuous stunting or spotting.

Bulb mites (*Rhizoglyphus* species) are a particular problem on imported bulbs, such as lilies or tulips. These mites feed on the bulb, causing weakened plants, stunted, off-color leaves and deformed flowers. Furthermore, their damage can be the ideal breeding ground for pathogens. Their control is difficult because bulb mites are located between the inner scales of bulbs, where they are difficult to reach with sprays or predators. Sclerotia of *Botrytis* spp. or other pathogens on bulbs are also resistant to treatment, and serve to introduce disease to potted plant production.

Table 22.4 Key pests and diseases of common flowering potted plants

Crop	Pests	Diseases
African violet	Thrips, cyclamen mites, mealybugs	Powdery mildew, Phytophthora crown rot (*Phytophthora nicotianae*)
Amaryllis	Bulb mites, aphids, mealybugs, spider mites, thrips, fungus gnats	Leaf scorch/red fire (*Stagonospora curtisii*), *Hippeastrum mosaic virus* (HiMV), TSWV
Anthurium	Aphids, thrips, spider mites, scales, potworms, *Duponchelia*	Bacterial blight (*Xanthomonas axonopodis* pv. *dieffenbachiae*)
Azalea	Tarsonemid mites, Azalea leafminer, black vine weevil	Phytophthora root rot, Cylindrocladium blight, azalea leaf gall (*Exobasidium japonicum*), Rhizoctonia web blight
Begonias (Hiemalis, non-stop, etc)	Aphids, mealybugs, mites, thrips, whiteflies	Bacterial blight (*Xanthomonas axonopodis* pv. *begoniae*), powdery mildew, Botrytis blight, INSV, TSWV
Bougainvillea	Aphids, brown soft scale, thrips, bougainvillea looper *Disclisioprocta stellata* (Guenee), whiteflies	Magnesium deficiency; bacterial leaf spot (*Burkholderia andropogonis*); crown rot (*Phytophthora nicotianae*)
Bulbs, potted (tulips, daffodils, hyacinth etc)	Bulb mites	Fusarium wilt, Pythium root rot, Botrytis blight
Calla lily (*Zantedeschia* sp.)	Thrips, fungus gnats	Bacterial soft rots (*Pectobacterium* and *Dickeya* spp.), *Dasheen mosaic virus* (DMV), TSWV, *Turnip mosaic virus* (TuMV), *Zantedeschia mosaic virus* (ZaMV), *Zantedeschia mild mosaic virus* (ZaMMV), *Konjac mosaic virus* (KoMV) and *Carnation mottle virus* (CarMV)
Chrysanthemum	Thrips, spider mites, leafminers, *Duponchelia*, aphids	Chrysanthemum white rust (*Puccinia horiana*), Chrysanthemum brown rust (*P. chrysanthemi*), TSWV, Pythium root rot (*Pythium aphanidermatum*)
Cyclamen	Thrips, fungus gnats, cyclamen mite, potworms	Fusarium wilt, anthracnose, Botrytis blight
Gerbera	Thrips, tarsonemid mites incl. broad mites, leafminer, whiteflies	Phytophthora crown rot (*Phytophthora cryptogea*), Fusarium wilt, Powdery mildew, Botrytis blight
Gloxinia	Aphids, thrips	TSWV, INSV, Phytophthora crown rot
Hellebore (Lenten rose)	Aphids, thrips	Botrytis blight, TSWV, INSV, *Hellebore net necrosis virus* (HeNNV), downy mildew
Hibiscus	Aphids, whitefly (especially *Bemisia)*, two-spotted spider mite, thrips	Bacterial leaf spot (*Pseudomonas cichorii* and others), powdery mildew, *Hibiscus chlorotic ringspot virus* (HCRSV)

(continued)

Table 22.4 (continued)

Crop	Pests	Diseases
Holiday cactus (*Hatiora*, *Schlumbergera truncata* and *Schlumbergera* hybrids)	Fungus gnats, thrips	Bacterial soft rot, Pythium and Phytophthora root and stem rots, Bipolaris blight (*B. cactivora*), and Fusarium basal stem and root rot, TSWV, INSV
Hydrangea	Aphids, two-spotted spider mite	Botrytis blight, powdery mildew, *Hydrangea ringspot virus* (HdRSV)
Kalanchoe	Thrips, aphids, fungus gnats, potworms	Bacterial soft rot (*Dickeya* and *Pectobacterium* spp.) powdery mildew, Stemphylium leaf spot, INSV, TSWV
Lilies —Easter, Asiatic, etc. (*Lilium* spp.)	Bulb mites, aphids, fungus gnats	Pythium/Globisporangium root rot, Rhizoctonia root rot, Botrytis blight (*Botrytis elliptica* and *B. cinerea*), *Lily symptomless virus* (LSV) and *Lily mottle virus* (LMoV)
Mandevilla	Aphids, mealybugs, scales, whitefly (especially *Bemisia*), thrips, two-spotted spider mite	Fusarium root rot, Phytophthora root rot, Southern wilt, anthracnose, Cercospora leaf spot, Corynespora leaf spot, *Cucumber mosaic virus* (CMV)
Mini-rose	Thrips, two-spotted spider mite, aphids, fungus gnats	Powdery mildew, Cylindrocladium root rot, Rhizoctonia root rot, downy mildew
Phalaenopsis orchid	Fungus gnats, mealybug, scale, thrips, mites, potworms	Bacterial leaf spot (*Acidovorax* sp.), Bacterial soft rot (*Pectobacterium* and *Dickeya* sp.) *Cymbidium mosaic virus* (CymMV); *Odontoglossum ringspot virus* (ORSV)
Poinsettia	Whiteflies (both greenhouse whitefly and *Bemisia*), Lewis mite, Fungus gnats	Xanthomonas leaf spot (*Xanthomonas axonopodis* pv. *poinsettiicola*), root rot (*Pythium aphanidermatum*), Botrytis blight, Powdery mildew, (*Pseudoidium poinsettiae*)
Ornamental pepper	Aphids, thrips, two-spotted spider mite, tarsonemid mites	Bacterial leaf spot (*Xanthomonas campestris* pv. *campestris*), INSV, TSWV
Primula	Aphids	Botrytis blight

22.2.3.2 Growing Medium

Pests associated with the growing medium are similar to those of bedding and foliage plants. When rooted cuttings are brought into the greenhouse, root rot pathogens such as *Phytophthora*, *Pythium*/*Globisporangium*, *Rhizoctonia* or *Thielaviopsis* spp. may easily be introduced. Using unrooted cuttings brings partial protection against introducing root pathogens to the greenhouse, but low levels of inoculum on leaves and stems of cuttings are still possible. One occasional pest, attacking roots of several potted plants (e.g. phalaenopsis, anthurium, kalanchoe), is potworm. There are different species that are all called potworm, mainly from the Keroplatidae (*Lyprauta* sp.) or Mycetophilidae (*Scophila* sp.). Potworm larvae damage the roots and create a layer of unsightly fungus-like webbing on top of the substrate.

22.2.3.3 Production Time and Season

In general, flowering potted plants have intermediate-length production cycles (generally longer than bedding plants)—about 10 weeks or longer, which means that pests and diseases have to be controlled fast to avoid visible damage at sale time. In addition, the whole plant is sold, so there is little tolerance for visible damage.

One of the challenges of year-round, weekly production of potted flowers (e.g. chrysanthemum, mini-roses, gerbera, kalanchoe, phalaenopsis) is the constant presence of susceptible plant material. Older plants can be a source of infection for younger plants and the greenhouse is never empty for a complete disinfection. It is for example very difficult to manage thrips or leafminer in a weekly production of chrysanthemums without physically separating infested plants from new plants in different greenhouse compartments. Airborne spore inoculum (of powdery mildew or downy mildew) presents a similar challenge.

In holiday crops like poinsettia or Easter lily, the time of year can create unique challenges. Conditions during the finishing of poinsettias are extremely favorable for the development of powdery mildew (*Pseudoidium poinsettiae*), which is fostered only after greenhouse temperatures stay below 30°C. Poinsettia crops are started during the hottest part of the summer, ideal conditions for whiteflies even in temperate areas of North America and Europe. Only around October do cooler temperatures naturally lead to a slow-down of whitefly population growth. Summer propagation also positions poinsettias and chrysanthemums for problems with *Pythium aphanidermatum*, a heat-loving root rot pathogen. Easter lilies have the opposite problem: this crop is started in winter, when pest pressure is low. However, warmer temperatures in spring just before shipping can stimulate pests like aphids and growers have to find a fast-acting method to control these pests and limit damage before the lilies are shipped. In terms of disease challenges, Easter lilies with their cooler, early-season start are particularly prone to Botrytis blight and root rots caused by *Globisporangium ultimum* (syn. *Pythium ultimum*) or *Thielaviopsis basicola*. In the past, temperatures for poinsettias were lowered at the end of production to hold them, leading to a cascade of root rot problems from cool-temperature loving *Pythium* spp. that originated from soil in the growing media. Because the crop is finished earlier in the fall now, in soilless mixes, this late-season root rot has been virtually eliminated.

22.2.4 Cut Flowers and Cut Foliage

The greenhouse cut flower industry is dominated by a few countries that supply the world with products. The main production areas are located in Colombia, Ecuador, Kenya, Ethiopia, the Netherlands and Malaysia. The principal reasons for growing cut flowers outside Europe and the US are the better climate, lower costs for labor, land and energy, and the economic value to the less developed countries. This arrangement also lowers retail prices and increases the choice of cut flower species for consumers. The United States import the most cut flowers (17%), followed by Germany (15%), UK (14%) and the Netherlands (11%) (van Rijswick 2015). Consequently, cut flowers are shipped all over the world by airplane and increasingly by sea container. Post-harvest conditions and procedures are of utmost importance to guarantee good flower performance at retail and for the consumer. In addition, all shipped plant material has to be essentially pest- and disease-free to comply with phytosanitary regulations at the border. Cut flowers go to auction and/or pass through several distribution and wholesale channels before they are sold at florists' shops, markets and supermarkets. Many European and North American countries still maintain a domestic cut flower industry for certain crops, like cut gerbera and other flower species that are more difficult to transport, so in this section we will discuss challenges for both temperate and subtropical climates. The most popular cut flower crops are roses, chrysanthemums, carnations and gerberas (see Table 22.5 for a more extensive list).

22.2.4.1 Starting Material

Some of the most important cut flower crops, such as carnations and chrysanthemums, are started from culture-indexed and virus-indexed stock. Cuttings from these indexed stock plants are certified as free from significant systemic diseases. For carnations, the most important consideration is freedom from *Fusarium oxysporum* f. sp. *dianthi*, while chrysanthemums must be grown from cuttings that are free from *Fusarium oxysporum* f. sp. *chrysanthemi*. Roses and gerberas are more likely to be propagated in-house, but the highest quality material is obtained from stock maintained free from known viruses. However, it is more difficult to guarantee that starting material is completely free of insect and mite pests (see discussion on infested cuttings in previous sections).

22.2.4.2 Substrate

For cut flowers, the growing substrate varies. For crops such as chrysanthemum and snapdragon, it is often amended field soil, in ground beds. The soil used for cut flower culture is periodically disinfested by steam pasteurization. Amendments employed might include composts or coconut coir. In addition to fungi, soilborne

Table 22.5 Key pests and diseases of common cut flower crops

Plant	Key Pests	Key Diseases
Alstroemeria	(foxglove) aphids, thrips	*Alstroemeria mosaic virus* (AlMV); *Puccinia*, *Aecidium*, *Uromyces* and *Uredo* rusts
Anthurium	Mites, scales, mealybugs	*Xanthomonas axonopodis* pv. *dieffenbachiae*
Carnation	Two-spotted spider mites	*Fusarium oxysporum* f. sp. *dianthi, Pseudomonas andropogonis,* fairy ring spot-*Mycosphaerella dianthi* (syn. *Cladosporium echinulatum*)*, Uromyces dianthi, Botrytis cinerea, Carnation mottle virus* (CarMV), root knot nematode
Chrysanthemum	Leafminer, thrips, two-spotted spider mites, aphids (including chrysanthemum aphid)	Fusarium wilt, *Fusarium oxysporum* f. sp. *chrysanthemi*; White rust, *Puccinia horiana*; Brown rust, *P. chrysanthemi*, Bacterial leaf spot, *Pseudomonas cichorii*, *Tomato spotted wilt virus* (TSWV), crown gall (*Agrobacterium tumefaciens*)
Daffodil	Bulb mites	Fusarium wilt (*Fusarium oxysporum* f. sp. *narcissi*)*, Sclerotinia narcissicola, Stagonospora curtisii*
Freesia	Aphids, bulb mites, thrips	*Freesia sneak virus* (*FreSV*)*, Fusarium oxysporum* f. sp. *gladioli*, *Bean yellow mosaic virus* (BYMV), *Botrytis cinerea* and *B. gladiolorum*
Gerbera	Thrips, mealybugs, greenhouse whitefly, leafminer, broad mites, aphids	*Impatiens necrotic spot virus* (INSV), *Botrytis cinerea*, Fusarium wilt, powdery mildew (*Golovinomyces cichoracearum*), *Phytophthora cryptogea,* and *Tomato spotted wilt virus* (TSWV),
Gladiolus	Bulb mites	Fusarium corm rot, gladiolus rust, Curvularia leaf spot, *Cucumber mosaic virus* (CMV) and *Bean yellow mosaic virus* (BYMV)
Gypsophila	Leafminer, mites, aphids, thrips	TSWV; Alternaria leaf spot; Pythium, Phytophthora, and Rhizoctonia root and stem rots; powdery mildew
Iris (Dutch)	Aphids, thrips	Pythium and Rhizoctonia root rot, Penicillium blue mold, Fusarium bulb rot
Lily (*Lilium* spp. – Easter, Asiatic, Oriental)	Bulb mites, aphids	Pythium root rot, Rhizoctonia root rot, Botrytis blight (*Botrytis elliptica* and *B. cinerea*), *Lily symptomless virus* (LSV) and *Lily mottle virus* (LMoV)
Calla lily (*Zantedeschia*)	Thrips, aphids	Bacterial soft rots (*Pectobacterium* and *Dickeya* spp.), *Dasheen mosaic virus* (DMV), TSWV, *Turnip mosaic virus* (TuMV), *Zantedeschia mosaic virus* (ZaMV), *Zantedeschia mild mosaic virus* (ZaMMV), *Konjac mosaic virus* (KoMV) and *Carnation mottle virus* (CarMV)

(continued)

Table 22.5 (continued)

Plant	Key Pests	Key Diseases
Leatherleaf fern (*Rumohra adiantiformis*)	Mealybugs, scale, two-spotted spider mites	*Calonectria theae* leaf spot, Cercospora leaf spot, Rhizoctonia blight, Cylindrocladium blight, and Pythium root rot
Lisianthus	Fungus gnats, thrips	Fusarium stem rot, *Tomato spotted wilt virus* (TSWV)
Rose	Thrips, mealybugs, scale, two-spotted spider mites, aphids, whitefly	*Rose rosette virus* (RRV), powdery mildew, downy mildew, crown gall (*Agrobacterium tumefaciens*)
Snapdragons	Aphids, two-spotted spider mite, thrips	Downy mildew, *Impatiens necrotic spot virus* (INSV), *Tomato spotted wilt virus* (TSWV)
Stephanotis	Thrips	*Tomato spotted wilt virus* (TSWV)
Stock (*Matthiola*)	Aphids, leaf rollers, thrips	Bacterial blight (*Xanthomonas campestris* pv. *incanae*), Rhizoctonia and Phytophthora root and stem rots
Tulip	Bulb mites, aphids	Botrytis blight (*Botrytis tulipae*), *Fusarium oxysporum* f. sp. *tulipae,* Pythium root rot

bacterial problems such as crown gall (caused by *Agrobacterium tumefaciens*) or Southern wilt (caused by *Ralstonia solanacearum*) and plant-parasitic nematodes (particularly root-knot nematode) can be problematic in ground beds. In order to circumvent the soil disease management problems inherent in growing in ground beds, soil-free production systems for crops such as roses and gerbera utilize rock-wool, coco fibre (coir) or bags of custom-made mixes with various ingredients. Bulb crops such as tulips often use a completely hydroponic growing system (Fig. 22.4).

22.2.4.3 Climate

In frost-free areas, plants may be grown in relatively open structures. Plastic sheets over wooden structures and open-sided structures are typical. The year-round climate in tropical/subtropical parts of the world is favorable for insect pests as well as for crops, but note that the more open growing environment is also favorable for native or endemic biocontrol agents, which may enter structures freely. This is a very different environment from the glasshouses used in temperate climates, which are most often steel structures with vents that may be screened. Winter annually eliminates the movement of pests and pathogens from outdoors for some months, while production in frost-free areas means that that pests and pathogens may gain entry to the greenhouse all year long.

Fig. 22.4 Many cut tulips in the Netherlands are produced hydroponically

22.2.4.4 Long Crop Cycles

In some cases, cut flower crops are grown perennially: roses, for example, are kept for 5 years or more. There may also be sequential crops of different ages grown within the same structure, as for snapdragon, making it easy for accumulated pests and pathogens to move from older crops to younger. The constant presence of flowers with pollen favors thrips population development, although most cut flowers are harvested and sold before the flowers are fully open and showing pollen. On the positive side, biocontrol agents have the opportunity to become well established in a long-term crop.

22.2.4.5 Pests Specific to This Crop Type

The pests common to other floral crops will affect cut flowers as well. Less mobile pests with longer generation times, including mealybugs and scales, take on a higher importance in cut flowers because the crop is in place for a long time.

22.2.4.6 Phytosanitary Regulations for International Trade

Most countries have strict phytosanitary regulations regarding imported plant material. Because many cut flowers are shipped all over the world, the tolerance for pests and diseases is effectively zero. This places high pressure on IPDM programs to deliver pest- and disease-free flowers, a standard that is increasingly difficult to meet. Losses of 10–20% due to pests like thrips in roses are common—and roses don't have the additional danger of quality loss from thrips-borne tospoviruses that threaten snapdragons, lisianthus, gerbera, and many other cut flower crops. Pesticide resistance, environmental regulations and worker safety concerns restrict the choice of pesticides and biological control strategies often do not deliver the required levels of control. One reason is the lack of biological control agents. At present, in Colombia, very few biological control agents are commercially available because the Colombian government has very strict regulations regarding importation of non-native organisms. In Europe or North America, where a wide range of biological products is available, pest control in cut flowers uses biological control where possible, but still depends a lot on chemical pesticides, especially for flowers that are exported.

22.2.4.7 Post-Harvest

A unique feature of cut flower crops is that the harvested flower stems must be maintained for weeks after harvest. This requires skilled refrigeration and environmental management (including ethylene avoidance) to slow physiological flower deterioration while simultaneously avoiding blight from *Botrytis cinerea*. Post-harvest disease control for cut flowers is as important as disease management during production. Conidia of *B. cinerea* can remain viable under dry conditions for more than a year (Salinas et al. 1989), so reducing inoculum formation during production and avoiding conditions for disease development during storage and shipment are key.

22.3 Techniques and Tools for Accomplishing IPDM

Ornamentals production is often quite profitable per unit area, and thus growers are able to invest in personnel (e.g. scouts to monitor), extra equipment, or control products to protect against both pathogens and pests. Consequently, relatively elaborate integrated pest and disease management (IPDM) programs have been devised. This section will discuss each of the elements of IPDM in turn, explaining how they have been used for reducing pest management problems across a range of ornamental crops. For a helpful listing of techniques applied to individual diseases and pests, the reader is referred to Gullino and Wardlow 1999.

Monitoring for Pests and Diseases

Monitoring, or scouting, is the basis for IPDM programs. To design and implement effective pest and disease management strategies, it is essential to know what pests and diseases are present, where they are in the crop, where they come from and how their numbers change over time. Good record keeping will allow growers to discover trends and consistencies over time, crop cycles and growing seasons, to predict outbreaks and to act preventively. Scouting often entails regular visits from an independent individual with pest management experience who reports to the management. Within some of the larger operations, the IPDM manager is an employee and can immediately take action when problems are identified. In greenhouses, weekly scouting is the norm, but all workers should also be trained in identifying symptoms and reporting to their supervisor any time something unusual is encountered. Scouting varies with crop and time of year: some crops or crop stages are simply more susceptible to insect, mite or disease problems and need closer and more frequent observation to catch problems at their inception. Lists such as the Key Pest/Key Disease lists provided in 22.2 above can guide scouts in knowing what symptoms and signs to be watching for. Greenhouses should have lists (and, ideally, color illustrations) to guide the scouting for each of their major crops.

The greatest benefit comes from scouting at the beginning of the crop. Inspection of the foliage and roots (when present) of plug seedlings and cuttings on arrival is the first step in IPDM, providing an opportunity to exclude pests and diseases by rejecting contaminated shipments, or holding them in a separate area to diagnose and treat infected/infested plants before adding them to the greenhouse. Once the crop is established in the greenhouse, scouting includes systematic and structured inspection of the crop itself for diseases and non-flying arthropod pests and life stages, and use of yellow sticky cards for flying insect pests. Occasionally, it is necessary to monitor specific pests using other monitoring devices. Common examples are blue sticky cards for western flower thrips [although some literature (Gillespie and Vernon 2014) suggests that there is no difference in attraction of this pest to yellow or blue cards], potato discs for fungus gnat larvae (Harris et al. 1995), indicator plants (fava beans or petunias) for tospoviruses (Smith 2015) and pheromone or light traps for lepidopteran pests. Because pests like thrips, aphids and whiteflies can vector certain plant viruses—that have no cure—their monitoring is especially vital.

IPDM programs in greenhouse ornamentals are by nature preventive. Use of tools like action thresholds which guide the timing of (mostly chemical) interventions, does not work in most of these crops: due to the extremely low tolerance for any visible damage of the end product, thresholds are likewise very low. Also, with a greater role of biological control in IPDM programs, growers cannot afford to wait until a certain threshold is reached before initiating a biological control strategy, as pest populations will be too large to be brought under control.

The future of monitoring will definitely include automation: Remote sensing with high tech cameras or other sensors is now able to detect differences between plants due to production practices, pathogen infection or pest feeding

(Martinelli et al. 2015), and this technology is being successfully integrated into different aspects of biological control, including scouting (Nansen 2016). Further automation of IPDM processes such as the use of drones or robotics to collect scouting data and to apply a treatment will be available in the near future. Yet machines may not be the only tools for pest and disease detection, as is demonstrated by the ability of sniffer dogs to detect bacterial infection of plants (Berger 2014), or to find hidden pests like pepper weevils (Sparks 2017), bed bugs or brown marmorated stink bugs.

In addition to direct scouting for pests, symptoms and signs in greenhouses, it is also important to monitor and record the factors that can affect pest and disease outbreaks such as environmental conditions, plant and substrate nutrient levels, substrate EC and pH. This data is essential for cultural management of pests and diseases, as well as for maintaining the crop's physiological health.

Diagnostic Services

Laboratories with the ability to culture pathogens and to utilize microscopy, serological methods, PCR and sequencing are needed as the backstop for greenhouse scouts, extension educators and private consultants. Proper and prompt identification is key for IPDM efforts to be effective. In addition, newly-introduced invasive species must be promptly identified to avoid widespread distribution through ignorance. Table 22.1 shows some of the new problems that have arisen since the turn of the century, as well as re-emerging problems. Increasing globalization of the ornamentals industry is directly responsible for the distribution of new and re-emerging diseases and arthropod pests. There is an ever-increasing need for taxonomic skills, research and development because of the fast pace at which new pest management challenges come to light.

It is now possible for specialized laboratories using molecular analytic methods to be able to separate cryptic pathogens, such as distinguishing *Globisporangium cryptoirregulare* (syn. *Pythium cryptoirregulare*) from *Globisporangium irregulare* (syn. *Pythium irregulare*) even though the two are highly similar morphologically. Specific primers allow polymerase chain reaction (PCR) tests to distinguish the Race 3, Biovar 2 strain of *Ralstonia solanacearum*, which determines whether a bacterial isolate is a Select Agent according to USDA-APHIS (APHIS-PPQ 2004; Weibel et al. 2016) (see Clean Stock section below). Whitefly and chilli thrips strains may be distinguished as well. Tests using PCR and/or sequencing of pest and pathogen DNA are not routine, but are available when circumstances require. Fine distinctions, impossible with earlier technology, are important for understanding the ecology and management of pests and diseases—new pests and new strains of familiar problems are frequently introduced because of the global nature of the ornamentals industry. Although these methods are expensive, the ornamentals industry, particularly at the propagator level, requires the power and precision that they offer. More traditional methods, such as culturing pathogens or using bioassays for virus detection, remain useful and are sometimes an important check on new methods, especially because molecular methods do not distinguish between dead or live organisms.

Systems Approach to IPDM

The usual approach to greenhouse IPDM is to make a list of key pests/pathogens for crops being grown, then choose the appropriate biological control agents and pesticides, check if there are any conflicts (like incompatibility among natural enemies or pesticide side-effects) and settle on an application schedule. However, if we do not understand the reason why there are pest outbreaks, IPDM will always be an uphill battle. Managing a system with inherent flaws takes a lot of effort and is expensive. Instead, the underlying weaknesses of the production ecosystem that are making it favorable to pests have to be addressed first (Buitenhuis 2014). By definition, the systems approach is a pest management strategy where the influence of all factors affecting pest abundance is considered. The goal is to create a system that is inherently more robust, where pests rarely reach damaging levels, plants are better able to tolerate feeding injury and conventional pesticides are rarely required (Lewis et al. 1997; Bale et al. 2008; Skirvin 2011). When switching from a pesticide-based program to a true IPDM approach, people should not limit pest and disease management to the application of biological control agents. This would assume that pest outbreaks are only caused by the absence of natural enemies. Yet this is only part of the problem. For best results, we also have to pay equal attention to plant resistance and environmental factors. Every decision that is made in the greenhouse will affect how vulnerable the crops are to pests and disease—from which crops are grown, to the source of the plugs or cuttings, to what growth regulators are used, to what fertilizer level is applied. Growers should make the best decisions for the whole system as they plot out their strategies for crop production.

22.3.1 Plant Solutions

22.3.1.1 Plant Breeding for Resistance

A key aspect of IPDM is choosing which crops to grow. Annual battles with particular insect or disease problems can be sharply reduced if a grower critically examines the species and cultivars grown and how pests and diseases affect them. Highly susceptible cultivars should be eliminated from production and replaced with others. Although market demands affect the cultivars grown, because of the wealth of ornamental cultivars for many crops it may be possible to eliminate or reduce the production of a susceptible cultivar and replace it with a more resistant one having similar desirable characteristics. Plant propagation companies can minimize economic losses from pests and diseases for all growers by discontinuing cultivars that are discovered to be very prone to a disease or insect/mite problem, substituting ones that are lower maintenance. The more moderately susceptible varieties can serve a useful purpose for IPDM, by acting as indicators for pests and diseases, thus making monitoring programs more efficient. Pest and disease issues on these indicator varieties can also be managed by making them focal points for intensive biological control programs.

Apart from developing new cultivars based on color and form, commercial plant breeders now also aim to improve the pest and disease tolerance/resistance of the crops (Deng 2017). In the past, the diversity of ornamental plant species and cultivars and the fast turn-over of popular varieties made breeding ornamentals an expensive process. However, the development of new breeding techniques, such as marker-assisted breeding, will make selection of specific resistance traits easier, faster and cheaper.

A recent study (Kos et al. 2014) showed that chrysanthemum cultivars varied considerably in resistance to western flower thrips, celery leafminer and two-spotted spider mite. In addition, many cultivars showed cross-resistance, where selection for increased resistance to one herbivore results in enhanced resistance to another herbivore. Of course, changing plant defense characteristics like metabolites (e.g. toxins, volatiles) or morphological defenses (e.g. trichomes, waxy layers) to make plants more resistant against herbivores may also have a negative effect on the natural enemies used for pest management (Prado et al. 2015), so new traits should be carefully considered for how they will fit into a production system.

Currently major efforts are underway to improve the genetic resistance of the most popular bedding plant, *Impatiens walleriana*, the common impatiens, to the downy mildew disease caused by *Plasmopara obducens* (Wegulo et al. 2004, Harlan et al. 2017). This pathogen became a problem in the bedding plant industry worldwide beginning in 2003 when it was first seen in the United Kingdom; previously it had been recorded only as a disease of wild impatiens in North America and parts of Europe (Daughtrey 2012, 2014). The disease had dramatic effects on infected bedding plants: flowering ceased, leaves yellowed and wilted, and then there was catastrophic leaf drop, leaving only bare stems where there had been impatiens flowering in the garden. The value of this major crop consequently fell precipitously, from $111 million wholesale value in 2010 to only $60.4 million in 2015 (USDA-NASS 2011; USDA-NASS 2016) in the United States alone (figures represent sales of flats, hanging baskets and potted plants for 15 states). The European experience has been similar. Because there is resistance in *Impatiens hawkeri* and certain other members of the genus *Impatiens* (Keach et al. 2016), traditional plant breeding efforts with other species in the genus could allow the development of new F1 hybrid impatiens with desirable traits including resistance to *P. obducens* (Keach and Bridgen 2015). University and commercial plant breeding programs are underway to develop impatiens bedding plants with much less susceptibility to downy mildew, and some improved plants are already commercially available. The new Imara XDR and Beacon series of impatiens have both shown high resistance to downy mildew, retaining their flowers and foliage when earlier cultivars exposed to downy mildew under the same environmental conditions become entirely defoliated (M. Daughtrey, unpublished).

There are a few trials of relative cultivar susceptibility to other diseases reported in the recent literature. *Plant Disease Management Reports* includes some of this information: the Crystal and Profusion series of zinnia (Holcomb et al. 2007), Profusion Orange and *Zinnia angustifolia* (Hagan 2009) were shown to be very resistant to bacterial leaf spot caused by *Xanthomonas campestris* pv. *zinniae*. Verbena cultivars varied from no symptoms of powdery mildew (*Podosphaera xanthii*) to

56% leaf coverage (Daughtrey and Tobiasz 2008). Variation in coleus cultivars with regard to downy mildew susceptibility was reported by the American Floral Endowment (Daughtrey et al. 2014). The ornamentals industry will be better able to make decisions about crop improvements if provided with information about the range of responses to pests and pathogens seen in cultivars grown today.

22.3.1.2 Induced Resistance

In recent years, research on induced plant defenses has advanced considerably. We now know a lot about plant defense pathways and the factors and organisms that can turn these mechanisms on and off. However, little is yet known about how to apply this knowledge in real world cropping systems to reduce the negative effects of pests and diseases on plant health and yield. Future studies will reveal how to manipulate the plant's microbiome to enhance plant growth, nutrient use efficiency, abiotic stress tolerance and pest and disease resistance (Busby et al. 2017). Currently phosphorous acid materials (such as fosetyl Al and mono- and di-potassium salts of phosphorous acid) (Datnoff and Elmer 2017) and some pathogen bioantagonists like *Trichoderma* and *Streptomyces* spp. are providing a measure of induced resistance to diseases encountered in greenhouse ornamental crop production.

22.3.1.3 Transgenics

Transgenic ornamentals have been produced experimentally, although these are not in wide usage. Shinoyama et al., for example, produced chrysanthemums with an anti-microbial peptide and an anti-herbivore protein that conveyed reduced susceptibility to white rust caused by *Puccinia horiana* and four lepidopteran herbivores (Shinoyama et al. 2015). It is widely assumed that transgenics having pest and disease resistance will be accepted by consumers of ornamentals before this biotechnology will be embraced for edible crops.

22.3.1.4 Plant Nutrition

Both major and minor nutritional elements may play a role in increasing the speed of a plant's response to infection or in affecting a plant's tolerance to drought and other stresses (Datnoff and Elmer 2017). Studies suggest that high fertilizer levels may stimulate pest reproduction by providing insects with more free nitrogen (normally a limited resource in plant phloem). Research on several ornamental greenhouse crops has shown that reduced fertilizer rates decreased pest infestations for western flower thrips (Chau and Heinz 2006; Chow et al. 2012; Spiers et al. 2011) and aphids (Chau et al. 2005) with no adverse effects on plant quality. In greenhouse floriculture, nutrients are often oversupplied, even when technology can be used to regulate the supply of plant nutrients to meet plant needs (MacDonald et al. 2013) and reductions of 34–75% are possible without affecting crop production

(Shelp et al. 2017; Zheng et al. 2004, 2010). Effects of high nitrogen may cascade up trophic levels. Insects exposed to pathogenic microorganisms change their feeding habits from sources high in carbohydrate to ones high in protein (N); this provides necessary resources that enhance the insects' immune systems and improve their ability to overcome/resist infection (Cotter et al. 2011; Povey et al. 2013).

Similarly, plant nutrition has important effects on diseases (Datnoff and Elmer 2017) and avoiding excess nitrogen will in some instances help to curb disease outbreaks. Lower N may help with Pythium/Globisporangium root rot management, for example (Gladstone and Moorman 1989). Reducing nitrogen does not, however, benefit all pest or disease management systems: downy mildew diseases are in some cases reduced by higher levels of N fertility (Kenneth 1981). Disease management through nutrition will need to be designed for each crop, according to its particular key pests and pathogens.

Other nutrients or minerals can also influence the susceptibility of plants to pests or diseases: although the mechanisms are still poorly understood, application of silicon to certain plants, for example, can increase the plants' physical defense mechanisms, activate plant defense pathways and increase the efficacy of entomopathogens, parasitoids and predators (Reynolds et al. 2016). There are only a few studies on the effects of silicon on insect pests in ornamentals. The addition of potassium silicate increased the chrysanthemum's ability to withstand attack by leafminers (Parrella and Costamagna 2006). In contrast no direct effects of silicon on life history traits of mealybugs were seen on coleus (Hogendorp et al. 2009), or of aphids on zinnia (Ranger et al. 2009). Silicon has been used as a beneficial amendment in cucumber culture in glasshouses, and also to some degree in roses for powdery mildew management in Europe (Belanger et al. 1995; Voogt 1992). Effects of silicon are realized only in plants that accumulate the element significantly (Mattson and Leatherwood 2010). Calcium is another nutrient with important effects on pest management: Volpin and Elad observed decrease in ethylene production as well as a 55% reduction of postharvest Botrytis blight severity in naturally inoculated rose cut flowers provided with 3.5 mM calcium (Volpin and Elad 1991). Calcium has also been seen as a tool for control of soilborne diseases, such as those caused by zoosporic pathogens including *Phytophthora* spp. (von Broembsen and Deacon 1997). Periodic foliar analyses may be useful for keeping nutrients at levels that are inhibitory to certain disease outbreaks or insect infestations. Future studies of the nutrient requirements of specific crops should take into account opportunities to curb development of the crop's primary insect and disease problems.

22.3.2 Environmental Solutions

22.3.2.1 Greenhouse Climate

One of the three points of the disease triangle (in addition to host and pathogen) is the environment, which determines whether or not conditions favor disease. Duration of moisture on plant surfaces, greenhouse humidity and temperature regulate whether and when diseases develop significantly, if inoculum is present along with a susceptible host. Likewise, temperature regulates the speed of insect/mite life cycles, and humidity will have important effects on insect pathogens.

Understanding what environmental conditions favor a particular disease can allow appropriately timed fungicide applications in some cases, and can help guide monitoring efforts in others. For suppression of diseases such as Botrytis blight and powdery mildews, 85% relative humidity is generally quoted as a maximum set point because the relative humidity at the leaf surface may be 10% higher (Gullino and Garibaldi 2017). Temperature may be a limiting factor for diseases: powdery mildew on poinsettia (*Oidium* sp.) is not able to develop an epiphytotic until greenhouse temperatures are consistently below 30°C (Celio and Hausbeck 1998), hence monitoring for the beginning of outbreaks and making preventive treatments are particularly important as temperatures begin to cool in fall. Understanding the particular temperatures that speed up the life cycle of a pest or pathogen may inform choices in greenhouse culture; for example, symptoms of bacterial blight of geranium, caused by *Xanthomonas hortorum* pv. *pelargonii*, are reduced at both high (32–38 °C) or low (10–15 °C) temperatures, compared to optimal temperatures of 21–23 °C (Gullino and Garibaldi 2017). Optimal temperatures are in some cases used by growers as a tool when crop contamination is suspected, to expose the diseased plants so they can be rogued out.

Pest outbreaks can also be exacerbated or reduced by greenhouse climate conditions. For example, spider mites thrive under dry conditions, while foxglove aphids seem to perform best under spring and fall conditions (Jandricic et al. 2010). Most pests will die when temperatures rise above a certain threshold. If the greenhouse is empty between crops, heat treatment can be an effective way to remove pest infestations. If temperatures are maintained at >40 °C and humidity at <50% for 3–4 days, insect and mite pests will be effectively controlled (Shipp and Gillespie 1993). Similarly, most pests will become less active or inactive at low temperatures. In temperate climates, pests will be less of a problem in winter when temperatures and light levels are lower and days are shorter.

Knowledge of expected weather conditions may also be important for natural enemy release, just as it may be relevant for assessing the likelihood of phytotoxicity from a spray application. For example, applying beneficial nematodes is best done at the end of the day when there is no direct sunlight and a greenhouse is humid. Slow release sachets of predatory mites should be hung inside the plant canopy, and not exposed to direct sunlight (Buitenhuis et al. 2014). Also, to avoid injury from oil application, good drying is of paramount importance so low humidity is desirable.

22.3.2.2 Substrate Conditions

The choice of the substrate can make a large difference in insect and disease management: some media are more attractive to fungus gnats than others (Cloyd et al. 2007; Lindquist et al. 1985), and differences in the characteristics of commercial growing media may strongly affect root diseases such as root rot of geranium caused by *Pythium* or *Globisporangium* spp. (Pasura and Elliott 2007).

Sometimes specific management strategies may be used to control anticipated problems, such as lowering the growing medium pH of crops such as poinsettia or pansy that are known to be very susceptible to black root rot caused by *Thielaviopsis basicola*. Black root rot is not favored at pH <6.2, but one must be careful not to lower the pH excessively for a flower crop, in a way that reduces crop quality. Poinsettias, for example, cannot be grown successfully at a pH as low as 5.2, which would provide strong disease suppression (Daughtrey and Chase 2016). A contrasting management technique for Fusarium wilt control in chrysanthemum, and perhaps other hosts such as gerbera and argyranthemum, is to keep pH high, between 6.5 and 7.0 (Trolinger et al. 2017). Fusarium diseases on chrysanthemum, carnation, cyclamen and gladiolus are also lower in severity when a nitrate form of nitrogen is used, while ammonium nitrogen reduces severity of diseases caused by *Verticillium* and *Thielaviopsis* spp. (Datnoff and Elmer 2017). Which ion is combined with N in a fertilizer may also have an effect on disease suppression (Datnoff and Elmer 2017).

All substrates should be monitored by regular testing to ensure that soluble salts levels are ideal for crop growth and not unnecessarily conducive to particular diseases or insects. Fertilizing so that soluble salts do not accumulate in the growing medium may help with disease management. High soluble salts have been shown to injure root tips and make crops more susceptible to Phytophthora (Swiecki and MacDonald 1988) and Pythium root rot (Moorman 2000). Leaching in order to reduce salts, of course, may have negative effects on groundwater, so production systems in which fertilizer is applied only at the rate needed by the plant are ideal.

Irrigation (often tied to fertilization) is one of the most important skills for a greenhouse grower. Both drought and overwatering cause plant stress and can interfere with plant defenses against pests and disease. Overwatering also has a direct effect on plant susceptibility to pathogens such as *Pythium/Globisporangium*, *Phytophthora* and *Thielaviopsis* spp. that are favored by wet soil conditions.

22.3.2.3 Sanitation and Exclusion

Careful biosecurity and phytosanitary practices are key to effective IPM (Copes 2017). Most countries have biosecurity guidelines available and every greenhouse operation should develop and apply their own standard operating procedures. For example, work/traffic flow should go from areas of low risk to higher risk. Quarantine/isolation areas should be available for high-risk plants. Plants with major insect or mite infestations or severe disease symptoms should be rogued out immediately upon detection and removed from the greenhouse in a manner not to spread the infestation or infection to healthy plants. Organic debris from a finished crop should be carefully removed and the area where the crop was sitting should be disinfested. Quaternary ammonium, peroxide and sodium hypochlorite materials are typically used for disinfestation of container or bench surfaces (Copes 2017). Weeds, pet plants and old crops retained in a greenhouse can all provide a refuge for pests and act as a reservoir for diseases. To avoid unwanted pathogenic microbes but retain beneficial microorganisms, growers who use mineral soil in flats and packs ideally utilize aerated steam at 60 °C or 71 °C for 30 minutes as a pasteurization treatment. Even the organic components added to soilless media such as coir, peat moss and bark should be tested for contamination and disinfested if necessary before use (Rosskopf et al. 2017). Media components must be stored carefully to avoid recontamination, and pots and trays must be disinfested before re-use.

For major flower crops grown from cuttings, clean stock programs at propagating facilities are extremely important (VanDerMeij and Warfield 2011). The high value of chrysanthemums, carnations and geraniums, in particular, allowed the development of technology to ensure that propagation material was certified free from known systemic bacterial, fungal and viral pathogens. These programs set a high standard for the cleanliness of certain ornamental propagules, but unfortunately it has not been feasible for other crops to be held to the same standard. In clean stock production, laboratory procedures are typically used to test either tissue culture or cutting stock for culturable bacteria or fungi. Once certified free from fungal or bacterial pathogens, a virus-indexing procedure employing methods such as enzyme-linked immunosorbent assay (ELISA), polymerase chain reaction (PCR) and/or indicator plant inoculation is used to determine whether known or unknown viruses are present. The titre of virus is often very low in tissue culture plants, and virus particles may be unevenly distributed in the plant tissues, so improvements in the efficiency of virus detection are much needed in this production system. Heat therapy may also be used in conjunction with testing methods to produce virus-free meristems that may be used to generate a virus-free plant line. Clean stock programs have been very beneficial to the crops for which they are used; in chrysanthemum, for example, some diseases such as Verticillium wilt common in the 20th century are not generally seen in the 21st (Trolinger et al. 2017).

The vegetatively-grown geranium crop has been the subject of some recent refinements in sanitation procedures, testing and exclusion because of the possibility that it could be the means of moving an important potato pathogen. The United States Department of Agriculture's Bioterrorism Protection Act of 2002 lists *R. solanacearum* race 3 biovar 2 as a Select Agent because it could pose a severe threat to plant health. It causes brown rot of potato, Southern wilt of geranium, and bacterial wilt of tomato and eggplant. The pathogen can be transmitted by contaminated soil, water, equipment, and on workers' hands or clothing. It can also spread when infected plants, tubers, or cuttings are moved from one place and planted in another. As a result of incidents in which *Ralstonia solanacearum* race 3 biovar 2 was introduced to the United States, APHIS established minimum sanitation protocols for offshore greenhouse facilities to more carefully exclude this pathogen. By ensuring that all offshore facilities meet or exceed minimum standards for greenhouse construction, sanitation, production, and pest management, APHIS can mitigate the risk of *R. solanacearum* before plant cuttings reach the United States (APHIS-PPQ 2004). This concerted effort to produce *Ralstonia*-free cuttings has reduced the overall disease management risk for geranium growers. Similar programs would be helpful for other major greenhouse crops, particularly petunia and vegetatively-propagated begonias. Regulatory agencies such as EPPO (The European and Mediterranean Plant Protection Organization) are working towards systems in which clean stock would be maintained for crops to eliminate pathogens (McNamara et al. 1996).

Screening vents and other openings in the greenhouse to prevent entry of pests is increasingly becoming common practice in temperate climates. Growers using screening see a decrease in common greenhouse pests such as thrips, aphids and whiteflies, as well as some less common pests such as plant bugs and various lepidopteran pests. In warmer climates, where pests occur outside year-round, screening would make a big difference in the number of pests entering the greenhouse. However, a major concern for growers is that screening will reduce airflow, making it difficult to maintain the correct environment, resulting in higher temperature and humidity gradients. This can partially be addressed by increasing the surface area of the vent or by using forced ventilation (Teitel 2007). To further mitigate these problems, new screening materials are being developed to optimize airflow, while still excluding pests. It may also be possible to vary optical characteristics of screens (e.g. color) to manipulate the behavior of pests so that they do not enter the greenhouse, even if the pore size of the screen is large enough to let the pest through (Ben-Yakir et al. 2013).

Exclusion of pests and pathogens is a challenge because any plant material brought into the greenhouse may be a source of infection or infestation. Although it is important, monitoring the cleanliness of the plant material entering the system is not sufficient: low levels of pests or microscopic inoculum will invariably escape inspection efforts. From the North American perspective, arthropod pests on imported propagative material may include cosmopolitan pests (e.g. western flower thrips, *Bemisia* sp.), insecticide resistant insect strains (e.g. American serpentine leafminer), and/or invasive alien species (e.g. chilli thrips, melon thrips, red palm mite, pink hibiscus mealybug, light brown apple moth). Surveys of international trade found at least 20% of cuttings and 12% of plants infested with western flower thrips (Romero 2011; Kirk 2002). The whitefly *B. tabaci* has been regularly intercepted in the UK and Canada on imported plant material, in particular on poinsettias (Cuthbertson et al. 2011; Frewin et al. 2014). Dipping (immersing) cuttings in reduced-risk pesticides, either alone or in combination with microbial biopesticides, significantly reduced *B. tabaci* populations on infested poinsettia cuttings and would allow growers to knock down populations to a point where they can be managed successfully thereafter with existing biocontrol strategies (Buitenhuis et al. 2016). Similar dip treatments are being developed against other pests like thrips and spider mites. The potential benefits of these dip treatments for arthropod management need to be weighed against the potential for spread of pathogens, particularly bacterial diseases. Other options to disinfest plant materials are hot water treatments (e.g. Hara and Jacobsen 2005 for tropical cuttings, or Conijn 1992 for mites on bulbs), irradiation (Osouli et al. 2013) and controlled atmosphere (Liu 2011).

22.3.2.4 Mass Trapping

Mass trapping for insects, either in the form of sticky cards, sticky tape or trap plants, is a common sight in commercial ornamental greenhouses worldwide (Fig. 22.5). Although mass trapping by itself will not protect a crop, as part of an IPDM system it has been proven very successful. In combination with the application of predatory mites and spinosad sprays, sticky tape significantly reduced

Fig. 22.5 Yellow sticky cards or tapes used for mass trapping may be an important component of an IPDM program for greenhouse flower crops

western flower thrips damage in strawberry grown in high tunnels (Sampson and Kirk 2013). Large sticky cards or long ribbons of sticky tape can remove large numbers of pests like thrips, whiteflies and fungus gnats from a greenhouse, a practice favored by organic growers in particular. In general, growers of ornamentals use yellow sticky cards or tape as this is an attractive color for many insects, although white and blue traps are also used, depending on the target species.

Trap plants may be selected to trap a specific pest, based on their high attractiveness to these pests compared to the crop. Buitenhuis et al. (2007) showed that yellow flowering chrysanthemum plants can be used to trap western flower thrips, but marigolds and gerberas have also been used for this pest (Skinner et al. 2013). Eggplant has been tested as a trap plant against whiteflies in poinsettia, but results were dependent on several factors, including the species of whitefly (Lee et al. 2009). However, eggplants are highly effective at trapping whitefly in mandevilla and potentially could also be used in hibiscus crops (Jandricic 2017). An advantage of trap plants is that they can also be used as a focus for the release of biocontrol agents so that they act simultaneously as a banker plant.

For all mass trapping devices, placement is critical for their efficacy. For most pests, traps should be placed where pests are moving into or through the greenhouse. Generally, traps do not attract pests that are established on a crop plant (e.g. thrips, Buitenhuis and Shipp 2006), unless they are induced to leave or disperse by pheromones or disturbance as part of a push-pull strategy (Cook et al. 2007; Holden et al. 2012). It is also important to position the traps close to the plants (Pinto and Vänninen 2013): in ornamentals, ideal placement would be just above the plant canopy.

22.3.3 Control Agents

22.3.3.1 Biological Control, General

Biological control agents used for pest and disease control in greenhouse ornamentals can be predators, parasitoids or microorganisms (including entomopathogenic nematodes, fungi, bacteria, viruses, protozoa and yeasts). The term biopesticide should not be confused with biological control. Although biopesticides include living microorganisms that are biological control agents, by US Environmental Protection Agency (EPA) definition they also include biochemical products (naturally-occurring substances that control pests) and plant-incorporated protectants (pesticidal substances produced by plants containing added genetic material).

Barriers to biological control are still being cited: lack of biocontrol registrations in some countries (e.g. Colombia), the challenges of shifting from a pesticide-based program to a biologically based one, the need to adapt biocontrol programs to local conditions and crop type, and the difficulty of coping with new pests, which arrive without ready-made biocontrol solutions. The real and potential benefits are equally compelling, however: chemical applications and their labor costs are minimized, pesticide resistance crises no longer threaten, and subtle or overt crop damage from pesticides is eliminated—while premium customer satisfaction is associated with crops grown without pesticides. The adoption of biological controls for diseases continues to lag behind the use of insect biocontrols, but a distinct biocontrol industry is developing for plant disease management (McSpadden Gardener and Fravel 2002).

Biological control programs for greenhouse ornamentals will vary between locations. Although there will be many similarities, there are no universal recipes for biocontrol success. What works in Europe may not be the best solution in North America or anywhere else because of differences in climate, production practices, crop varieties or other factors. In addition, not all biocontrol products are available worldwide due to regulations on the importation of non-native species. Therefore, this chapter will not describe all possible pest and biological control agent combinations, but rather describe the general approach and principles used to design biological control based IPDM programs for ornamentals.

The adoption of biological control as part of IPDM programs in ornamentals is still increasing. Although biological control against insects and mites has become more common, growers are increasingly including biological products into their disease control strategies as well. Structured surveys to determine the percentage of growers using biological control are mostly lacking, but some numbers are available, especially in places where adoption is high: in Ontario, Canada, a survey in 2014 found that 69% of greenhouse ornamental growers, mainly producing potted ornamentals, use some form of biocontrol (Summerfield et al. 2015). Three quarters of these used biocontrol agents regularly, while the remainder used biological control only at certain times, typically at the start of production. The same survey showed that use of biological control for diseases was 45%. In the US, adoption varies widely: anecdotal reports indicate use for pest management is between 10% and 90%, varying among the different states, but it seems that biological control is more often used in propagation, and that small farms use more biological control than big farms (S. Gill, D. Smitley, pers. comm.). Similar numbers are reported from Europe.

22.3.3.2 Biological Control for Insect and Mite Pests

The species of biological control agents used for insect and mite control in greenhouse ornamentals are very similar to the ones used in greenhouse vegetables and include hymenopteran parasitoids, predatory mites and beetles, entomopathogenic nematodes and fungi, bacteria, bacterial toxins and viruses. However, biological control programs developed for greenhouse vegetables cannot be directly applied to floriculture crops. As discussed previously in this chapter, most ornamental crops have short production cycles and no or few food sources (e.g. pollen or alternative prey), so biological control agents do not have time to establish in ornamental crops, necessitating frequent inundative releases or other strategies to ensure the continued presence of biological control agents. The presence of multiple plant species and varieties, different plant stages and complex growing procedures require careful consideration of the best combination of biological control agents. Finally, there is little margin for error, because little cosmetic damage is tolerated (Buitenhuis et al. 2015).

Biological control agents are selected according to the pest complex present or expected in the crop, their adaptation to the host plant and environmental conditions and their compatibility with each other. For many pests, a combination of natural enemies is needed, either to target different life stages of the pest or to adjust as conditions in the crop change as plants grow and flower. See example on thrips management below. It is important to consider the season when selecting biological control agents, because some predators, like *Orius sp*. or *Aphidoletes aphidimyza* will diapause at low light and low temperature conditions found in winter. In Ontario, Canada, many growers use the thrips predatory mite *Amblyseius swirskii* in summer because it performs better than *Neoseiulus cucumeris* under warm conditions, but in winter they use the less expensive *N. cucumeris* as both predators have similar performance under cooler conditions (Hewitt et al. 2015). The host plant also determines the choice of biological control agents: some of the generalist phytoseiid predators prefer smooth, glabrous plants, while others benefit from trichomes (McMurtry et al. 2013; Schmidt 2014). Finally, there are many studies that show that biological control agents can feed on, parasitize or infect each other (i.e. intra-guild and hyperpredation), which potentially affects the efficacy of biological control programs. Few of these interactions have been validated under commercial production practices. A review by Messelink et al. (2012) concludes that although the potential risk of intraguild predation disrupting biological control appears to be low in many cases, there are also examples of negative effects of intraguild predation on biological control. Greenhouse biological control means building an artificial ecosystem, and creating and manipulating biodiversity to maximize pest control.

Example: Management of Western Flower Thrips in Potted Chrysanthemum in Ontario, Canada

- Identify resistant/tolerant/susceptible varieties.
  - If possible, choose less susceptible varieties.
  - Increase monitoring and control inputs on susceptible varieties.
- Identify entry routes of thrips.
  - From outside: screen vents, keep doors closed
  - On previous crops or weeds: strict sanitation protocols
  - On introduced plant material: scout incoming material, disinfest cuttings, quarantine.
- Start biological control program early.
  - 1–2 applications of *Dalotia coriaria*, *Stratiolaelaps scimitus*
  - 3–4 applications of entomopathogenic nematodes (*Steinernema feltiae*) to the substrate until plant canopy closes.
  - 3 applications of entomopathogenic fungi (*Beauveria bassiana* or *Metarhizium brunneum*).
- Continue throughout the production cycle.
  - Weekly applications of predatory mites or slow release sachets (*Neoseiulus cucumeris* or *Amblyseius swirskii*), could be supported by supplemental food (e.g. cattail pollen)
  - If needed, *Orius insidiosus*. Could be supported by ornamental pepper banker plants.
  - Mass trapping with large sticky cards or sticky tape.
  - If needed, application of entomopathogenic fungi (*B. bassiana* or *M. brunneum*).
- If needed, apply a clean-up spray of a chemical pesticide at the end of the production cycle.
- Assess the efficacy and cost of the program and make changes as needed for future crops.

It is commonly assumed that biological control agents only suppress pest populations by consuming them. However, non-consumptive mechanisms can also play an important role. The mere presence of biological control agents may reduce pest fecundity or survival by reducing the amount of time pests spend feeding, and failed attacks by predators or parasitoids may result in the injury and eventual death of potential prey. For example, the predatory mite *Neoseiulus cucumeris* does not prey on second instar western flower thrips, but its 'harassment' led to reduced feeding and less survival to adulthood of thrips, and resulted in less plant damage (Jandricic et al. 2016). Also, aphids interrupted feeding and showed costly defensive behaviors, including dropping off the plant, in reaction to the presence of a non-enemy parasitoid wasp (Ingerslew and Finke 2017).

Another indirect effect of biological control agents on pests is the induction of plant defenses. Certain natural enemies (especially mirid and anthocorid bugs) can feed on the host plants of their prey, invoking a plant defense response that ultimately will negatively affect the prey. For example, compared to undamaged tomato plants (i.e., not exposed to the mirid), plants on which young or mature nymphs, or adult males or females of *Nesidiocoris tenuis* fed and developed were less attractive to the whitefly *Bemisia tabaci*, but were more attractive to the parasitoid *Encarsia formosa*. (Naselli et al. 2016). Similarly, plant feeding by the predator *Orius laevigatus* induced plant defenses (repellency) in sweet pepper against western flower thrips and whiteflies (*B. tabaci*). Again, the whitefly parasitoid *E. formosa* was significantly attracted to *O. laevigatus*-punctured plants (Bouagga et al. 2018). Although all these studies were done in vegetable crops, it is reasonable to assume similar effects could be achieved in greenhouse floriculture crops.

For greenhouse floriculture IPDM programs, it is recommended to start releases of natural enemies early, even as early as propagation. Given that most cutting producers still rely heavily on pesticides, any pests that arrive on cuttings are likely to have been exposed to a range of chemistries, and may have developed resistance. As most pests have extremely rapid life cycles and high reproductive potential, early release of biocontrol, before pests have had the chance to build up large numbers, will be most successful. Early releases are also more economical, because young plants are often spaced closer together, and releases are made on a smaller area. In addition, release rates of biological control agents may be higher in floriculture than in vegetables, because short crop cycles mean there is no time to expect the natural enemies to establish and build up their populations over time.

To help insect biological control agents to rapidly increase their numbers and to persist in the crop, banker plants and supplemental food are used as supporting strategies (Huang et al. 2011; Messelink et al. 2014). In this manner, a population of biological control agents is maintained in the greenhouse even in the absence of prey, to be ready when pests arrive. The most common examples of banker plants are barley plants infested with aphids (*Rhopalosiphum padi*) to maintain populations of the aphid parasitoid *Aphidius colemani*, and ornamental pepper plants to breed *Orius* sp. predators. Supplemental food is added to the crop in the form of pollen (e.g. *Typha* sp.), eggs of *Ephestia kuehniella*, *Artemia franciscana* cysts or mites of stored products (similar to the mites used in mass rearing of predatory mites).

22.3.3.3 Biological Control of Diseases

In disease management, bioantagonists based on bacteria, fungi and actinomycetes as active ingredients are labeled for use in greenhouses on ornamentals (Paulitz and Belanger 2002). These are used primarily against powdery mildews and *Botrytis cinerea* and also for a range of soil organisms including *Pythium/Globisporangium*, *Rhizoctonia* and *Fusarium* spp. Well-established products are based on *Trichoderma*, *Bacillus*, *Pseudomonas*, and *Streptomyces* spp. Recently a *Ulocladium oudemansii* strain was registered in the US for control of Botrytis and Sclerotinia diseases. These biological controls work by various mechanisms including competition, antibiosis, and induction of plant defenses (Karthikeyan et al. 2007). For effective disease biocontrol, treatments have to be in place before the challenge from the pathogen. Daughtrey and Benson (2005) pointed out the high failure rate of biological controls in published efficacy trials from university research, and suggested that the inoculum level typically used for trialing may be inappropriately high for biocontrol agents, even though these methods are appropriate to evaluate chemical fungicides.

Since the beginning of the publication of *Plant Disease Management Reports* by the American Phytopathological Society in 2007, tests of fungicides have far outnumbered tests of bioantagonists of pathogens, and there have been few reports of trials in ornamentals. Recently published disease biocontrol trials showed failures of *Bacillus subtilis* product treatments against downy mildew on impatiens (Warfield 2012) and of four biocontrol products against Botrytis blight on poinsettia (Hausbeck and Harlan 2012) (Hausbeck et al. 2017), but another trial indicated effectiveness of a Pseudomonas product drench (plus Capsil) against Rhizoctonia root rot on zinnia (Hausbeck et al. 2016). In spite of the paucity of published trial work from the research community, there has been increasing adoption of biocontrols by greenhouse growers producing ornamental crops in the US. This shows that, among other factors, there is a market for non-chemical disease control options. Biological controls are not likely to be stand-alone methods for disease management, but can be an important component within an IPDM program employing sound sanitation practices and cultural controls. The cleanliness of the plant material used for production is also of paramount importance.

Learning how to integrate bioantagonists with chemicals may be an option in the disease management arena, even though mixing biological and chemical control is often not an option for managing insect and mites because of direct and indirect toxicity side-effects. Bacterial biofungicides are compatible with many of the chemicals used on greenhouse floral crops: seed treatment with a strain of *Pseudomonas fluorescens* plus mefenoxam or strobilurin fungicides protected tomato seedlings against *Globisporangium ultimum* (syn. *Pythium ultimum*) (Salman and Abuamsha 2012).

Our knowledge of biological control of diseases is the greatest for the systems where chemical control has been inadequate. A 2016 review of biocontrol methods for Fusarium wilt (Lecomte et al. 2016) indicated that there were 26 biological control products registered globally for the control of Fusarium wilt. These include as active ingredients (alone or in combination) a wide variety of bacteria and fungi: *Bacillus pumilus*, *B. subtilis*, *Gliocladium catenulatum*, *Pseudomonas cepacia*, *P. chlororaphis*, *Pythium oligandrum*, *Streptomyces griseoviridis*, *S. lydicus*, *Trichoderma asperellum*, *T. harzianum*, *T. polysporum*, and *T. virens*. In spite of this diversity of biocontrol tools, the authors conclude that an immense amount of research is still needed in order to learn how to integrate biocontrol measures with the other key tools (resistant plants and other cultural measures) to manage disease successfully.

Biocontrol is an IPDM tool that will need continuing research in order to function well for greenhouse growers.

22.3.3.4 Chemical Control of Insect and Mite Pests

Up to the turn of the century, pest control in ornamentals was mainly achieved by pesticide sprays. As mentioned before, many growers are now moving to integrate biological control agents into their pest management programs due to issues with pest resistance, worker health and environmental issues and consumer demand. However, integrating pesticides with biological methods is not as simple as it seems. Many factors need to be considered: often, pesticides are not compatible with biological control agents. Negative side effects can range from direct toxicity, which is mostly expressed as percent mortality of the biological control agent, to sub-lethal effects, where the biological control agent survives the pesticide treatment, but its fitness, e.g. reproduction, lifespan or searching/predation capacity is impaired, reducing its effectiveness. All major biocontrol producers have side-effects lists available that provide information on the acute toxicity of the product against various biological control agents. In practice, growers that are committed to the use of biological control as their main pest control strategy for insects and mites will use biological control as long as they can to keep pest populations low and prevent build up of resistance, then apply a clean-up spray to eliminate pests at the time when plants are sold. Growers using biocontrols against pathogens as crop protectants will employ them unless a disease outbreak is detected, and then switch to chemical treatments directed against that specific problem. When using insecticides, it is important to check Insecticide Resistance Action Committee (IRAC) group designations when choosing products (see Table 22.6). Treatments should be rotated among chemicals from different mode of action groups to delay development of resistance in the target pest.

22.3.3.5 Chemical Control of Diseases

Despite the increase in uptake of biological control and the refinement of cultural methods, chemical control is still a mainstay of IPDM in greenhouse ornamentals production (Palmer and Vea 2017). Tools available for chemical management of

Table 22.6 Insecticide/miticide management tools available for use against some greenhouse ornamental pests

		Registered by US EPA for some uses against these insects or mites				
Insecticide (or growth regulator)	IRAC group	Aphids	Thrips	Whitefly (Bemisia)	Two-spotted spider mite	Broad mite
Abamectin	6	X	X	X	X	X
Abamectin + bifenazate	6 + UN	X	X	X	X	X
Acephate	1B	X	X	X	X	
Acequinocyl	20B				X	
Acetamiprid	4A	X	X	X		
Azadirachtin	(Unknown)	X	X	X	X	
Bifenazate	25				X	
Bifenthrin	3	X	X	X	X	
Buprofezin	16			X		
Chlofentezine	10A				X	
Chlorofenapyr	13		X		X	X
Chlorpyrifos	1B	X	X		X	
Chlorpyrifos + cyfluthrin	1B + 3	X	X	X	X	
Cyantraniliprole	28	X	X	X		
Cyflumetofen	25				X	
Cyfluthrin	3	X	X	X		
Cyfluthrin + imidacloprid	3 + 4A	X	X	X		
Diflubenzuron	15			X		
Dinotefuran	4A	X	X	X		
Etoxazole	10b			X	X	
Fenazaquin	21			X	X	X
Fenpropathrin	3	X		X	X	
Fenpropathrin + acephate	3 + 1B	X	X	X	X	
Fenpyroximate	21				X	
Flonicamid	9C	X	X	X		
Fluvalinate	3	X	X	X	X	
Hexythiazox	10A				X	
Hort oil	M	X	X	X	X	
Imidacloprid	4A	X	X	X		
Insecticidal soap	NS	X	X	X	X	
Kinoprene	7A	X	X	X		
Lambda-cyhalothrin	3	X	X	X	X	X
Methiocarb	1A	X	X		X	
Naled	1B	X		X	X	
Novaluron	15		X	X		
Neem oil	18B + NS	X		X	X	
Permethrin	3	X	X	X		

(continued)

Table 22.6 (continued)

		Registered by US EPA for some uses against these insects or mites				
Insecticide (or growth regulator)	IRAC group	Aphids	Thrips	Whitefly (Bemisia)	Two-spotted spider mite	Broad mite
Pymetrozine	9B	X		X		
Pyridalyl	UN		X			
Pyrethrins + piperonyl butoxide	3 + 27A	X	X	X	X	
Pyridaben	21			X	X	X
Pyriproxyfen	7C	X		X		
Spinosad	5		X		X	
Spiromesifen	23			X	X	X (SLN NY)
Spirotetramat	23	X		X	X	
Thiamethoxam	4A	X	X	X		

diseases are fairly comprehensive: there are effective materials for most fungal problems other than the systemic diseases. Even when materials are "effective," however, they are not an economical way to fight disease without integrating them with other methods. Considering Botrytis management, for example, infections on petal tissue are especially damaging to salability of an ornamental, but this delicate plant part is the one most easily harmed by fungicides. Some (e.g. chlorothalonil products) are even prohibited from use on crops in flower. Thus, the other cardinal components of IPDM and not just chemicals must be used for effective Botrytis management: sanitation practices that remove organic debris that could otherwise develop spore inoculum, biological controls that compete with or inhibit Botrytis, fertilization practices that do not increase disease susceptibility, and thoughtful irrigation and environmental management practices that prevent condensation on plant surfaces.

Growers of ornamentals are becoming more familiar with using Fungicide Resistance Action Committee (FRAC) group designations when making their treatment choices. Now that these numbers appear on product labels they are a convenient way to plan treatments that rotate among chemicals from different mode of action groups and thus delay development of resistance in the target pathogen. This is especially important for Botrytis blight, downy mildew and powdery mildew. To preserve usefulness of highly effective active ingredients prone to resistance development (single-site materials), companies have begun to offer combination products, a recent example being the FRAC Group 11+7 category that brings together a strobilurin with a succinate dehydrogenase inhibitor (SDHI) fungicide.

Botrytis blight management in the greenhouse is facilitated by fungicide choices from many different FRAC groups (See Table 22.7). In addition, there are combination

Table 22.7 Fungicide management tools available for use against some greenhouse ornamental diseases

		Registered by US EPA for some uses against these diseases				
Fungicide (or group)	FRAC group	Botrytis blight	Powdery mildews	Downy mildews	Rusts	Pythium root rot
Thiophanate-methyl	1	X (R)	X		X	
Iprodione	2	X (R)				
DMI fungicides	3	X	X		X	
Mefenoxam	4			X (R)		X (R)
Piperalin	5		X			
Flutolanil	7				X	
QoI fungicides	11	X	X	X (R)	X	X
Fludioxonil	12	X				
Etridiazole	14					X
Fenhexamid	17	X (R)				
Polyoxin D	19	X	X	X		
Cyazofamid	21			X		X
Phosphorous acids	33	X	X	X (R)		X
Dimethomorph, mandipropamid	40			X		
Fluopicolide	43			X (R)		X
Oxathiapiprolin	49			X		
Copper	M1	X	X	X	X	
Sulfur	M2	X	X		X	
Mancozeb	M3	X		X	X	
Chlorothalonil	M5	X	X		X	
Potassium bicarbonate	NC	X	X	X	X	
Mineral oil	NC		X		X	
Neem oil	NC	X	X	X	X	
Hydrogen dioxide plus peroxyacetic acid	NC	X	X	X	X	X
Reynoutria sachalinensis extract	P	X	X	X	X	X

No claims are made for effectiveness of these registered materials; effectiveness may vary widely among the different active ingredients

X indicates that the active ingredient is registered in the US for use on some greenhouse ornamentals for the indicated disease

DMI fungicides = demethylation inhibitor fungicides, also known as SI (sterolbiosynthesis inhibiting) fungicides

QoI fungicides = quinone outside inhibitor fungicides, including the strobilurins

(R) = Resistance to this fungicide (or fungicide group) for this use in an ornamental crop reported. e.g. Impatiens downy mildew (Warfield, 2017)

products with 2 or more chemistries: strobilurin + DMI (FRAC Group 11+3), strobilurin + SDHI (11+7), aniline-pyrimidine + phenylpyrrole (9+12) and carboxylic acid amide + triazolo-pyrimidylamine (40+45) materials, all of which provide some

Botrytis blight management as well as broad-spectrum activity against additional diseases.

There is now a choice of chemicals for downy mildews (a pathogen group that has been especially problematic on ornamentals in the past two decades). Because chemicals used against oomycetes (which include both *Phytophthora* spp. and downy mildews) are available from different FRAC groups, there are enough to use in rotation during the times of year that a particular downy mildew may pose a threat. Combination materials should slow the development of fungicide resistance, and are simpler for the grower to use than a tank mix. For downy mildews, combinations of FRAC Groups 11+3, 11+7 and 40+45 are available for use on greenhouse ornamentals.

Powdery mildews also may be addressed with preventive fungicide applications (see Table 22.7) made in response to the first sighting of powdery mildew colonies within a crop. Crops prone to powdery mildew, such as poinsettias and gerberas, must be scouted carefully to avoid either unnecessary preventive treatments or crop losses due to inattention.

For rust and leaf spot management, the strobilurins have been a particularly effective management tool in recent decades when used in combination and rotation with contact fungicides—along with careful irrigation management. Combinations of active ingredients in FRAC Groups 11+7, 11+3, M5+1 and M1+M3 are on the market for use against rusts and various leaf spots/anthracnoses. Some additional fungicide combination materials are sold for use against certain leaf spots on ornamentals in greenhouses: materials in FRAC Groups 9+12, 1+2, and M5+2+1+3.

Phytotoxicity from pesticide misapplications may result in symptoms that are confused with those caused by pathogens. Foliage injury destroys ornamental crop value quickly: growers of ornamentals must always check product labels carefully for prohibitions against treating certain kinds of plants and also be careful to apply when the crop is not stressed from other factors.

Soilborne diseases in greenhouse ornamentals production are minimized by the use of soilless mixes. Widespread root disease losses in greenhouse ornamentals are uncommon today because inoculum of root diseases is largely from sanitation lapses (e.g. carelessly stored containers or reuse of pots from previously diseased crops) or from occasional contamination associated with rooted cuttings or plug seedlings received from another greenhouse. Preventive treatments early in the crop using biological controls have become commonplace; fungicides are used either preventively or in response to outbreaks (biological controls are not expected to curb an established root disease problem). Two categories of fungicide are needed for broad-spectrum treatment of root diseases in ornamentals, with one ingredient to counteract oomycetes (*Pythium* and *Phytophthora* spp.) and one to counteract true fungi (e.g. *Rhizoctonia*, *Fusarium* and *Thielaviopsis* spp.). Some products are designed to provide this spectrum of activity in one product, e.g. combining thiophanate-methyl with etridiazole, or fludioxonil with mefenoxam. Once symptomatic individuals have been discarded, laboratory identification of the disease can inform the choice of which fungicide will be the most helpful to protect the remainder of the crop. The root disease with the fewest effective chemical controls is Pythium root rot (Table 22.7)—there are more options for Phytophthora management. Development of more effective fungicides and biological controls for Pythium management would be extremely helpful to the greenhouse ornamentals industry.

22.3.4 Extension Methods

Educational materials supporting IPDM programs for producers of greenhouse ornamentals are now available to provide growers with timely information about insect/mite problem and disease sightings as well as pest and biocontrol identification. These communications have already evolved from mailed subscription newsletters to emailed alerts, blogs and Facebook® pages. The timeliness and local relevance of the information is a key benefit of this electronic distribution system. Greenhouse trade magazines and university IPDM and other extension programs as well as plant propagation, plant protection and greenhouse supply companies are utilizing the internet to provide growers with information they need. Webinars and educational information that has been collected at sites such as eGro (https://e-gro.org – Electronic Grower Resources Online) allow international exchange of information, some of it in real-time and some archived for future reference. Apps have also been developed to assist scouts in their decisions in the greenhouse, e.g. the Pocket IPM Greenhouse Scout Mobile App from Cornell University https://tinyurl.com/y9korbhr that aids in scouting and pest identification.

22.4 Conclusion

Because the unchecked development of pests or pathogens on ornamentals can lead to 100% crop losses from cosmetic injury, death, or regulatory action, investments in improved pest management are worthwhile for all growers. Globally, one recent estimate suggested that there could be as much as $10 billion USD annual loss in floriculture crops to plant diseases alone (McGovern and Elmer 2017). The need for research efforts to speed up the development of more greenhouse system-wide biocontrol for floriculture crops is obvious. One of the main reasons given by growers for not using biological control was that they did not know enough about biocontrol to use it effectively (Sulecki 2015). Also, improving the availability of biological control agents in all major production countries will help the adoption.

In cases where pesticides are still the main pest and disease control method, new safe chemistries with low environmental impact are needed to replace some existing materials and to provide rotational partners where choices are limited. Crops with high customer appeal and low pest and disease susceptibility are the highest priority, which should be attainable with modern methods of plant breeding. It seems very likely that some form of genetic modification will be utilized towards this important goal in the near future.

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Chapter 23
Implementation of IPDM in Greenhouses: Customer Value as Guideline

J. S. Buurma and N. J. A. van der Velden

Abstract The objective of this chapter is to provide IPDM researchers and advisers with ideas on how to enhance the implementation of innovative IPDM knowledge and tools into practice. The chapter is based on research into innovation dynamics in food chains, willingness to pay of consumers, quality standards of high market segments, product prices in different market segments and motivations of greenhouse growers. The challenge of innovation in food chains rests in joint action between knowledge partners, primary producers and value chain partners. Experience has taught that reduction of pesticide use and substitution of chemical pesticides by biocontrol alone is not enough to make a distinction in the market. New product concepts have to be supplied to provoke a willingness to pay amongst consumers. The resulting higher consumer prices generate more money to be shared among the partners in the value chain. The main motivations of greenhouse growers are to produce a customer product (market-oriented subgroup), grow a healthy crop (crop-oriented subgroup) and achieve a lower cost price (cost-oriented subgroup). Implementation of IPDM technologies has best chances in the market-oriented and crop-oriented subgroups. They are more willing and able to integrate customer values in new product concepts and production systems than their cost-oriented colleagues.

Keywords Innovation dynamics · Willingness to pay · Value chain · Product concepts · Vegetables

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23.1 Introduction

Experience shows that the implementation of Integrated Pest and Disease Management (IPDM) in practice is challenging. Adoption of IPDM technologies progresses slower in most cases than researchers and advisers had in mind. However, this problem is not new nor specific for IPDM. Several social scientists, such as Rogers (1962, Diffusion of innovations) and Moore (1991, Crossing the chasm), have dedicated their lives to understanding the mechanisms of, and designating incentives for, the implementation of new technologies. Still, the challenge remains. Recently, the European Commission (CORDIS 2014) again identified this challenge and framed it as ‘the research and innovation divide’.

Many IPDM researchers and advisers believe that the solution is in further improvement of innovative IPDM tools and knowledge supply. The leaders of ENDURE (European Network for Durable Exploitation of crop protection strategies), e.g., aimed at making knowledge supply more flexible, locally adapted and practical (Barzman et al. 2015). In our opinion, however, the solution rests in paying attention to the motivations of growers and the values and incentives of value chain partners.

The objective of this chapter is to provide IPDM researchers and advisers with ideas on how to enhance the implementation of innovative IPDM knowledge and tools into practice by sharing knowledge on:

(i) The dynamics of innovations in food chains;
(ii) The position of growers in innovation processes;
(iii) The roles of input suppliers and value chain partners.

23.2 Dynamics of Innovation in Food Chains

Analyses of public debates on crop protection in the Netherlands revealed a recurring pattern. The pattern has been summarised in a flow chart (Fig. 23.1).

The flow chart starts with social unrest (through actions and campaigns of activist NGOs) and (5–8 years later) results in customer value. Between start and result several activities and changes take place. The urgency created by activist NGOs is picked up by moderate NGOs. In the right half of the triangle, they work with knowledge partners to find technical solutions and develop standards. In the top segment of the triangle, they further develop and implement innovative tools and knowledge with primary producers. In the left half of the triangle, they negotiate and strike deals with retail companies and food service providers. Actions and campaigns of activist NGOs help to convince the value chain partners to make moves. These actions and campaigns also help to make consumers aware of the values missing or needed in consumer products.

The kernel of the dynamics described is coordinated action (gearbox in Fig. 23.1) of knowledge partners (including input suppliers), primary producers (i.e. green-

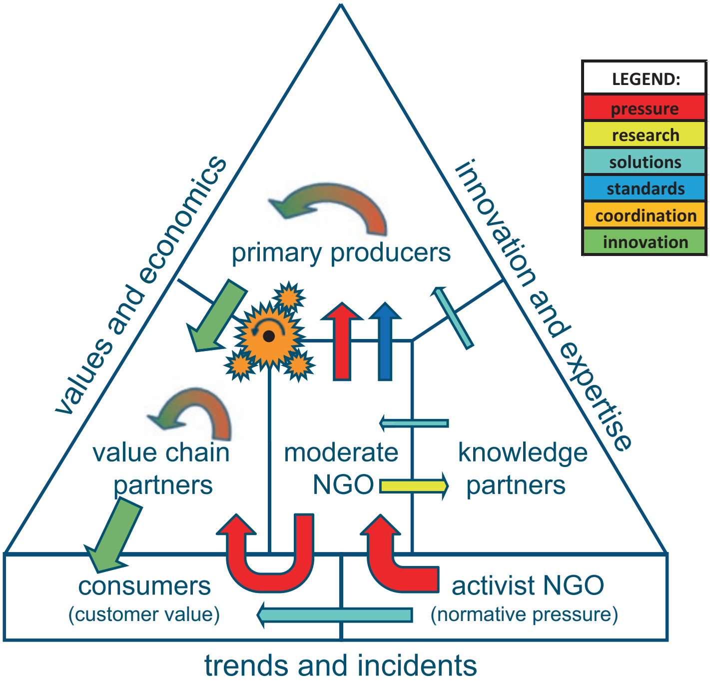

Fig. 23.1 Flow chart of the dynamics of societal pressure and innovations in food chains

house growers) and value chain partners. A series of experiments with an agent-based simulation model revealed that activist NGOs, proactive retailers and open-minded producer organisations are crucial for bringing this coordinated action concerned to a successful conclusion (More information on the social dynamics in public debates and the simulation model can be found in Buurma et al. 2017).

23.3 Product Concepts

Actions and campaigns of NGOs on the environmental impact of pesticides and/or exceeding maximum residue levels (MRLs), in principle, strengthen the position of IPDM grown products in the market. However, experience has taught that reduction of pesticide use and substitution of chemical pesticides by biocontrol alone does not result in higher product prices. The difference in consumer quality is just too small to make a distinction on the shelf. To attract the attention of the consumer and provoke a willingness to pay, new product concepts have to be supplied. The idea of product concepts is explained in Fig. 23.2.

In May 2018, the traditional loose tomatoes in the illustration were sold for €1.39 per 500 g, the more modern vine tomatoes for €1.79 per 500 g, and the new snack tomatoes for €2.99 per 500 g. The differences in consumer prices suggest that new

Loose tomatoes, 500 gram, €1.39

Vine tomatoes, 500 gram, €1.79

Snack tomatoes, 500 gram, €2.99

Fig. 23.2 Three product concepts of tomatoes with corresponding product prices. (Photos Shutterstock)

product concepts (in this case tasty and residue-free snack tomatoes in a transparent plastic box) provide a win-win situation for all partners in the value chain. The consumer is willing to pay a higher price and thus there is more money to be shared among the partners in the value chain. The higher price is partly necessary, because of the lower crop yield (kg/ha) and consequently higher costs price (€/kg) of snack tomatoes.

Traditional product concepts (e.g. loose tomatoes) often are at the end of their life cycle and pushed down to shrinking market segments. As a result, the fixed value chain costs have to be earned back with shrinking product volumes. Partial product improvements (e.g. through IPDM) may stretch the life cycle and delay the decline in market share but usually offer little room for price recovery.

A new product concept (e.g. snack tomatoes) includes an integration of several consumer quality aspects in a vegetable or ornamental product and the underlying production system. Van der Velden (2015) identified these quality aspects in an exploratory survey among tomato seed companies and tomato trade companies in southern Europe. These quality aspects were, in the first place, taste and flavour, in the second place, physical appearance such as shelf life, product type, colour and package, and in the third place, low pesticide residue levels.

This array of consumer quality aspects implies that IPDM and low residue levels alone are not enough to get access to higher market segments and secure higher product prices. The clue is in integrating tasteful cultivars and product types, advanced agronomy, adequate crop management, attractive packaging and low pesticide residue levels in one inclusive product concept, and thus achieving a license to deliver for higher market segments with corresponding higher prices.

23.4 Economic Evidence

The suggestion that new product concepts provide a win-win situation for all partners in the value chain requires further substantiation. After all, a higher consumer price is no guarantee for a higher producer price. Indications for higher producer prices being paid for new product concepts were obtained in exploratory surveys on crop protection challenges in greenhouse tomato production in southern Europe (Van de Velden et al. 2012). In those surveys, growers and traders complained about the strict pesticide residue requirements of German supermarkets.

This observation led to the hypothesis that the growers and traders concerned were eager to export tomatoes to Germany, because of attractive prices, but that they were not able to meet the quality standards (including strict residue requirements) of the demanding German supermarkets. To check the hypothesis of attractive prices for exports to Germany, detailed export data of fresh vegetables (tomatoes, sweet peppers and cucumbers) were extracted from Eurostat's Comext database and analysed.

In the analysis, the main exporting countries of both tomatoes and sweet peppers and cucumbers were first identified: Italy, Spain, France, Belgium and the Netherlands. Subsequently, the exports data of each of these countries were divided into two segments representing: (1) exports to Germany, and (2) exports to the rest of the EU. For these two segments, average export prices per year were calculated (total values divided by total volumes). This was done for the exports of both tomatoes and sweet peppers and cucumbers over the years 1999 through 2015. The differences in average export prices between the two segments (i.e. price premium for Germany relative to the rest of the EU) for tomatoes are presented in Fig. 23.3.

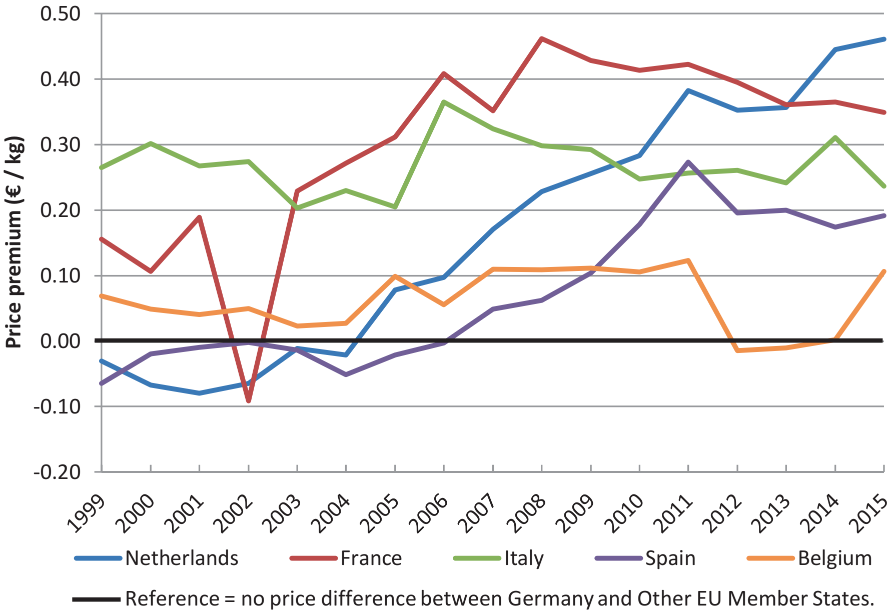

Fig. 23.3 Price premium for tomatoes exported to Germany relative to tomatoes exported to the rest of the EU, specified for the main exporting countries. The green line represents the price differences for Italy. The black line represents the X-axis of the figure, where the price difference between exports to Germany and to the other EU Member States is € 0.00. The price differences for exports from Spain, France, Belgium and the Netherlands are presented by the purple, red, orange and blue lines respectively

In 80% of the cases (i.e. the values above the X-axis in Fig. 23.3) the prices of tomatoes exported to Germany were higher than the prices of tomatoes exported to the rest of the EU. The 20% of cases (i.e. the values below the X-axis in Fig. 23.3) with lower prices of tomatoes exported to Germany than to the rest of the EU can be attributed to exports from Spain and the Netherlands in the years before 2007. In those years, tomatoes from the two countries concerned did not meet the quality requirements of the German supermarkets. From 2007 onwards, in nearly all cases the export prices to Germany exceeded the export prices to the rest of the EU. In 2012 and 2013, Belgium was an exception to this rule, probably as an aftermath of the EHEC crisis in 2011. The other exporting countries also saw their price premiums for Germany drop in 2012.

In 25% of the cases (i.e. the values above the 0.30 line in Fig. 23.3) the price difference was larger than 0.30 €/kg, compared to the reference of 1.20 €/kg. In 2015, the price difference varied between 0.10 €/kg for Belgium and 0.45 €/kg for the Netherlands. The difference between Belgium and the Netherlands can be explained by product types. According to seed suppliers (Van der Velden 2016), tomato production in Belgium included a high percentage of beef tomatoes (traditional market), whereas tomato production in the Netherlands included a high percentage of specialty tomatoes (trendy market).

Similar patterns, but to a lesser extent, were found for sweet peppers. Cucumber exports to Germany did not yield higher prices than exports to other EU Member States. This variation between the different products is related to product innovation: the higher prices in higher market segments can only be secured with modern types/cultivars of existing products (tomatoes) and not with traditional types of existing products (cucumbers).

23.5 Entrepreneur Types

As mentioned in the introduction, the motivations of growers represent an important factor in the implementation of new technologies. So, for a successful implementation of IPDM in greenhouses it is useful for IPDM researchers and advisers to have some notion of the motivations of growers and entrepreneur types. Buurma and Smit (2016), in a study on the adoption of an innovative climate management concept in Dutch greenhouse horticulture, captured those motivations and entrepreneur types. They identified three subgroups of growers (Table 23.1).

The three subgroups differ in attitude with regard to implementation of new knowledge and tools: the market-oriented subgroup can be characterised as ‘ambitious’, the crop-oriented subgroup as ‘attentive’ and the cost-oriented subgroup as ‘ambiguous’. These characteristics are reflected in the motivations and resulting search and control agendas of the subgroups. The market-oriented entrepreneurs develop knowledge on how to integrate novel findings on customer demands, crop

Table 23.1 Motivations of three subgroups of growers involved in the adoption of an innovative concept for climate management in greenhouses in the Netherlands

Element	Market-oriented entrepreneurs	Crop-oriented entrepreneurs	Cost-oriented entrepreneurs
Motivation	Customer product	Healthy crop	Lower cost price
Search agenda	Crop physiology	Climate improvement	Climate equipment
Control agenda	Plant robustness	Climate and hygiene	Chemical control
Attitude[a]	'Ambitious'	'Attentive'	'Ambiguous'

Source: Buurma and Smit (2016)

Background information on the methodology applied for capturing the motivations of growers can be found in Buurma and Smit (2016) and in Buurma and Van der Velden (2016)

[a] Characterisation of entrepreneurial behaviour by the researchers

Table 23.2 Economic and social characteristics of three subgroups involved in the adoption of an innovative concept for climate management in greenhouses in the Netherlands

Characteristics	Market-oriented entrepreneurs	Crop-oriented entrepreneurs	Cost-oriented entrepreneurs
Greenhouse area (ha)	5–15	4–8	2–6
Construction period	2010–2014	2000–2009	1995–2004
Role of crop adviser	Thinks along	Comes round	Keeps off
Desired support	Plant monitoring	Exchange insights	Subsidies/courses
NCC[a] application	Step by step	Radical/careful	Reserved

Source: Buurma and Smit (2016)

[a] *NCC* new cultivation concept

physiology and plant robustness in new product concepts. The crop-oriented entrepreneurs focus on gathering and integrating actual experience on greenhouse climate and farm hygiene in order to grow a healthy crop (and low crop losses). The cost-oriented entrepreneurs focus on the purchase of climate equipment and the use of pesticides to achieve a good production with lower costs. So, the span of control of the three entrepreneur types varies from relatively wide and complex (value chain) to relatively narrow and simple (equipment).

In addition, Buurma and Smit (2016) collected economic and social characteristics of the growers in the three subgroups to gain an understanding of their respective business contexts (Table 23.2).

The greenhouse areas and construction periods show that the market-oriented entrepreneurs had relatively large and new greenhouses. They were able to invest in new greenhouses after the financial crisis of 2008. The crop-oriented entrepreneurs had smaller and older greenhouses. They stopped investing in new greenhouses after the financial crisis (including poor economic results) of 2008. The cost-oriented entrepreneurs had (on average) the smallest and oldest greenhouses. They already stopped investing in new greenhouses in 2004. These economic differences indicate a favourable position for the market-oriented entrepreneurs, a moderate position for the crop-oriented entrepreneurs and a difficult position for the costs-oriented entrepreneurs. More than half of the latter subgroup indicated that they had financial problems and/or wanted to sell their business.

The role of crop advisers also differed among the three subgroups. The market-oriented entrepreneurs were actively supported with the introduction of the new concept. The crop-oriented entrepreneurs first had to convince the advisers, whereas the cost-oriented entrepreneurs were warned against the risks of the new concept. The desired support line shows that the market-oriented entrepreneurs asked support for the development of novel plant monitoring software. In contrast, the crop-oriented colleagues asked support for the organisation of on-the-spot exchange of actual insights with colleagues. The cost-oriented entrepreneurs asked for subsidies and courses. The desired support corresponds with the search agendas (crop physiology, climate improvement and climate equipment) of the three subgroups. These differences again indicate a strong position for the market-oriented entrepreneurs, a moderate position for the crop-oriented entrepreneurs and a difficult position for the cost-oriented entrepreneurs.

The result is an accumulation of positive economic and social circumstances in the market-oriented subgroup, moderate economic and social circumstance in the crop-oriented subgroup and weak economic and social circumstances in the cost-oriented subgroup, which also materialises in the innovation rate in the three subgroups. These findings indicate that new concepts such as IPDM have a better chance of adoption in the market-oriented and crop-oriented subgroups than in the cost-oriented subgroup.

In crop protection projects, such as the EU-projects ENDURE and PURE, the technical experts usually consider effective pest/disease control, low input costs and good production as their terms of reference and subsidies and courses as means to promote adoption (e.g. Barzman et al. 2015). The terms concerned are remarkedly similar to the jargon of the cost-oriented entrepreneurs and indicate a (probably unintentional) preference for the cost-oriented entrepreneurs as target group.

However, the problem is that more than half of this subgroup have financial problems and/or plans to sell their business. Knowledge investments in this subgroup, then will in many cases not lead to adoption of new crop protection solutions. Supporting the learning process of market-oriented and crop-oriented entrepreneurs and their advisers has a greater chance of success.

23.6 Take-Home Message

The supply of knowledge and technologies alone is not enough for the implementation of IPDM in practice. The motivations of the growers and the support of their value chain partners also play an important role. The figure in Annex 23.1 depicts this notion in a nutshell.

The main motivation of the most motivated growers (i.e. market-oriented subgroup) is achieving a license to deliver for higher market segments with their corresponding higher product prices. However, experience has taught that getting access to higher market segments and achieving higher prices requires more than just implementation of IPDM. To attract the attention of the consumer and a willingness to pay, new product concepts have to be supplied.

The differences in consumer prices between traditional product concepts (e.g. loose tomatoes; €1.39 per 500 g) and new product concepts (e.g. tasteful and residue-free snack tomatoes in a plastic cup; €2.99 per 500 g) provide a win-win situation for all partners in the value chain. Due to the higher prices for new product concepts, there is more money to be shared among the partners in the value chain. Growers and their sales/export organisations also profit from the higher prices. Analyses of export statistics revealed 10–20% higher export prices for tomatoes and sweet peppers supplied to the highly demanding German market.

A new product concept includes an integration of several consumer quality aspects in a vegetable or ornamental product and the underlying production system. The clue rests in integrating tasteful cultivars and product types, advanced agronomy, adequate crop management, attractive packaging and low pesticide residue levels in an inclusive product concept, and thus achieving a license to deliver for higher market segments with corresponding higher prices.

For a successful implementation of IPDM in greenhouses it is useful to keep the motivations and characteristics (economic and social circumstances) of growers and entrepreneur types in mind. The main motivations are producing a customer product (market-oriented subgroup), growing a healthy crop (crop-oriented subgroup) and achieving a lower cost price (cost-oriented subgroup). Because of their stronger economic and social positions, market-oriented and crop-oriented entrepreneurs are more willing and able to integrate customer values (including IPDM) in new product concepts and production systems than their cost-oriented colleagues.

In summary, successful implementation of IPDM in greenhouses depends on integrating customer values such as tasteful cultivars and product types, attractive physical appearance and packaging, and low pesticide residue levels in inclusive product concepts to achieve a license to deliver for higher market segments with corresponding higher prices.

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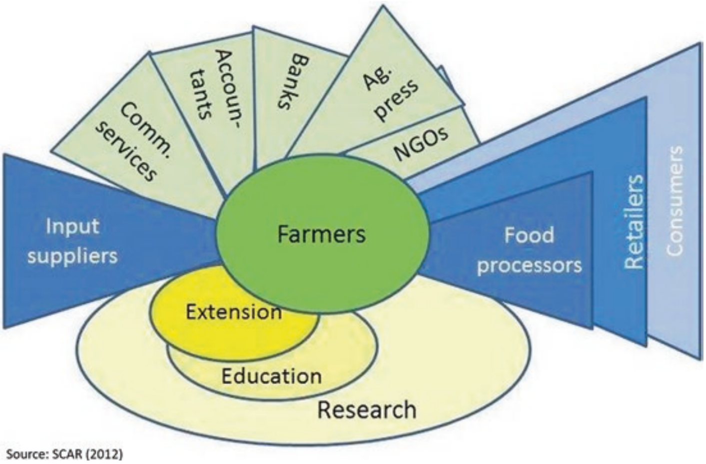
Annex 23.1: The Position of Farmers in Agricultural Knowledge and Innovation Systems

The Standing Committee on Agricultural Research (SCAR) of the European Commission in a foresight paper (SCAR 2016) considered the position of farmers and growers in agricultural knowledge and innovation systems. Their view is presented in Fig. 23.4.

SCAR (2016) pointed out that 'although different AKIS-components – Extension, Education and Research – are often stressed, it is important to realise that there are many more actors in the food chain that directly influence the decision making of farmers and their innovations'. The SCAR-view implies that IPDM researchers and advisers have to make a turn from vertical thinking (yellow and light green actors in Fig. 23.4) to horizontal thinking (blue actors in Fig. 23.4).



Source: SCAR (2012)

Fig. 23.4 Actors in Agricultural Knowledge and Innovation Systems (AKIS) directly relevant for agricultural innovation in the food chain (Commercial services include laboratories, veterinarians, management software, notaries, land brokers, whereas accountants have been mentioned separately as being in some countries very influential for strategic decisions)

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