Chapter 6
Allium Breeding Against Biotic Stresses

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Abstract Among *Allium* species, onion (*Allium cepa* L., $2n = 2x = 16$) and garlic (*Allium sativum* L, $2n = 2x = 16$) are cultivated throughout the world for their culinary, medicinal and therapeutic values. The production, productivity and inherent nutritional potential of these crops is immensely affected by various biotic stresses before and after harvesting. Onion breeding techniques are in several aspects less developed than those available and employed in other horticultural and agricultural crops. The major biological limitations that hampers onion breeding programmes are its biennial nature, photosensitivity, outcrossing flowering behavior, combined with a high inbreeding depression. Apart from these, the huge genome size (16 GB) with highly repetitive non-coding DNA is also a big constraint to complement marker-assisted breeding. Recently, a garlic genome was completely sequenced, as the first Allium species. With the recent release of the first draft genome assembly of onion, hopefully this would help to augment onion breeding possibilities through developing more and reliable genomic resources for resistance breeding against various insect-pest and diseases. This chapter summarizes the main diseases and pests threatening onion production in tropical and temperate regions, the efforts in breeding for disease and pest resistance, the development of tools for marker assisted selection and the potential of genomic tools for the development of resistant cultivars.

Keywords *Allium cepa* L. · Biotic · Stress · Onion · Garlic

6.1 Introduction

Onion (*Allium cepa* L.) is the main *Allium* cultivated species and is grown throughout the world for its culinary and medicinal values. Onion ranks second after tomato

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among vegetable crops regarding the produce (FAOSTAT 2019). The production, productivity and inherent nutritional potential of onions is affected by many pre- and post-harvest diseases, pests, and viruses (Agrios 2005). This chapter summarizes the main diseases and pests threatening onion production in tropical and temperate regions, the efforts in breeding for disease and pest resistance, the development of tools for marker assisted selection and the potential of genomic tools for the development of resistant cultivars.

Plants live in nature in contact with a wide spectrum of microorganisms, arthropods, and a range of other potential enemies. Plants possess an immunity system to prevent that any microorganism can feed from live plant tissues (Niks et al. 2011). As a consequence of this general defense system, only a few microbes and arthropods co-evolved with specific *Allium* species to develop pathogenicity and virulence mechanisms to become pathogens, parasites, or pests. Pathogenicity may be either restricted to a specific plant species or taxa or extended to a broad spectrum of host species (Agrios 2005). As examples, onion is affected by downy mildew caused by *Peronospora destructor*, a pathogen able to infect only onion and few closely related *Allium* species (Kofoet and Zinkernagel 1989; Scholten et al. 2007). In contrast, *Botrytis cinerea*, a generalist pathogen able to cause brown stain in mature onion bulbs as well as flower blight at onion blooming (Steentjes et al. 2021), can cause grey mold in over 200 cultivated plant species, including tomato, grape vine, strawberry, and Cannabis (Williamson et al. 2007).

6.1.1 Passive Defenses

Plant immunity system involves different levels of defenses, briefly described in these sections. Some passive defense mechanisms are developed and present in plants as adaptative barriers (Niks et al. 2011). *Allium* species are characterized by the production of allicins, a family of cysteine-sulfoxides that upon damage are metabolized releasing thiosulfinates with antimicrobial activity against gram positive and negative bacteria (Ankri and Mirelman 1999, Reiter et al. 2020). To visualize its relevance, pathogenicity of *Pantoea ananatis* strains causing bulb rotting, requires the gene cluster *alt* (allicin tolerance), codifying for enzymes that confer tolerance against thiosulfinates (Stice et al. 2020).

Another pre-formed defense is given by the catechin, a skin phenolic pigment present in pigmented onion (yellow and red bulbs) with antioxidant activity (Beretta et al. 2017). Onion smudge caused by *Colletotrichum circinans* affects white onions, as small black flecks on the bulb surface with the sign of the pathogen. Smudge disease is not observed in pigmented onions (either with yellow or red skins) due to the inhibitory effect of catechin on spore germination and fungal growth, a ubiquitous example of passive defenses in plants (Link et al. 1929).

6.1.2 Active Defenses

In addition, active defense mechanisms are triggered once the presence of a potential pathogen or damage is perceived by plant tissues (Li et al. 2020). The early phase is a broad-spectrum resistance, triggered by the recognition of pathogen associated molecular patterns (PAMPs) by plant recognition receptors (PRR). This defense is called PAMP triggered immunity (PTI) (Jones and Dangl 2006). The main PTI signaling pathway is a cascade of mitogen activated protein kinases (MAPKs) leading to cellular responses that comprise the production of reactive oxygen species (ROS), synthesis of antimicrobial compounds like phytoalexins and phytohormones, reinforcement of the cell wall, cell wall appositions, and programmed cell death (Ponce de Leon and Montesano 2013). Some typical PAMP conserved molecules recognized by PTI are the bacterial flagellin and EF-Tu, and the fungal chitin (Panstruga et al. 2009).

Pathogens can hamper effective defenses by the release of effectors, proteins that, for instance, suppress early steps before the MAPK signaling pathway is activated (He et al. 2007). Then, the result is plant host susceptibility mediated by pathogen effectors (Jones and Dangl 2006). Like in an arm race, plants have developed the recognition of effectors by specific molecules (R proteins) triggering a resistance response called effector triggered immunity (ETI). This resistance occurs later in the infection process than PTI, when the plant and the pathogen establish an intimate contact (e.g., post-haustorial in obligate pathogens) (Niks et al. 2011). ETI is a highly effective resistance, typically leading to programmed cell death with no visible disease symptoms and controlled by a single R gene coding for the R protein, two reasons that make it very attractive for breeders. As constraints, effector mediated resistance is specific, only effective for those strains carrying the recognized effector, making a strong evolutive pressure in favor of other strains in the field or strains mutated at the recognized effector (Niks et al. 2011).

Plant recognition receptors and R proteins are a family of molecules with perception (ecological) activity. Most of them share the presence of a conserved region, like the nucleotide binding sequence (NBS), and a more variable region like the leucine rich repeats (LRR), the region with activity in the recognition of PAMP or effectors (Hammond-Kosack and Parker 2003). PTI is associated with the activation of jasmonic acid (JA) and ethylene (ET) activities, leading to high or partial resistance responses in plant genotypes either for necrotrophic or biotrophic pathogens. ETI is associated with the activation of salicylic acid (SA), leading to high resistance to complete resistance in plant genotypes (Panstruga et al. 2009). Throughout the action of mobile phytohormones like JA, ET, and SA, both PTI and ETI express additional systemic responses, activating defense reactions in plant tissues far apart from the infection points (Pieterse et al. 2009).

6.2 Breeding *Allium* Species

6.2.1 Rudimentary Genetics

Onion ($2n = 2x = 16$) breeding techniques are in several aspects less developed than those available and employed in other crops. Besides the minor economic relevance of *Allium* crops, some of the main biological constraints addressed in the literature are the biennial life cycle, the photothermal (seasonal) requirements, and the outcrossing flowering behavior of the crop combined with a high inbreeding depression (Shigyo and Kik 2008; Havey 2012; Khar and Singh 2020; Singh et al. 2021a). These onion features point Havey (2012) to qualify onion genetics as rudimentary, as only genes for a few agronomic traits were known and mapped at that time and until now. Among these mapped genes, few are disease resistance genes (Table 6.1).

The huge genome size for onion (*Allium cepa*, 32–33.5 pg·cell^{-1}), even larger than *A. roylei* (28–30 pg·cell^{-1}) and shallot (*A. fistulosum*, 22.5–23.5 pg·cell^{-1}) genomes (Ricroch et al. 2005), add to the list of constraints, has prevented and delayed the availability of fully sequenced genomes as a resource for molecular breeding. In comparison to other crops used as model plants, rice has a genome estimated in 490 Mb and tomato 1038 Mb, whereas onion genome is estimated at 17,500 Mb (Leitch et al. 2019). Fortunately, Finkers et al. (2021) have recently communicated the first draft genome available for onion, with 14.9 Gb assembled, and 2.2 Gb arranged in the eight pseudomolecules, with a high synteny with garlic (*Allium sativum*) genome (Sun et al. 2020). The advent of genomic resources is particularly good news and will accelerate the progress in molecular genetics and marker assisted selection.

Table 6.1 Few disease resistance genes identified and/or mapped for onion breeding

Disease resistance	Source	Gene	Chromosome	Marker system	References
Downy mildew	*A. roylei*	*Pd1*	3	SCAR	Kik et al. (1997)
				AFLP	Scholten et al. (2007)
				Simple PCR	Kim et al. (2016)
Fusarium basal rot	*A. cepa*	–	1	SNP	Taylor et al. (2019)
		–	6	SNP	
		–	8	SNP	
		–	Unmapped	SNP	
Purple blotch	*A. cepa*	*Apr-01*	Unmapped	STS, SSR	Chand et al. (2018)

Diverse molecular marker systems have been applied in genetic traits analysis and genetic diversity analysis in onion, summarized by Klaas and Friesen (2002) and Khosa et al. (2016): random amplified polymorphic DNA (RAPDs), restriction fragment length polymorphism (RFLP) and amplified fragment length polymorphism (AFLP) (van Heusden et al. 2000). The development of simple sequence repeat (SSR) markers was successful only after based on expressed sequence tags (ESTs) (EST-SSR; McCallum et al. 2008; Khar et al. 2011). A step further was given by the upcoming of next generation sequencing (NGS) technologies, setting up the base for the development of highly dense linkage maps based on single nucleotide polymorphism (SNP) markers (Duangjit et al. 2013; Scholten et al. 2016).

6.2.2 Genetic Resources

Onion is a cultigen not found as such in nature. The center of origin as postulated by Vavilovi is Central Asia, where its close relative *A. vavilovii* is found (Fritsch and Friesen 2002). McCallum et al. (2008) studied a global panel of onion germplasm diversity based in EST-SSR markers and distinguished an Indian–Iranian gene pool separated from a SD and a LD gene pools of European and American germplasm, suggesting divergent adaptation of eastern and western onion gene pools. Similarly, Taylor et al. (2019) studied a world onion accessions panel using SNP markers developed by Duangjit et al. (2013), and accessions were grouped according to photoperiodic requirements and geographical regions.

A comprehensive strategy to identify sources of resistance is needed. Most of the research work has focused on Fusarium basal rot and downy mildew under temperate conditions. In tropical countries, research on purple blotch has only focused on management and phenotypic screening.

Wild relatives of Alliums have been evaluated and found carrying diverse degrees of resistance to various diseases and pests, as summarized in Table 6.2. Wild relatives of crops have been used to introduce genetic variation in crops for several plant families, mainly for diseases and pest resistance (Hajjar and Hodgkin 2007). Nevertheless, crosses between onion and resistant wild species have not been as successful as needed for introgression traits, due to pre- and post-fertilization barriers. Development of interspecific F1 having non-bulbing traits and poor to none male fertility have also hampered the interest of breeders to use these wild species in conventional breeding programs (Kik 2002). The only successful example of interspecific hybridization has been the crossing of *A. cepa* and *A. roylei* for the development of downy mildew resistant onions (Scholten et al. 2007).

The gene pool classification from Harlan and De Wet (1971) yields a very narrow gene pool 1 for onion (defined as viable crosses within the cultivated species and crosses with very narrow species producing completely fertile progenies). Viruel et al. (2021) proposed to consider crop wild relatives (CWRs), summing up information of phylogenetic distance and biological information on crossing compatibility. This kind of integrated information for onion related species was shown by van Raamsdonk

Table 6.2 Summary of some resistance reports against diseases and pests in onion (*Allium cepa* L.) and onion relatives

Resistance source	Disease resistance	Varieties	References
Allium cepa	Purple blotch	CBT-Ac77, Arka Kalyan	Nanda et al. (2016)
		Red Creole, Yellow Creole	Bock (1964)
		Red Creole, Red Shallot	Natural Resources Institute (1990)
		Red Creole	Montes (2004)
		Red Creole, Kaharda	Abubakar et al. (2006)
	White rot	Sweet sandwich	
	Thrips	VI038552, VI038512, AVON1067	Njau et al. (2017)
	Fusarium basal rot	Rossa Savonese	Galván et al. (1997)
		NMSU00-25	Gutiérrez and Cramer (2005)
		Ailsa Craig prinzewinner White Lisbon	Taylor et al. (2013)
	Downy mildew	Regia	Arias et al. (2020)
	Thrips	White Persian	Jones et al. (1934)
		IPA-3	Hamilton et al. (1999)
		Meshkan; Sefid-e-Kurdistan	Alimousavi et al. (2007)
Allium fistulosum	Anthracnose		Galvan et al. (1997)
	Stemphylium Blight		Pathak et al. (2001) Dangi et al. (2019)
	Fusarium basal rot		Holz & Knox (1974) Galvan et al. (2008) Rout et al. (2015)
	Pink root	Nebuka, Winterhecke, White Welsh	Porter & Jones (1933), Felix (1933) Ludwin et al. (1992), Netzer et al. (1985)
	Botrytis squamosa		Walters et al. (1996), Bergquist & Lorbeer (1971), Currah & Maude (1984)
	Smut	Nebuka	Jones et al. (1934)
	Thrips	Nebuka	Jones et al. (1934)
Allium roylei	Anthracnose		Galvan et al. (1997)
	Purple blotch		Nanda et al. (2016)

(continued)

Table 6.2 (continued)

Resistance source	Disease resistance	Varieties	References
	Fusarium basal rot		Rout et al. (2015)
	Downy mildew		Kofoet and Zingernagel (1989)
	Botrytis squamosa		De Vries et al. (1992) Walters et al. (1996)
A. schoenoprasum	Fusarium basal rot		Galvan et al. (2008) Rout et al. (2015)
	Purple blotch		Nanda et al. (2016)
Allium galanthum	Anthracnose		Galvan et al. (1997)
A. tuberosum	Root knot nematode		Huang et al. (2016)
A. aflatunense	Penicillium decay		Dugan et al. (2011)
A. atroviolaceum	Penicillium decay		Dugan et al. (2011)
A. stipitatum	Penicillium decay		Dugan et al. (2011)
A. telavinense	White rot		Bansal and Broadhurst (1992)

et al. (2003). Only few closer onion related species yield F1 viable seed in interspecific crosses with *A. cepa, e.g., A. vavilovii, A. galanthum, A. fistulosum, A. roylei*, but obtained interspecific F1 plants are frequently unfertile or of low fertility plants. Crossing *A. cepa* with other more distant *Allium* species may require embryo rescue techniques. The bridge cross concept is another applied approach to be exploited in introgression strategies (Khrustaleva and Kik 2000; Kik 2002).

6.3 Featured Examples in *Allium* Breeding for Resistance

6.3.1 Purple Blotch

Purple blotch caused by *Alternaria porri* (Ellis) Cifferi is an important onion disease throughout the world (Schwartz and Mohan 2008). This disease is widely prevalent in warm and humid environments (Suheri and Price 2000; Shahanaz et al. 2007), and therefore is relevant in tropical climates and as a late season disease in temperate climates. This fungus attacks leaves and flower stalks, and reductions in the range 62 to 92% in foliar production has been noticed (Bock 1964; Suheri and Price 2001). Purple blotch causes heavy yield losses in both bulb and seed crops ranging from 2.5 to 97% during *kharif* season (Nanda et al. 2016). Some reports suggest a yield loss of 30% (Everts and Lacy 1990) and 100% seed crop loss under favorable conditions (Schwartz 2004).

Research on identification of purple blotch resistance has been ongoing for several decades (Bock 1964; Pathak et al. 1986; Daljeet et al. 1992; Lakra 1999; Chethana et al. 2011; Behera et al. 2013). Breeding for resistance against purple blotch revealed that Red Creole (hybrid), Red Creole (open pollinated), Yellow Creole (Bock 1964), VL-1, PBR-1, PBR-5, PRR and Arka Niketan (Daljeet et al. 1992), Red Creole and Red Shallot from Ethiopia (Natural Resource Institute 1990), Red Creole from Honduras (Montes 2004), Red Creole and Kaharda from Nigeria (Abubakar et al. 2006) were identified as resistant cultivars. Abubakar and Ado (2008) demonstrated that onion hybrids resistant to purple blotch can be developed. Exploitation of heterosis in onion to develop resistant hybrids is one of the viable options (Singh and Khar 2021).

Field resistance can break down under artificial conditions due to high disease pressure. Screening under normal epiphytotic conditions and artificial conditions is important to identify the resistant cultivars. The onion variety 'Arka Kalyan' and the accession 'CBT-Ac77' were identified as highly resistant to purple blotch whereas *A. schoenoprasum* and *A. roylei* were identified as moderately resistant (Nanda et al. 2016). Studies on inheritance revealed that purple blotch disease is controlled by a single dominant gene christened as *ApR1* (Chand et al. 2018). Molecular mapping for disease resistance led to development of one SSR marker (AcSSR7) and one sequence tagged site (STS) marker (ApR-450) linked closely to the *ApR1* locus in coupling phase at 1.3 and 1.1 cm, respectively (Chand et al. 2018). These markers can be used for introgression breeding of resistant locus in onion accessions for development of resistant genotypes.

6.3.2 Stemphylium Blight

Stemphylium blight (*Stemphylium vesicarium*) was first reported by Miller et al. (1978) to cause significant damage in onions (Fig. 6.1). It is a potentially important pathogen in winter grown *Allium* crops (Suheri and Price 2001). Warm humid conditions with temperatures ranging from 18 to 22 °C and relative humidity (RH) above 85% favor disease development; but the pathogen can also cause infections at lower temperatures (10 °C), as well as can develop at higher temperatures (Suheri and Price 2000).

Screening of onion and *A. fistulosum* accessions revealed that onion is susceptible whereas some lines of *A. fistulosum* were resistant to Stemphylium blight (Pathak et al. 2001). A possible dominant gene control of the resistance was observed based on F2 and F3 generation. Pathak et al. (2001) first reported natural and controlled screening against Stemphylium blight and identified two resistant *A. fistulosum* accessions. Most of the research has focused on screening against purple blotch and Stemphylium blight under both natural (Dhiman et al. 1986; Behera et al. 2013; Tripathy et al. 2013) and controlled conditions (Nanda et al. 2016; Dangi et al. 2019). After the first report by Pathak (2001), Dangi et al. (2019) identified 'Pusa Soumya' (*A. fistulosum*) and 'Red Creole2' (*A. cepa*) as moderately resistant and 'Red Creole1'

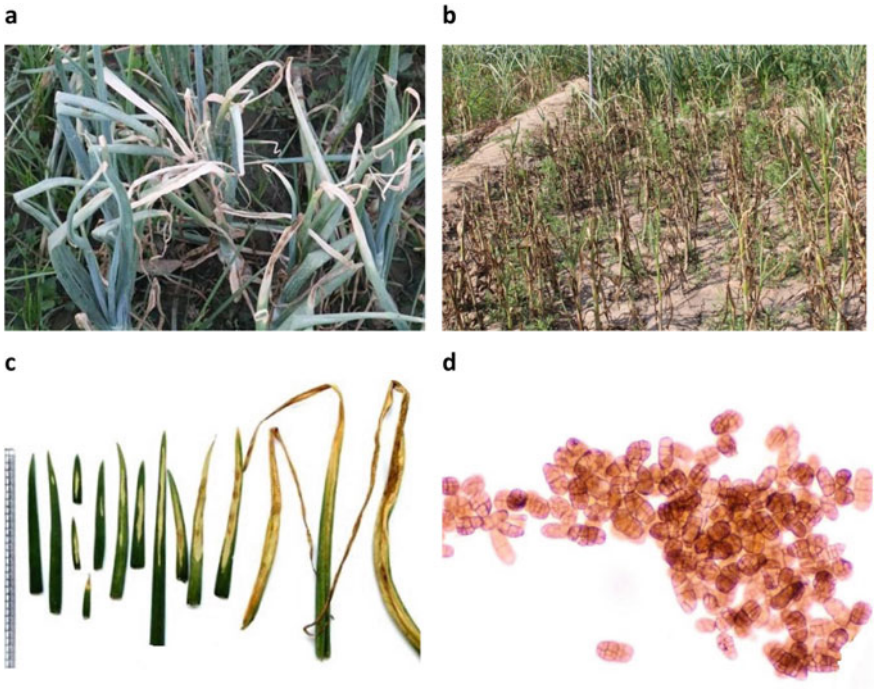

Fig. 6.1 (**a**) Stemphylium blight on onion in India; (**b**) Stemphylium blight outbreak in garlic; (**c**) different stages and levels of Stemphylium blight attack in onion as a scale in selection for resistance; (**d**) microscopical checking of *Stemphylium vesicarium* multicellular ovoid conidia, confirming field infections and symptoms in onion

as susceptible. Significant variation in morphological and biochemical traits was observed and it was suggested that dry matter and total foliar phenol content can be used as biochemical markers for high throughput screening against Stemphylium blight at preliminary screening stage.

In the absence of credible sources of resistance against Stemphylium, Kamal et al. (2008) advised application of benzothiadiazole (Bion®) and di-potassium phosphate salt (K_2HPO_4) to onion. Application of salicylic acid (2 mM) also suppressed 40.39% disease development after 15 days of inoculation under greenhouse conditions (Abo-Elyousr et al. 2009).

6.3.3 Anthracnose

Onion and shallot anthracnose or twister disease is a relevant cause of crop yield losses in tropical regions of Asia, Africa, and South America. The causal agent is

traditionally described as *Colletotrichum gloeosporioides* Penz. (teleomorph *Glomerella cingulata* (Stonem.) Spould & Schrenk). This airborne fungus is a saprophytic pathogen that infects onion leaves, but also seedlings and harvested bulbs (Maude 1990; Lopes et al. 2021). A collection of pathogen isolates from Brazilian regions were identified using sequencing of several genes (Lopes et al. 2021), and isolates were found to belong to the *C. gloeosporioides* and *C. acutatum* species complexes. The species *C. theobromicola* from the *C. gloeosporioides* cluster was predominant in the collection (Lopes et al. 2021).

Rodriguez and Hausbeck (2018) described that anthracnose caused by *Colletotrichum coccoides* is a relevant disease in Michigan. They tested favorable conditions for the disease and reported that the combination of high temperature (>25 °C) and extended (>24 h) high RH resulted in high (>20% leaf area affected) disease severity 28 days post-inoculation.

The scant breeding efforts within the genetic base of onion crop only revealed quantitative differences or partial resistance. Wordell Filho and Stadnik (2008) assessed the response of 20 commercial Brazilian cultivars and identified those with lower levels of disease severity after experimental inoculation in controlled conditions. Earlier, in São Paulo, Brazil, Melo and Costa (1983) evaluated the survival rate of onion cultivars affected by anthracnose. A cross between the highly resistant cv. "Barreiro" and the susceptible "Texas Early Grano 502" suggested that resistance was polygenic and quantitatively expressed.

Galván et al. (1997) screened shallot and its wild relatives for anthracnose (*Colletorichum gloeosporioides* Penz.). *Allium cepa* and *A. oschaninii* were most susceptible, whereas *A. altaicum*, *A. fistulosum*, *A. galanthum*, *A. psekemense* and *A. roylei* were partially resistant. Highly resistant reactions were observed in *A. galanthum* and *A. fistulosum* accessions (Fig. 6.2). Genetic analysis based on a cross *A. cepa* x *A. roylei* revealed that resistance from *A. roylei* was dominantly inherited and determined by more than one gene (Galván et al. 1997).

6.3.4 Fusarium Basal Rot

Fusarium basal rot (FBR) is an important soil-borne disease of *Allium* crops throughout the world, which can affect seedlings, mature plants, and stored bulbs as well. In onion the disease is caused mainly by *Fusarium oxysporum* f. sp. *cepae* (FOC). Other *Fusarium* species may cause FBR in onion and garlic. *Fusarium proliferatum* (du Toit et al. 2003; Valdez et al. 2004; Stankovic et al. 2007; Galván et al. 2008) calls the attention because of the potential fumonisins toxins production and the risks for human consumption. Other less frequent *Fusarium* species have also been identified (Entwistle 1990; Galván et al. 2008).

Field and storage losses up to 23% have been reported under soils naturally infested with *Fusarium* (Bacher et al. 1989). The fungus attacks seedlings leading to damping off, root rot and enters the basal plate of onion bulbs causing stem plate discoloration and bulb rot in the field and storage (Abawi and Lorbeer

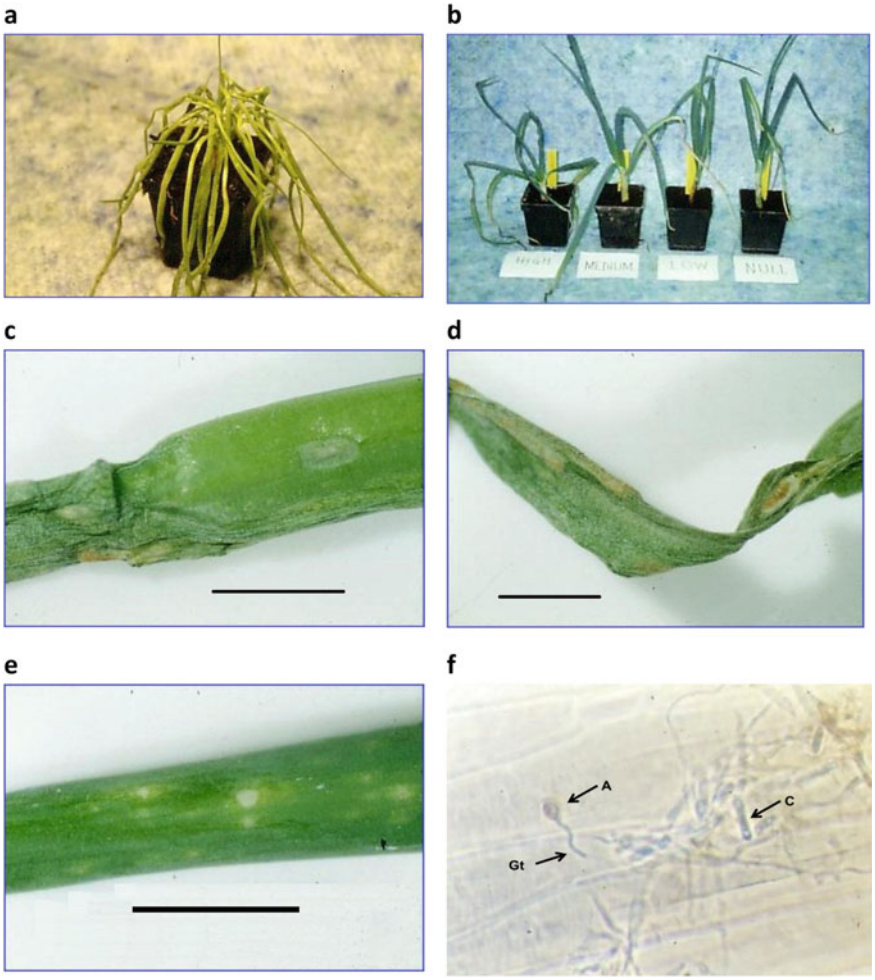

Fig. 6.2 Screening for anthracnose (*Colletotrichum gloeosporioides*) resistance under controlled conditions with experimental inoculation (Galván et al. 1997); (**a**) a severely affected shallot (*A. cepa*) pot plant; (**b**) evaluation scale from severely diseased (left) with typical curly leaves or '*vira cabeza*' symptoms, up to a non-affected healthy plant (right); (**c**, **d**) anthracnose spots on susceptible *A. cepa* genotypes with orange sporulation areas; (**e**) resistance reaction on *Allium fistulosum*, with small flecks and no sporulation; (**f**) microscopic observation 24 h after inoculation; the arrows point to cylindrical conidia (C) producing a germination tube (Gt) ending up an appressorium (A) attached to leaf epidermis. Pathogenicity in *Colletotrichum* species is characterized as hemi-biotrophic, with a brief biotrophic initial phase. Black bars depict 1 cm

1971). The first stages of emerging seedling and bulbing plants are the most susceptible phenological phases of the crop, suggesting an age-related resistance (defense) host system (Galeano et al. 2014). A temperature range of 25 to 28 °C is optimum for disease development (Sumner 1995) and used in experimental screening like the seedling test, with *Fusarium* inoculation during the germination phase (https://haveylab.horticulture.wisc.edu/wp-content/uploads/sites/66/2016/05/Fusarium-screening-in-onion.pdf).

FBR may be the only onion disease where systematic research on resistance has been conducted. Two recent reviews refer to FBR; Le et al. (2021) covering diverse aspects of the disease, whereas Cramer et al. (2021) point at the advances in breeding for resistance.

Fusarium oxysporum is a natural inhabitant in soils with non-pathogenic and pathogenic forms, and a generalist pathogen able to infect diverse plant families. Pathogenicity on a specific host or just the ability to multiply on a range of plant hosts is acquired in a quantitative manner (Dhingra and Cohelo Netto 2001; Leoni et al. 2013), with quantitative differences among isolates in virulence. Genetic diversity within FOC was reported with isolates distributed in two main clades by Galván et al. (2008) and three clades by Taylor et al. (2016), among those clades reported for this species complex by O'Donnell et al. (1998). Virulence differences among isolates are not linked to evolutionary genetic differences (Galván et al. 2008; Taylor et al. 2016). Pathogenicity related genes present in FOC were studied by Taylor et al. (2016) and ten effectors were identified. Seven secreted in xylem (SIX) genes out of 14 tested were identified, and their sequences were found specific for FOC, despite a high homology with corresponding six genes for other *forma specialis*. In addition, two genes with signal peptides and RxLR motifs (CRX1/CRX2) and a gene with uncharacterized domain (C5) are present in FOC isolates (Taylor et al. 2016).

Selection methods and the way to perform phenotypic evaluations have been under concern. Improvements in screening methods aim to increase heritability in recurrent selection for resistance. Gutierrez and Cramer (2005) developed a method of slicing the basal plate of the bulbs to quantify FBR infections, and identified 'NMSU00-25' as resistant cultivar with lowest disease severity and incidence in two years evaluation. A rapid, simple and repeatable seedling assay for high throughput screening of onion seedlings was employed by Taylor et al. (2013). Two onion cultivars 'Ailsa Craig Prizewinner' and 'White Lisbon' showed the highest level of resistance. In disease resistance programs, isolate and inoculum concentration are vital factors for identification of resistant germplasm. The use of low virulence isolates or low inoculum density for resistance breeding leads to false resistant reactions which prove to be susceptible under field conditions. Caligiori Gei et al. (2014) reported that an inoculum density of 10,000 microconidia/g of substrate was most effective for all tested *Fusarium* isolates.

Strong correlation between seedling and mature plant assays suggests that a high throughput phenotyping for resistance screening against FBR is a viable option (Taylor et al. 2019). Caligiori Gei et al. (2020) employed an integrated approach of laboratory screening complemented with field screening for resistance breeding

against FBR. This new technique not only minimizes the time to develop resistant material but also helps in selecting suitable material in a fast and cost-effective manner. At the same time, Mandal and Cramer (2020) implemented a successful inoculation method by placing on the basal plate of each bulb a plug of a growing media containing a suspension of conidia.

Resistance to onion *Fusarium* isolates was tested in several *Allium* species by Galvan et al. (2008). High levels of resistance were found in *A. fistulosum* and *A. schoenoprasum* against *F. oxysporum* and *F. proliferatum* isolates from onion. *Allium pskemense*, *A. roylei* and *A. galanthum* exhibited an intermediate level of resistance, as well as the Italian onion variety 'Rossa Savonese'. A counterintuitive result is how *A. fistulosum* accessions behaved resistant against onion isolates (Galván et al. 2008), but FBR is an important disease for Welsh onion (*A. fistulosum*) cultivation in Japan (Dissanayake et al. 2009), which suggest that pathogen divergent host specialization occurs. Preliminarily, a quantitative trait locus (QTL) from *A. fistulosum* for resistance against FOC was identified in the long arm of chromosome 8 (Galván 2009).

Selection for resistance in diverse onion breeding programs led to the obtention of resistant selections. Inheritance studies using onion segregant populations suggest a single major gene, two genes or polygenic control of resistance (Cramer 2000). However, the resistance response has not been stable in other regions, most likely due to conduciveness of the environment for the disease and differences in virulence factors in the *Fusarium* populations. A worldwide panel of onion accessions was tested for resistance by Taylor et al. (2019). Using SNP markers developed by Duangjit et al. (2013), three markers linked to FBR resistance on Chromosome 1, Chromosome 6 (linkage group 6B), Chromosome 8 and other two unmapped SNP markers were identified. In another approach, a set of monosomic addition lines was a tool to identify a steroidal saponin from shallot (*A. cepa*) on Chromosome 2 that plays a role in defense against FBR (Abdelrahman et al. 2017). Using RNA-seq analysis, 50 genes related to saponin synthesis were upregulated, and among these, some key genes are located on chromosome 2. The knowledge on genetics (QTLs), gene expression (transcriptome) and gene products (proteome) involved in FBR resistance can be integrated in ongoing onion breeding programs around the world, opening a new phase in FBR resistance breeding.

6.3.5 Downy Mildew

Downy mildew is an onion leaf devastating disease caused by *Peronospora destructor* Berk. (Casp.) prevalent in temperate to cold climates (Schwartz and Mohan 2008). The pathogen belongs to the Oomycete, a group of heterotrophic eukaryotic organisms with filamentous growth and spores as a means of dissemination and reproduction (Lamour and Kamaoun 2009). Oomycete cell walls are composed of polysaccharides like cellulose and glucans, but not chitin. The mycelia are coenocytic and diploid, except when gametangia are formed (Hardham 2007). The oomycete is a

group of important crop pathogens within the supergroup *Chromalveolata,* which also comprises autotrophic chromista algae (Kamoun et al. 2015). Although the monophyletic status of the supergroup has been under discussion (Lamour and Kamoun 2009; Kamoun et al. 2015), based on molecular sequencing and evidence from evolutionary anatomical comparisons, Beakes et al. (2012) postulates that *Oomycete* evolved from holocarpic marine parasites. The filamentous growth pattern as well as the gametangia and sexual reproduction were the main changes to adapt to land lifestyle, but parasitic ability was already present (Beakes et al. 2012).

Within the Oomycete, onion downy mildew belongs to the *Peronosporaceae* family, which comprises the important plant pathogenic genera *Peronospora* and *Phytophthora*, among others (Beakes et al. 2012). The family is characterized by obligate pathogenicity causing leaf blight on the whole plant, including young and turgent leaves, progressing dramatically in brief periods of time (Agrios 2005). Chemical management for onion downy mildew may be effective (Araujo et al. 2020), though may carry risks and negative consequences on laborers and consumers' health, the environment and farmers' profitability. Forecast systems like 'Downcast' (Jesperson and Sutton 1987; de Visser 1998) based on the environmental conditions required for pathogen sporulation and infection were developed to reduce the number of chemical interventions during the season (Lorbeer et al. 2002; Ullah et al. 2020). However, no significant spray reductions are obtained if environmental conditions for sporulation and infection frequently occur (Wright et al. 2002; Maeso 2005; Scholten et al. 2007).

Host resistance is an alternative disease management way, economically and environmentally sound. Early studies reported resistance to *P. destructor* in red onion lines (Jones et al., 1939; Warid and Tims, 1952). Recent studies have also identified and described highly resistant onion varieties (Galván et al. 2016a; Alves et al., 2018; Ullah et al., 2020). However, complete resistance was not available within the genetic base of the crop (Kofoet and Zingernagel, 1989) until the introgression of a simple dominant gene from *Allium roylei*. Among related onion species, an *A. roylei* accession was characterized as downy mildew resistant with a simple genetic control (Kofoet et al. 1990). The *Pd* gene was mapped to a telomeric position of Chromosome 3 (van Heusden et al. 2000), as proved also using cytogenetic tools (Khrustaleva et al. 2019). The gene was introgressed, overcoming dragged negative effects of lethal gene(s) linked to *Pd* from *A. roylei,* that caused distorted segregations. A recombinant with a crossover between the *Pd* gene and the deleterious effects was found, and homozygous *Pd* lines were obtained (Scholten et al. 2007). Currently, downy mildew resistant cultivars are available (Scholten et al. 2007), though the use of this resistance in onion cultivars adapted to diverse growing regions is a long-term process.

Specific molecular markers tagging *Pd* were initially developed as a sequence characterized amplified region (SCAR) marker (Kik et al. 1997; van Heusden et al. 2000) and AFLP markers (Scholten et al. 2007). More recently, Kim et al. (2016) developed a simple PCR marker to assist selection processes, based on cDNA sequences for the telomeric region of long arm of Chromosome 3 from the high-density linkage map developed by Duangjit et al. (2013) and transcriptome sequences

(RNA-Seq analysis). The nature of the codified molecule and mechanisms of resistance triggered by *Pd*-gene have not been studied. Programmed cell death is probably involved, as usually no symptoms at all are observed in comparison with susceptible or partial resistant varieties, except for atypical lesions observed in experimental inoculations (Galván 2011; Vu et al. 2012). The analysis of transcriptome and histopathological relationships may contribute to determining the mechanisms involved and the association with durability of resistance, an issue absolutely under concern for breeders and growers.

Partial levels of resistance in onion varieties might be due to basal resistance mechanisms triggered by the recognition of pathogen associated molecular patterns. These quantitative differences are expressed as epidemiological parameters leading to a slowdown of disease development (Niks et al. 2011), and those differences are exploited in onion breeding to reduce the negative effects on crop yields and contribute to an integrated crop management (Niks et al. 2011). The genetic basis of partial resistance is usually polygenic and has shown to be durable (Niks et al. 2011). Alves et al. (2018) evaluated a set of 46 onion cultivars in agroecologically managed experiments (organic agriculture) in Santa Catarina (Brazil) and selected two open pollinated experimental cultivars for their lower AUDPC for downy mildew, in combination with yield and storage ability.

A screening for sources of resistance in Uruguay led to the identification of 'Regia' as a highly resistant source to downy mildew (Fig. 6.3). Crosses 'Regia' x 'Pantanoso' for South Uruguay (Galván et al. 2016a), and 'Regia' x (Naqué x Casera) for North Uruguay (Galván et al. 2016b) aimed to combine the resistance of the former with favorable agronomic traits from the latter varieties. The analysis of initial steps of the infection process after experimental inoculation revealed a lower rate of successful infection and suggested that the lack of recognition as a potential host before the establishment of the infection could be a first mechanism of resistance in 'Regia' (Galván et al. 2016a). The resistance from 'Regia' has been proposed as determined by various genes with additive and eventually recessive effects (Arias et al. 2020). The segregation of resistance in six offspring from crosses between susceptible cultivars and 'Regia' resulted in skewed segregations towards susceptibility, with transgressive segregation in five of six progenies. Recessive inheritance was reported also in earlier studies by Warid and Tims (1952) in the USA, with 2.8 to 24% of resistant plants in F2 families. The recessive inheritance could be associated with loss of susceptibility mechanisms (Pavan et al. 2010), e.g., the lack of a target host receptor for a successful pathogenicity. Downy mildew severity was positively correlated with histological differences in the proportion of infected stomata, with 'Regia' presenting the lowest severity and the highest percentage of healthy stomata (Arias et al. 2020). The identification and selection of resistant F1S2 lines would allow the development of downy mildew resistant cultivars combining agronomic favorable traits like bulb yield, bulb quality traits and postharvest behavior (Arias et al. 2020).

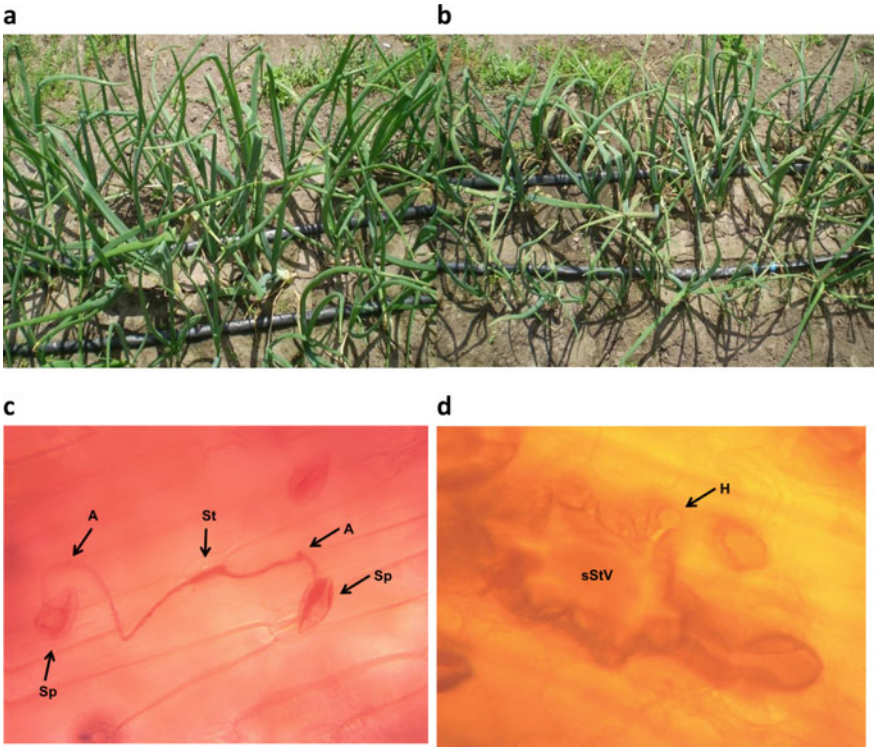

Fig. 6.3 Resistance against downy mildew (Arias et al. 2020). (**a**) Experimental plot of resistant onion 'Regia', (**b**) experimental plot of susceptible cv. 'Pantanoso del Sauce'. (**c**) Microscopical observation 24 h after experimental inoculation. Arrows point to lemon shaped sporangia (Sp), the appressoria (A) and the epidermal stomata (St) as penetration point. (**d**) Microscopic observation of a downy mildew infected leaf with a sub-stomatal vesicle (sStV) where the leaf parenchyma has collapsed, and a typical haustoria (H) with head and neck, as found in other Peronosporales pathogens

6.3.6 White Rot

White rot (*Scleotium cepivorum*) is highly specific to *Allium* species since their sclerotia germinate only in the presence of *Allium* specific root exudates (Entwistle 1990). It is thought to persist in soils for more than 20 years in the absence of host plants by means of sclerotia. White rot may become a devastating disease for both onion and garlic in farming systems with infected soils.

A fungal toxin (oxalic acid) secreted by the fungus degrades the plant cell walls and makes them amenable to this pathogen (Maude 2006). Licona-Juarez et al. (2019) developed a PCR based assay for *Sclerotium* detection in mycelia and infected garlic cloves. In vitro selection techniques using oxalic acid as the selective agent in the growth medium have led to initial success in resistance callus cultures of the variety Beheri Red (Sayed et al. 2016). Al-Safadi et al. (2000) started mutation breeding of

garlic to get mutants resistant to white rot using gamma radiation and successfully achieved resistant mutants. Utilization of induced mutagenesis could be another cheaper option to develop disease resistant mutants in Alliums (Khar et al. 2020; Singh et al. 2021b).

6.3.7 Rhizoctonia Seedling Stunt

In the cereal-onion cropping system, cereals like winter wheat (*Triticum aestivum* L.) or barley (*Hordeum vulgare* L.) are used as windbreak crops to protect onion seedlings against sand blasting during windy spring conditions. When herbicides are applied to kill the cover crop, the dying cereal roots provide substrate for the growth of saprophytic fungus *Rhozoctonia solani*. This fungus may infect onion seedling roots that result in significant stunting of onion plants in patches. Sharma et al. (2015) evaluated 35 onion genotypes for resistance to stunting and identified four genotypes that can be the base to develop cultivars partially resistant to *R. solani*.

6.3.8 **Pantoea** *sp. (Onion Center Rot)*

Onion bacterial diseases cause small flecks on onion leaves and seed stalks, leaf strep and even fully wet leaf rotting. As a postharvest disease, center bulb rot up to complete bulb rotting, among other diverse symptoms caused by bacteria constitute an economically relevant source of losses in onion storages (Schwartz and Mohan 2008). Besides environmental prevalent conditions like rainfall during the bulbing phase and the weeks before harvest, the occurrence of downy mildew and thrips damage will increase bacterial rotting during storage. Onion center rot was found to be caused by the genera *Pectobacterium* spp., *Pseudomonas, Dickeya (Erwinia)* and *Enterobacter* (Maude 1990). However, some strains from *Pseudomonas* spp. have been reclassified as *Burkholderia* (Yabuuchi et al. 1992), whereas *Dickeya* spp. strains were renamed as *Pantoea* (Gavini et al. 1989).

Among pathogenic bacteria, *Pantoea* species were identified as a relevant cause of onion center rot in Georgia and other regions in the USA. Center rot caused by *Pantoea ananatis* may appear as a leaf infection that later progresses towards the bulb. At harvest, onion plants may have a wetish bulb neck with a viscous content after pressuring the neck (Snowdon 2010).

Pantoea species identified as involved in center rot of onion are *P. agglomerans*, *P. ananatis*, *P. allii*, *P. dispersa* and *P. stewarti* subsp. *indologens* (Stice et al. 2021). Virulence in *Pantoea ananatis* has been extensively studied. The species lacks the typical bacterial virulence T2 and T3 secretion systems but holds the T6SS (De Maayer et al. 2017). Pathogenicity of *P. ananatis* on onion is supported by the HiVir cluster in combination with the *alt* (allicine tolerance) gene, leading to necrotrophic infection (Stice et al. 2020). The HiVir cluster is not extensively present in other

Pantoea species pathogenic to onion, and therefore Stice et al. (2021) suggested that different virulence mechanisms beyond HiVir are depicted in this genera.

Ongoing host resistance studies revealed quantitative differences among onion cultivars in leaf lesion length (de Armas et al. 2019), and open prospects for selection for resistance against bacterial diseases.

6.3.9 Thrips

Thrips are the major insect pests of onions throughout the world. Application of insecticides for thrips management is widely employed. As in fungicides, regular and indiscriminate use of pesticide has led to environmental pollution and risk of insecticides into our food basket. Thrips have direct damage, but also are vectors for IYSV, *Pantoea* species and give opportunity for *Alternaria* infections. Development of resistant plant material is a viable option. In onion, thrips resistance can be achieved through selection on family basis instead of single plant selection since the heritability is extremely low (Hamilton et al. 1999). An increase in thrips tolerance by selection was reported by Singh and Cramer (2019), though no progress in associated resistance to IYSV was achieved.

Genetic and agronomic factors affect the susceptibility of onion cultivars (Martin and Workman 2006). Various morphological traits viz., leaf arrangement (Jones et al. 1934), round or flat sized leaves, open plant architecture (Coudriet et al. 1979), wider contact angle between leaves (Patil et al. 1988), pH of the plant (Monzen 1926), waxiness (Molenaar 1984; Khosa et al. 2020) and bulb color (Verma 1996) have been associated with thrips resistance. Jones et al. (1934) identified 'White Persian' as the resistant variety with wide angled circular leaves that provide less protection to thrips. Alimousavi et al. (2007) evaluated Iranian onion accessions and identified 'Meshkan', 'Sefid-e-Kurdistan', 'Sefid-e-Qom' and 'Eghlid' as resistant accessions. Diaz-Montano et al. (2010) suggested that resistant cultivars had yellow-green foliage whereas susceptible one had blue-green foliage.

The role of morphological traits towards thrips resistance has been evaluated by various researchers. In cultivar Alfa São Francisco RT, a wider central angle (16.4°), a thinner cuticle, a larger amount of epicuticular waxes, and stomata on the surface of leaves accounted for resistance. In contrast, in cultivars BR 29 and Sirius, the presence of resistance-conferring substances or high amounts of some component in the chemical composition inferred resistance (Silva et al. 2015). Ferreira et al. (2017) observed negative correlations between bulb yield and central angle of the plant, indicating that plants with lower angle of central leaves yield higher under thrips pressure. Njau et al. (2017) screened onion accessions under Tanzanian conditions. A significant negative correlation between leaf angle, leaf toughness and thrips damage were observed. Total epicuticular waxes were weak and non-significantly related with thrips damage. Significant negative correlation between total phenol content and non-significant and inverse correlation between total foliar amino acids or total sugars and thrips damage was reported.

6.3.9.1 Onion Maggot

Onion maggot [*Delia antiqua* (Meigen)] is a major pest in temperate climates. Onion maggot has a limited host range within Alliums crops only. Nevertheless, this pest can destroy more than 50% seedlings in absence of proper control measures (Eckenrode and Nyrop 1995). In some fields where onions are grown continuously for several years, this pest becomes problematic.

Preliminary reports have shown little variation in resistance to onion maggot among onion accessions (Munger and Page 1974; Ellis et al. 1979), but *A. fistulosum* was reported to sustain low maggot damage (Ellis et al. 1979). Screening of onion and related species (McFerson et al. 1996) against this pest showed that no resistance existed in onion and seedlings, whereas mature plants of *A. ampeloprasum* sustained low injury. Hence, *A. ampeloprasum* holds mechanisms of resistance that need to be examined. This knowledge can be a tool for resistance against fly maggots in onion breeding.

6.4 Prospect for Genomic Breeding Against *Allium* Biotic Stresses

This chapter summarized *Allium* progress in breeding for resistance against diseases and pests, with emphasis in onion, and reflects a rather limited picture for the breeders in relation to marker assisted selection. The picture is even more limited for diseases relevant in tropical regions. Breeders rely on phenotypic differences among onion germplasm as resistance sources, phenotypic evaluation of breeding lines and recurrent selection towards enhanced resistance. Although molecular markers and QTLs discovery were tools available from the nineties, their use was scant in crop breeding, as reflected in the query from Lindhout (1995): to what extent, mapping disease resistance genes (in tomato, at that time) was 'a toy for the geneticist or a joy for the breeders?'.

Only recently, the availability of automation and the availability of large numbers of SNP markers, with 'a plus or minus' result and automatic marker reading for hundreds of breeding lines, or just to confirm the hybrid nature of a seed lot, have become regular processes in breeding companies in the last decades.

More emphasis to include genomic studies for identification of genes involved in resistance, their mode of action and how to use those genes for development of resistant varieties should be the focus in future. A recent compilation of genomic resources in *Allium* by Shigyo et al. (2018) gives a comprehensive coverage on genomic tools and their utilization in Alliums. Classical genetics and cytogenetic tools are enriched in the last decade with genomic markers from next generation sequencing (NGS) available tools (Duangjit et al. 2013; Scholten et al. 2016), analysis of transcriptome profiling and metabolomic profiles (Abdelrahman et al. 2017). Publication of chromosome level assembly of garlic genome (Sun et al. 2020) and first genome

assembly of onion (Finkers et al. 2021) supplemented with the transcriptomics and metabolomic atlas in both crops will serve as a guiding force to facilitate genomic breakthroughs in breeding for disease resistance in Alliums.

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