

Chapter 10

Cultural Methods for Greenhouse Pest and Disease Management



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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.

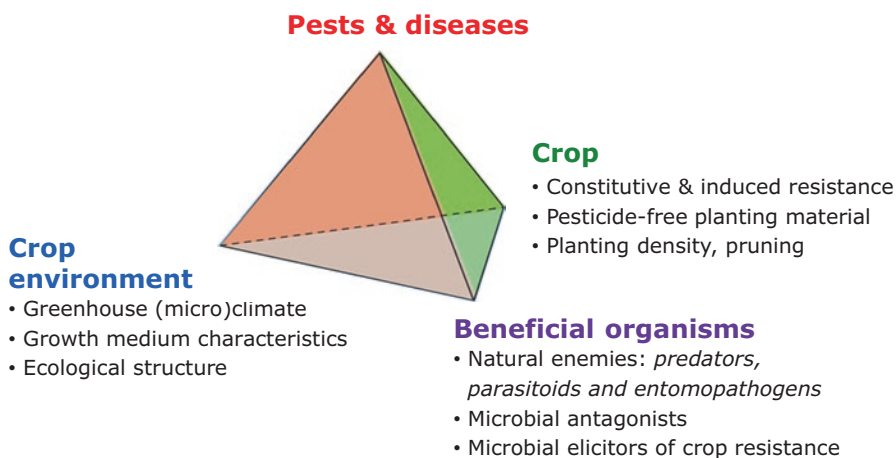


Fig. 10.1 Pest and disease tetrahedron, depicting the 4 main components of a systems approach to pest and disease management, as well as their interactions

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 coenzymes 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). Disinfecting greenhouse floors, rockwool slabs, bench top surfaces, support strings, trays, pots, and utensils will further reduce common pest reservoirs. Most disinfectants like alcohol, household 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 as 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 polypropylene 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 disinfestation 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. Perdakis 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 a 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 insulated 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 tetranychid 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 exosmoted 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 *Tetranychus 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 $55 \pm 10\%$ 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 above-ground 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 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/m² 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 W m^{-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 ($112\text{--}114 \text{ W m}^{-2}$) and long daylength (L:D = 16:8 h) than at low light intensity ($12\text{--}14 \text{ W m}^{-2}$) 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 nocturnal 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; Hiramata 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 greenhouse 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 $\text{Ca}(\text{NO}_3)_2$ 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 through 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 $\text{NH}_4\text{-N}$, whereas *Fusarium* diseases were almost consistently suppressed under $\text{NO}_3\text{-N}$ 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 $\text{NH}_4\text{-N}$ 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 (Ammann 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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