Chapter 16
Plant Pathogen Interactions: Crop Improvement Under Adverse Conditions

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1 Introduction

In the face of an expanding world population, we need more quantity of food, especially when the cultivated land resources are shrinking. It is estimated that to feed the world population by 2050 our food requirement will be 70% more, which means an increase in crop production at the rate of 44 million metric tons per year is required (Tester and Langridge 2010). The increasing food and energy demand calls for intensive crop production but it is also visualized that in intensive cropping systems the growth of plant pathogens is rapid and new virulence mechanisms appear in pathogen population, and minor pathogens become a major production constrain. Therefore, the incorporation of resistance is a major focus of many breeding programs. However, certain limitations like lack of resistance against many diseases in the primary gene pool, difficulty in transfer of resistance in desired host due to crossability barriers, rapid evolution of virulent pathogens, existence of high pathogenic variability amongst the pathogens, etc. override the advantages of traditional breeding. It is the consensus of plant breeders, geneticists, and other biologists that biotechnological approaches can play an important role in alleviating some of these problems.

Research on host–pathogen interaction in crop plants mainly has been focused on production of toxic substances. Recent advances in molecular biology, however, have offered efficient and precise tools for better understanding of plant–pathogen interactions. In the first half of this chapter, recent developments towards understanding of molecular aspect of plant immunity, mostly against the bacteria and fungi, have been described, although many of these pathways play an important role against other

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N. Tuteja and S. Singh Gill (eds.), *Plant Acclimation to Environmental Stress*,
DOI 10.1007/978-1-4614-5001-6_16,

pathogens also. This part is further divided into sections and subsections to provide clearly outlined apprehension of the topic. In the second half of the chapter various methods to achieve resistance against pathogens in crop plants have been discussed.

2 Plant–Pathogen Interactions

Plants are rich source of sugar, minerals, and water that attracts various organisms with heterotrophic lifestyle. The pathogenic organisms use host plant to serve basic aim of life, i.e., grow and reproduce. Plant diseases are comparatively less than the number and variety of potential pathogens in the surrounding environment of plants; this is due to the fact that they have developed a highly complex and multilayered immune system while coevolving with pathogens. The outcome of a plant–pathogen interaction can be either an incompatible (disease resistance/tolerance) or a compatible (pathogen infection and disease) interaction, which is governed by the genetic makeup of both the plant and pathogen. The ability of a pathogen to infect plants depends upon the repertoire of its effectors to suppress or evade plant immune responses and modulate host cellular metabolism for its own benefit. The plant resistance against a potential pathogen depends upon the capacity of the plant to recognize this pathogen as nonself and induce immune response to restrict its growth.

In an ecosystem, pathogens pass their life on host plants in different modes. Many pathogens have evolved to infect only a single plant species (narrow host range) while a few of these pathogens can implicate more plant species for their survival (broad host range). Based on their lifestyle on host, pathogens are classified as biotrophs, hemibiotrophs, and necrotrophs. The biotrophs are entirely dependent upon living host and keep their host alive throughout their life cycle, the hemibiotrophs keep host alive for some period and then kill them, and the necrotrophs feed on host plants by killing them. The evolution of such lifestyles in filamentous pathogens was correlated with gain/loss of genes by comparative analysis (Dodds 2010).

Molecular plant pathologists have broadly classified plant disease resistance operating in natural habitats into two categories: the host resistance and the nonhost resistance (Heath 2000). The nonhost resistance dominates in nature as every plant withstands the injurious effect of most of the potential pathogens while host resistance against a particular pathogen species is shown by the some genotypes of an otherwise host species. To define, the nonhost resistance is the ability of an entire plant species to resist infection by all isolates of a pathogen species. Many reports suggest that the defense signaling against host and nonhost pathogens is similar and many components of these resistance mechanisms are common but the final outcome of their interaction with pathogen or pathogen effectors differs (Thordal-Christensen 2003). It is opined that the components of host resistance were isolated earlier through forward genetics in many known plant–pathogen pairs; hence data towards host resistance seem to be unfair. Therefore, with the advancements in biotechnology biologists are prompted to use the components of nonhost resistance due to its effectiveness and durability.

3 Multilayered Plant Immune System

A simple way to define plant immune system is to define the obstacles that a pathogen must overcome to invade host tissue, proliferate, and cause disease (Thordal-Christensen 2003). Bacterial pathogens get access to host tissue through stomata or wounds. The filamentous pathogens make their entry in host through stomata and may even directly penetrate the cuticle layer. Plants try to restrict pathogens by preformed and induced defenses. The induced defense responses are controlled by PTI (pathogen-associated molecular patterns-triggered immunity) and ETI (effector-triggered immunity). Only pathogens that can evade/suppress/manipulate these defensive layers can cause disease.

3.1 Preformed Structural and Chemical Barriers

The cuticle covers the epidermal cell wall and functions as the first barrier for pathogens. It is composed of polysaccharides, cutin, and waxes, whose composition changes within each species and according to environmental conditions (Shepherd and Wagner 2007). After landing of pathogen on plant surface, the cuticle plays an important part in the plant–pathogen communications. Generally cuticle is considered as a barrier for the entry of pathogens but now it is clear that many pathogens like *Uromyces appendiculatus*, *Fusarium solani* f. sp. *pisi*, *Ustilago maydis*, *Magnoporthe oryzae*, *Colletotrichum gloeosporioides*, *Puccinia graminis* f. sp. *tritici*, etc. require signals from the host plant surface to differentiate and penetrate the host (Mendoza et al. 2009; Reina-Pinto and Yephremov 2009; Liu et al. 2011). Thus, the cuticle's role is important towards resistance against nonadapted pathogens. The phytopathogenic fungi secrete cutinase to liberate cutin that serves as a signal for differentiation in *M. grisea* and *Erysiphe graminis* but not in *Botrytis cinerea* (Bessire et al. 2007). In case of necrotrophic fungi like *B. cinerea*, *Alternaria brassicicola*, and *Fusarium graminearum* secreted lipases are important for pathogenicity. The *Blumeria graminis* release lipolytic activity containing protein, Lip1, to release cues from the wheat plant surface for promoting pathogen development and infection (Feng et al. 2009). The *Arabidopsis* CUTE plants with cell wall targeted fungal cutinase, lipase, and mutants with altered cuticle showed higher resistance to *B. cinerea* but not to other necrotrophs like *Plectosphaerella cucumerina*, *A. brassicicola,* and *Sclerotinia sclerotiorum* (Bessire et al. 2007; Chassot et al. 2008). The increased resistance against *B. cinerea* in these plants was correlated with the induction of few genes and higher fungitoxic activity. Clearly a single mechanism cannot be charted out for the role of cuticle against diverse pathogens but the studies on

Table 16.1 Mutants and transgenic plants with altered cuticle composition affecting plant–pathogen interaction

Mutants/ Overexpressed gene	Plant	Features	Reference
sma4 mutant and *lacs2*	*Arabidopsis*	Enhanced susceptibility to *Pst* DC3000 strain with *avr* genes but resistance to *B. cinerea*	Tang et al. (2007)
att1 mutant	*Arabidopsis*	Susceptible to *Pst*	Xiao et al. (2004)
Yeast D-9 desaturase overexpression	*Solanum lycopersicum*	Higher resistance to *Erysiphe polygoni*	Wang et al. (1998); Wang et al. (2000)
bodyguard (*bdg*) mutant and *Fusarium solani* f. sp. *pisi* cutinase A and *B. cinerea LIP1* overexpression	*Arabidopsis*	Increased resistance to *B. cinerea*	Chassot et al. (2007)
permeable cuticle (*pec*) mutant	*Arabidopsis*	Increased resistance to *B. cinerea*	L'Haridon et al. (2011)
botrytis-resistant 1 (*bre1*)/*lacs2* mutant	*Arabidopsis*	Increased resistance to *B. cinerea*	Bessire et al. (2007)
gpat4/*gpat8* mutant	*Arabidopsis*	Sensitive to *A. brassicicola*	Li et al. (2007)
delayed fruit deterioration (*DFD*) mutant	*S. lycopersicum*	Resistance against *B. cinerea*	Saladie et al. (2007)
acyl carrier protein4 (*acp4*), *long-chain acyl-CoA synthetase2* (*lacs2*), and *lacs9*	*Arabidopsis*	Compromised systemic acquired resistance	Xia et al. (2009)
glabra1(*gl1*), *gl3, and ttg1*	*Arabidopsis*	Compromised systemic acquired resistance	Xia et al. (2010)
sitiens	*S. lycopersicum*	Resistance against *B. cinerea* due to ABA deficiency leading to cuticle permeability	Curvers et al. (2010)

various cuticle-related mutants have shown that its composition affects the final outcome of plant–pathogen interaction (Table 16.1). The adhesion level of cuticle with cell wall also modulates the defense responses of plants. The glandular trichomes also release antimicrobial substances that can inhibit pathogen growth.

After alteration of cuticle, the pathogens adopt a course of action to break the host plant cell wall by mechanical force and degrading enzymes such as polygalacturonases, xylanases, cellulases, and proteinases. Changes in the host cell wall components like less *O*-acetylation of cell wall polysaccharides in *Arabidopsis thaliana's Reduced Wall Acetylation* (*RWA2*) mutant plants displayed increased tolerance towards *Botrytis cinerea*, but mutation had no effect on infection by powdery mildew (*Golovinomyces cichoracearum*) suggesting differential mechanisms of fungal infection and plant resistance against these pathogens (Manabe et al. 2011). In another case, the *atmyb46* mutants have high level of cell wall-associated peroxidases that are involved in phenolic cross-linking at cell wall and ROS scavenging leading to enhanced resistance against *B. cinerea* (Ramirez et al. 2011). Many other cell wall-associated genes had been reported to influence resistance and susceptibility to pathogens (Hückelhoven 2007; Cantu et al. 2008). The molecules released by cell wall breakdown of the host (i.e., endogenous elicitors) and the pathogen can induce plant defense response, which has been discussed under induced defenses.

The apoplastic space is the site where many pathogen and plant-derived molecules counteract each other. Molecules having antimicrobial activity are secreted in the apoplastic space constitutively by plant or they can be induced after pathogen perception. Many enzyme inhibitors block the activity of pathogen-released enzymes and the plant-derived lipid transfer proteins (LTPs) have inhibitory effects on fungal growth (Molina and Garcia-Olmedo 1997; Patkar and Chattoo 2006). The *sad* mutants of *Avena strigosa* can be infected by the nonhost fungal pathogens *Gaeumannomyces graminis* var. *tritici* and *Fusarium culmorum* due to the lack of avenacins, a type of saponin with antifungal activity (Papadopoulou et al. 1999).

3.2 Pathogen-Associated Molecular Pattern-Triggered Immunity

When pathogens are able to breach the constitutive defensive layers then they are recognized as nonself by plant cell membrane receptors, which recognize conserved microbial components (flagellin and chitin in bacteria and fungi respectively) or motifs present in them and molecules released by pathogen. These molecules, termed as PAMPs/MAMPs (microbe-associated molecular patterns), are mostly conserved within a class of microbes and are essential for microbial survival and fitness (Bent and Mackey 2007). They are non-race-specific inducers of plant defense so are often mentioned as exogenous elicitors in contrast to the endogenous elicitors, called damage-associated molecular patterns (DAMPs), released from the host plant by virtue of pathogen attack (Lotze et al. 2007). Some of the known pathogen-associated molecular pattern (PAMPs)/DAMPs are listed in Table 16.2. The importance of PAMP-triggered immunity (PTI) in plant defense is manifested from the fact that the adapted pathogens have evolved effectors to suppress it or they have evolved mechanisms to mask the recognition of PAMPs/DAMPs but in nonhost resistance growth of a nonadapted pathogen is effectively restricted by PTI. The PTI in plants is very similar to that of animals.

The typical responses initiated in plant cell after PAMP/DAMP perception are generation of ion fluxes across plasma membrane, enhanced Ca^{2+} concentration in cytosol, protein phosphorylation, GTPases activation, rapid increase in reactive oxygen species (ROS), generation of nitric oxide (NO) and ethylene (ET), and many more associated changes (Garcia-Brugger et al. 2006; Boller and Felix 2009). These

Table 16.2 PAMPs/MAMPs perceived by plant cells

PAMPs	Active motif	Pathogen	Reference
Flagellin	flg22	Bacteria	Gomez-Gomez and Boller (2000)
Lipopolysaccharides (LPSs) and peptidoglycan	-	Bacteria	Erbs and Newman (2012)
Harpin	-	Gram-negative bacteria	Lee et al. (2001), Kim et al. (2004)
Cold shock protein	RPN-1 motif	Bacteria	Felix and Boller (2003)
N-glycosylated peptide	-	Yeast	Boller (1995)
Sulphated fucans	Fucan oligosaccharide	Brown Algae	Klarzynski et al. (2003)
Transglutaminase	Pep13 motif	*Phytophthora* spp.	Brunner et al. (2002)
Elicitins (sterol binding proteins)	-	*Phytophthora* spp., *Pythium* spp.	Osman et al. (2001)
Cellulose binding lectin	-	*Phytophthora* spp.	Gaulin et al. (2006)
Arachidonic acid	-	Oomycetes	Boller (1995)
β (Beta)-glucans	Oligomeric and multimeric-β (Beta)-glucosides	Filamentous pathogens	Yamaguchi et al. (2000), Fliegmann et al. (2004)
Ethylene inducing xylanase (EIX)	TKLGE pentapeptide	*Trichoderma* spp.	Ron and Avni (2004)
Chitin	-	Fungi	Wan et al. (2008)
Ergosterol	-	Fungi	Granado et al. (1995), Laquitaine et al. (2006), Lochman and Mikes (2006)
Cerebrosides A and C	-	*Magnaporthe* spp.	Koga et al. (1998)

changes lead to the activation of calcium-dependent protein kinases (CDPKs), calmodulins, and mitogen-activated protein kinases (MAPKs) through cascade of events that ultimately activates the transcription of numerous defense-related genes (Boudsocq et al. 2010). Scientists generally use alkalization of the growth medium, MAPK activation, hydrogen peroxide (H_2O_2) generation, callose deposition, and expression of early induced genes as markers for the flagellin, chitin, and other PAMP-activated responses (Asai et al. 2002; Denoux et al. 2008). In terms of the quality, responses elicited by various PAMPs from virus, bacteria, oomycetes, fungi, and other pathogens are same but quantitatively they may differ. The cumulative effect of these responses can often lead to hypersensitive response (HR) that is characterized by localized cell death at the site of attack to limit the pathogen spread (Heath 1998; Bolwell 1999).

Many PAMPs have been defined at molecular level based on the activation of PTI responses but their corresponding plant receptors working as sentinels at plasma membrane are not so well defined (Zipfel 2009). The first PAMP receptor cloned from plants was for flagellin (flg22). It is *FLAGELLIN-SENSING 2* (*FLS2*) that encodes for a leucine-rich repeat receptor-like kinase (LRR-RK) (Gomez-Gomez and Boller 2000). The orthologs of *FLS2* are present in other higher plants also suggesting that flagellin-mediated signaling is present in both monocot and dicot branches (Takai et al. 2008). Unlike flg22 responsiveness seen in many higher plants, the Brassicaceae family is only responsive to the N-terminus (elf18/26) of a highly conserved and abundant bacterial protein Elongation factor Tu (a GTPase). Its receptor in *Arabidopsis*, EFR, is also an LRR-RK (Kunze et al. 2004). Such is also the case with the recognition of Ax21 by some specific rice cultivars. It is thus apparent that each plant does not recognize every PAMP and not every pathogen displays all PAMPs (Zipfel and Robatzek 2010).

The nonhost interaction of *Arabidopsis thaliana* with *Blumeria graminis* f. sp. *hordei* (Bgh) has emerged as an excellent system to study the role of early induced genes as the infection is localized at the epidermal cells. Analysis of mutant plants for the various genes like *PENETRATION* (*PEN1*- a syntaxin, *PEN2*-a glycosyl hydolase, and *PEN3*-an ABC transporter) have suggested their role in plant immunity towards nonadapted pathogens (Ellis 2006).

3.3 Effector-Triggered Immunity

To suppress the PTI and to modulate host metabolism for their own benefit, pathogens secrete a variety of effector molecules inside the host cell (Hok et al. 2010). Bacteria mainly use type III secretion system while filamentous pathogens utilize host machinery to deliver effectors into the plant cell (Göhre and Robatzek 2008; Chibucos et al. 2009). These effectors can be proteases, toxins, transcriptional activators, etc. suggesting that diverse pathogens have evolved various strategies to subvert plant responses (de Jonge et al. 2011; Gheysen and Mitchum 2011; Hogenhout and Bos 2011; Stassen and Van den Ackerveken 2011). In a recent study, related to the interaction of pathogenic effectors with their target plant proteins, it was concluded that two diverse pathogens have evolved their effectors to target a selected set of plant proteins besides other individual targets. These common plant protein targets, in general, form large interaction networks in plants suggesting that pathogens target those proteins inside a host plant that are important for a signaling or interaction hub (Mukhtar et al. 2011). In response to effectors, plants have evolved an array of *R* (resistance) genes that recognizes these effectors directly or indirectly to rapidly induce a strong defense response. Many of the R proteins are associated with multi-protein immune complexes (Friedman and Baker 2007). Models have been proposed and experimentally verified to explain the evolution of *R* genes and the recognition of pathogen effectors by R proteins. Relevant among them are gene-for-gene, guard model, and decoy model (van der Hoom and Kamoun 2008).

Most of the known R proteins are multidomain NB-LRR (Nucleotide binding site and leucine-rich repeat) type but other types of R proteins are also known like protein kinase (Rpg1), LRR-receptor-like kinase (Xa21), LRR-TM (Cf’s), etc. and

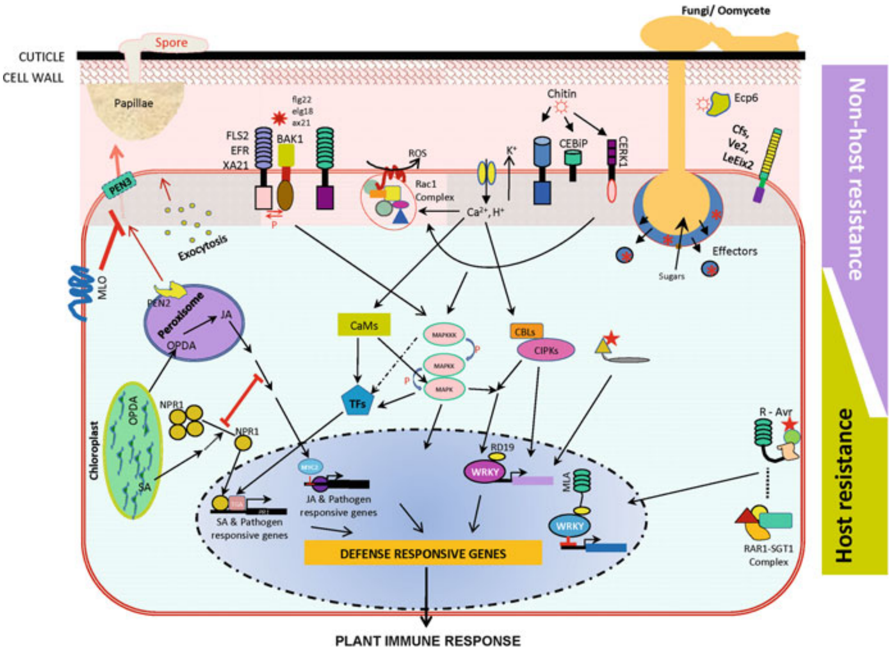

Fig. 16.1 The multilayered plant immune system

in some genes the promoter polymorphisms also genetically suggest it as *R* gene (Liu et al. 2007; Bogdanove et al. 2010; Chen et al. 2010). The NB-LRR proteins can be further subdivided based on N-terminal homology to TIR (Toll and Interleukin-1 Receptor; RPS4, SSI4, L6, etc.), CC (coiled-coil; RPM1, RCY1, Mi-1, etc.) or LZ (leucine-zipper; RPS5), and non-motif groups. The C-terminal LRR region binds to the decoy or the effector (direct Avr-R interaction) while the N-terminal is involved in transducing signals to the downstream components to initiate defense signaling. It is suggested that the intra-domain interaction or interaction with associated proteins keeps NB-LRR proteins under resting condition and with the perception of effectors or their activity the signaling is initiated (Caplan et al. 2008; Collier and Moffett 2009; Lukasik and Takken 2009). The signaling downstream to R-proteins is very complex, as some group of R-genes requires NDR1 (non-race-specific disease resistance 1) or EDS1 (enhanced disease susceptibility 1) or some are independent of these two parallel pathways. Further complexity appears in the requirement of RAR1 and SGT1 proteins (Thatcher et al. 2005; Shirasu 2008).

In model plant *Arabidopsis* and other crop plants various components of preformed and induced (PAMP and effector recognition-based) immunity have be isolated and from these analyses emerges a complex picture of plant immune responses (Fig. 16.1) (Thatcher et al. 2005; Chisholm et al. 2006; Knepper and Day, 2010; Nishimura and Dangl 2010; Zhang and Zhou 2010; Chen and Ronald 2011).

The signaling initiated by ETI and PTI shares many common points (Thomma et al. 2011) but the final outcome of defense response, i.e., plant immunity is brought by the cumulative effects of all these components some of which may also be involved in primary and secondary metabolism. A common feature associated with resistance against biotrophic pathogen is the development of hypersensitive response (HR) and systemic acquired resistance (SAR) along with some associated processes (Durrant and Dong 2004; Vlot et al. 2008). Plant hormones like salicylic acid (SA), jasmonic acid (JA), ethylene (ET), auxin, etc. also play an important role along with a myriad of small molecules and proteins in this complex plant response. Role of these components in plant immunity has been extensively reviewed (Lorenzo and Solano 2005; Roberts-Seilaniantz et al. 2007; Spoel and Dong 2008; Bari and Jones 2009; Pieterse et al. 2009; Ton et al. 2009).

4 Strategies to Develop Biotic Stress-Tolerant Crops

Since a number of crop species are cultivated under adverse stress conditions, Varshney et al. (2011) emphasized that the scientists should take up multiple approaches to develop biotic and abiotic stress-tolerant crops with adequate nutritional food value. This will be useful in meeting the food and biofuel security with the growing population and changing environment. As discussed earlier, the plant breeding has played a significant role in crop improvement; still we need to do more. In this context the impact of agrobiotechnology is both productive and benign. We can utilize the most cutting edge works associated with genetic mapping, molecular markers, and biotechnology to accelerate the crop development process. Methods through which crops with enhanced immunity can be generated are discussed in the following sections.

4.1 Molecular Plant Breeding

The plant breeding was the basis of the green revolution that led to increase in wheat and rice production in the twentieth century. The merger of biotechnology with conventional plant breeding techniques along with increase in our knowledge about basic plant biology has led to evolution of molecular plant breeding. Many reviews have discussed the molecular techniques and essential requirements for efficient use of molecular plant breeding in future crops (Jauhar 2006; Wenzel 2006; Moose and Mumm 2008; Hospital 2009; Torres 2010). A number of molecular markers based on simple sequence repeats (SSRs), single nucleotide polymorphism (SNPs), insert-deletions, and candidate gene markers are being developed in several crop species that will assist in genetic analysis and breeding programs (Feuillet et al. 2010). In recent years the next-generation sequencing (NGS) technologies have positively influenced the breeding programs (Varshney et al. 2005, 2010). A greater impact of NGS is noted on the comparative genomic studies which is expected to facilitate breeding programs.

The breeding for disease resistance is the greatest challenge because there is great variability both in plants and pathogens. Although our knowledge about disease resistance mechanisms has increased but still its application for developing resistant varieties is not an easy task because only the genes responsible for species level resistance (host resistance) can be transferred to elite varieties through breeding. Against many pathogens the plant resistance is a complex trait governed by QTLs having major or minor roles; with the advancement of molecular breeding technologies it will be possible to transfer many of the QTLs in elite varieties (Poland et al. 2009).

In breeding programs the field trials need to be well designed as various others environmental factors can also influence the final outcome of plant–pathogen interactions. It is visualized that next decade will be dominated by the high yielding and stress-tolerant varieties developed through traditional and molecular breeding due to the sociopolitical reasons associated with genetically modified (GM) crops.

4.2 Induction of Plant Immunity

Although breeding strategies are useful in enhancing species level resistance, they are time-consuming and have some drawbacks like linkage drag and nonavailability of effective resistant germplasms. The crop production can improve if we espouse environment friendly chemicals that enhance plant immunity, use nonpathogenic microbes as biocontrol agents that induce SAR, and raise transgenic plants with greater potential to recognize the pathogens and execute defense responses (Mourgues et al. 1998; Dita et al. 2006; Collinge et al. 2010; Gust et al. 2010; Shoresh et al. 2010; Wulff et al. 2011).

The initial transgenic crops were developed to overcome pathogen infestations and herbicide tolerance for industrial (ethanol, oil, textile, sugar) use of crops like corn, cotton, sugarcane, soybean, etc (Marshall 2010). When this trend shifted to crops for food consumption then various biosafety and ethical issues were raised, which were also raised for industrial crops but to a lower level. These issues were successfully overcome by the use of marker free transgenic, field trials, and well-designed experiments on animal models, so GM crops are making greater impact on the economy and accepted by people now (Carpenter 2010). Several genes are regularly being tried to get biotic stress-tolerant plants. Transgenic approaches to control herbivore pests are mainly expression of recombinant protease inhibitors and *Bacillus thuringiensis* endotoxins along with some alternate strategies (Bravo and Soberon 2008; Gatehouse 2008; Schlüter et al. 2010; Sanahuja et al. 2011). Some of the recent publications in this regard are mentioned in Table 16.3. The *cis*-engineering has provided promoters that precisely express the useful genes in an organ-specific and pathogen-inducible manner depending upon mode of pathogen infection (Venter 2006).

Table 16.3 Recent reports of enhanced tolerance against biotic stress by overexpression of gene(s)

Host transgenic plant	Gene(s) transformed	Tolerance against	Reference
Amorphophallus konjac	*Bacillus thuringiensis AiiA*	*Erwinia carotovora* subsp. *Carotovora* (Ecc) SCG1	Ban et al. (2009)
Arabidopsis thaliana	Pepper Mannose-binding lectin 1 (*CaMBL1*)	*Pseudomonas syringae* and *Alternaria brassicicola*	Hwang and Hwang (2011)
	B. vulgaris germin-like protein 1	*Verticillium longisporum* and *Rhizoctonia solani*	Knecht et al. (2010)
	Capsicum annuum ANTIMICROBIAL PROTEIN1	*P. syringae, H. parasitica*, *F.o.* f. sp. *matthiolae*, and *Alternaria brassicicola*	Lee et al. (2008)
	Solanum lycopersicumVe1	Race 1 of *Verticillium dahliae* and *V. albo-atrum*	Fradin et al. (2011)
	OsBSR1	*Colletotrichum higginsianum* and *Pst* DC3000	Dubouzet et al. (2011)
	Stellaria media SmAMP1 & 2	*Bipolaris sorokiniana*	Shukurov et al. (2012)
Arachis hypogaea	*Brassica juncea* defensin	*P. personata* and *Cercospora arachidicola*	Anuradha et al. (2008)
	OsChit-3	*Cercospora arachidicola*	Iqbal et al. (2012)
Brassica napus	*BnMPK4*	*Sclerotinia sclerotiorum* and *Botrytis cinerea*	Wang et al. (2009)
Brassica napus	*Triticum aestivum OXO*	*Sclerotinia sclerotiorum*	Dong et al. (2008)
Carica papaya	*Dahlia merckii DmAMP1*	*Phytophthora palmivora*	Zhu et al. (2007)
Colocynthis citrullus	*Wasabia japonica* defensin	*Alternaria solani* and *Fusarium oxysporum*	Ntui et al. (2010)
Daucus carota	*AtNPR1*	*Erysiphe heraclei*, *Xanthomonas hortorum*, *Botrytis cinerea*, *Alternaria radicina,* and *S. sclerotiorum*	Wally et al. (2009)
	HvChi-2 and *TaLTP*	*Alternaria radicicola* and *Botrytis cinerea*	Jayaraj and Punja (2007)
Gossypium hirsutum	*AtNPR1*	*V. dahliae* isolate TS2, *F.o.* f. sp. *vasinfectum*, *R. solani*, *Alternaria alternate*, and *Rotylenchulus reniformis*	Parkhi et al. (2010)
	NaPI and *StPin1A*	*Helicoverpa* spp.	Dunse et al. (2010)
	Xanthomonas oryzae pv. *oryzae Hpa1Xoo*	*Verticillium dahliae*	Miao et al. (2010)
	Momordica charantia McChit1	*Verticillium wilt*	Xiao et al. (2007)

(continued)

Table 16.3 (continued)

Host transgenic plant	Gene(s) transformed	Tolerance against	Reference
Hordeum vulgare	*D. melanogaster* metchnikowin	*F. graminearum*	Rahnamaeian et al. (2009)
L. esculentum	*CaMi*	*Meloidogyne incognita*	Chen et al. (2007)
	Bacillus thuringiensis Cry6A	*Meloidogyne incognita*	Li et al. (2007b)
Malus × *domestica* Borkh	*Nicotiana alata* proteinase inhibitor	*Epiphyas postvittiana*	Maheswaran et al. (2007)
Medicago sativa	*M. truncatula RCT1*	*Colletotrichum trifolii*	Yang et al. (2008)
Musa acuminata	*C. annuum* Hrap	*X. campestris* pv. *musacearum*	Tripathi et al. (2010)
N. benthamiana	*Momordica charantia McChit1*	*Phytophthora nicotianae*	Xiao et al. (2007)
	A. thaliana EFR	*Pss* B728a, *Pta* 11528, and *A. tumefaciens* A281	Lacombe et al. (2010)
N. tabacum	Protease inhibitor	*Spodoptera litura* and *Helicoverpa armigera*	Srinivasan et al. (2009)
	Brassica juncea defensin	*Phytophthora parasitica* pv. *Nicotianae* and *Fusarium moniliforme*	Anuradha et al. (2008)
	Gastrodia antifungal protein (GAFP-1)	*P. nicotianae*, *Meloidogyne incognita*, and *Rhizoctonia solani*	Cox et al. (2006)
	Hydronyche versuta Hvt1	*Heliothis armigera*	Shah et al. (2011)
	Stellaria media SmAMP1 & 2	*Thielaviopsis basicola*	Shukurov et al. (2012)
	Nicotiana megalosiphon NmDef02	*Phytophthora parasitica* var. *nicotianae* and *Peronospora hyoscyami* f. sp. *tabacina*	Portieles et al. (2010)
	Metarhizium anisopliae Chit1	*Rhizoctonia solani*	Kern et al. (2010)
	Zephyranthes grandiflora, Agglutinin	*Myzus nicotianae*	Ye et al. (2009)
	MsrA2 and Temporin A	*Fusarium solani*, *F. oxysporum*, *Alternaria alternata*, *Botrytis cinerea*, *Sclerotinia sclerotiorum, Pythium aphanidermatum*, and *Pectobacterium carotovorum*	Yevtushenko and Misra (2009)

Oryza sativa	*Trichoderma virens* endochitinase	*Rhizoctonia solani*	Shah et al. (2009)
	Xanthomonas hrf1	*Magnaporthe grisea*	Shao et al. (2008)
	OsBSR1	*Xanthomonas oryzae*, *Magnaporthe grisea*,	Dubouzet et al. (2011)
	Pleurotus cornucopiae tamavidin 1	*Magnaporthe oryzae*	Takakura et al. (2012)
	Allium sativum and *Galanthus nivalis* lectin genes	Brown planthopper , Green leafhopper, and Whitebacked planthopper	Bharathi et al. (2011)
	Raphanus sativus AFP2	*Magnaporthe oryzae* and *Rhizoctonia solani*	Jha and Chattoo (2010)
	Chimeric Cry1Ab/Vip3H	*Chilo suppressalis* and *Sesamia inferens*	Chen et al. (2010)
	Podisus maculiventris thanatin	*Magnaporthe oryzae*	Imamura et al. (2010)
	Allium sativum leaf agglutinin	Green leafhopper and Brown planthopper	Yarasi et al. (2008); Sengupta et al. (2010)
	B. rapa BrD1	*Nilaparvata lugens*	Choi et al. (2009)
	Potato carboxypeptidase inhibitor	*Magnaporthe oryzae* and *Fusarium verticillioides*	Quilis et al. (2007)
Ricinus communis	*cry1EC*	*Spodoptera litura*, Fabr and *Achoea janata*	Sujatha et al. (2009)
Saccharum officinarum	*B. thuringiensis mCry1Ac*	*Proceras venosatus*	Weng et al. (2011)
S. lycopersicum	Pepper methionine sulfoxide reductase B2 (*CaMsrB2*)	*Phytophthora capsici* and *P. infestans*	Oh et al. (2010)
	A. thaliana EFR	*R. solanacearum* GMI1000 and *X. perforans* T4-4B	Lacombe et al. (2010)
Solanum tuberosum	*Nicotiana megalosiphon NmDef02*	*Alternaria solani* and *P. infestans*	Portieles et al. (2010)
	S. chacoense SN1	*Rhizoctonia solani* and *Erwinia carotovora*	Almasia et al. (2008)

(continued)

Table 16.3 (continued)

Host transgenic plant	Gene(s) transformed	Tolerance against	Reference
Triticum aestivum	*TaPIEP1*	*Bipolaris sorokiniana*	Dong et al. (2010)
	Actinidia chinensis pectin methyl esterase inhibitor	*Bipolaris sorokiniana* and *Fusarium graminearum*	Volpi et al. (2011)
	Thinopyrum intermedium ERF1	*Rhizoctonia cerealis*	Chen et al. (2008)
	Stpk-V	*Blumeria graminis* f. sp. *tritici*	Cao et al. (2011)
	Barley class II chitinase	*Fusarium graminearum*	Shin et al. (2008)
	Raphanus sativus AFP2	*Fusarium graminearum* and *Rhizoctonia cerealis*	Li et al. (2011)
	PvPGIP2	*Fusarium moniliforme* and *Bipolaris sorokiniana*	Janni et al. (2008)
Vigna radiata	*BjNPR1*	*Rhizoctonia solani*	Vijayan and Kirti (2012)
Vigna unguiculata	*Phaseolus vulgaris αAI-1*	*Callosobruchus maculatus* and *C. chinensis*	Solleti et al. (2008)
Zea mays	UMV4 virus modified KP4	*Ustilago maydis*	Allen et al. (2011)
	HvCPI-6	*Tetranychus urticae*	Carrillo et al. (2011)

4.3 Manipulation of Susceptibility Factors

It is now very clear that for pathogenesis, plant pathogens manipulate host metabolism and suppress plant defense. In some cases plant proteins behave as susceptibility factors, i.e., plant proteins help in pathogen growth and reproduction leading to disease establishment. The role of a gene in susceptibility can be either because of its own function as negative regulator of plant defense or plant effectors may target its protein product for their own growth, although the gene may have role in plant growth and development in normal conditions (Eckardt 2002; De Almeida et al. 2005; Pavan et al. 2010). The elimination or modification of such plant factors from crop plants can also be a method to achieve resistance against pathogens, although modifications of gene should not have obvious negative consequences on plant health and yield. Many recessive genes that act as negative regulators provide resistance by activating the cell death (*cpr*, *lsd*, *cim*, *acd*, and *mlo*) or by unknown mechanisms independent of salicylic acid, jasmonic acid, and ethylene signaling pathways (*pmr6*).

In one of the best examples of a susceptibility gene, barley's *Mlo* (*Mildew Resistance Locus o*) gene is required for successful colonization by the ascomycete *B. graminis* f. sp. *hordei* (Humphry et al. 2006). Nonfunctional mutant alleles of this gene provide durable resistance in many elite varieties of barley after their introgression into them. Its role in powdery mildew pathogenesis has also been found in *Arabidopsis*, tomato, and pea plants (Consonni et al. 2006; Bai et al. 2008; Humphry et al. 2011). The gene seems to function as a suppressor of nonhost defense response components/signaling as resistance in *mlo* mutant plants and nonhost resistance share analogous features (Humphry et al. 2006). The *pmr6* mutants showed enhanced recessive resistance to *Erysiphe orontii* and *E. cichoracearum* but these mutant plants were susceptible to *P. parasitica* (Vogel and Somerville 2000; Vogel et al. 2002). The *pmr6* gene encodes for a pectate lyase-like protein with extended C-terminal, the mutations in this gene show pleiotropic effects on plant growth, and the cell wall of these plants have high pectin content. The eukaryotic translation initiation factor subunits (mostly elF4E and elF4G) act as susceptibility factors for viral infections mainly potyviruses (Robaglia and Caranta 2006; Piron et al. 2010). In *Arabidopsis* a pathogen-inducible patatin-like lipid acyl hydrolase (*PLP2*) facilitates fungal and bacterial colonization (La Camera et al. 2005) and in rice loss of a proline-rich protein (Pi21) confers durable disease resistance (Fukuoka et al. 2009). The transcription-activator-like (TAL) effector proteins of bacteria target many susceptible factors and in resistant plants they are recognized by many *R*-genes (Lewis et al. 2009; Bogdanove et al. 2010). A group of 'SWEET' sugar efflux transporters are induced by several pathogens and it was shown that TAL effectors in case of *Xanthomonas* spp. regulate their induction for pathogen growth (Chen et al. 2010).

The availability of genome editing in plants and further technology improvements will help scientists to manipulate the pathogen-induced expression or the whole susceptibility gene from plant. Thus, this powerful method can also increase the hope for improved GM crops with durable disease resistance (Weinthal et al. 2010).

4.4 Host-Induced Gene Silencing in Pathogens

The sequencing projects of various pathogens especially filamentous pathogens have revealed that their effectors are rapidly evolving as compared to other genes and their genomes are rich in transposons (Dodds 2010). This suggests that in near future more virulent strains of a pathogen will emerge like the highly virulent strain of *Puccinia graminis* f. sp. *tritici* Ug99 and events of host jumps may also be seen. In the long run, breeding and induced defense-based approaches will work only against pathogens that will evolve slowly but approaches that target the basic cellular and pathogenicity mechanisms of pathogens would provide long-lasting resistance. The RNA interference (RNAi; RNA-guided regulation of RNA transcripts) based approach would make an ideal choice against rapidly evolving pathogens, as it is known to provide resistance against viral infection in natural environment (Baulcombe 2004). Transgenic plants with RNAi constructs targeting specific genes of pathogens have shown resistance against viruses, parasitic nematodes, herbivorous insects, and parasitic weeds in many plants (Huang et al. 2006; Frizzi and Huang 2010; Niu et al. 2010; Wani et al. 2010). In an unsuccessful attempt, the *Plasmodiophora brassicae* gene was also checked for downregulation on transgenic *Arabidopsis thaliana* plants as this phytomyxea pathogen remains in intimate contact with host cell (Bulman 2006).

Considering the situation that ~70% of all major crop diseases are caused by fungal pathogens (Agrios 2005), this RNAi technology against fungi would greatly help to increase crop yield. Two prerequisites for successful silencing of fungal genes on transgenic plants would be the transfer of silencing-RNAs from host plant cell to the fungi and a functional RNAi machinery of the pathogenic fungi. Many independent groups have reported the silencing of genes using RNAi constructs in fungi suggesting that the RNAi machinery works in many fungi. The uptake of dsRNA from outside the fungal cells and subsequent silencing of the targeted fungal gene transcripts were claimed in two US patents (Van De Craen et al. 2006; Roberts et al. 2008). Tinoco et al. (2010) reported silencing of the *gus* transcripts in transgenic *Fusarium verticillioides* when it was inoculated on transgenic tobacco plants expressing RNAi construct against *gus* gene. Nowara et al. (2010) also showed that dsRNA or siRNA molecules were exchanged between cereal hosts and the obligate biotrophic fungal pathogen *Blumeria graminis* and they called this technique of downregulating pathogen genes as host-induced gene silencing (HIGS). Using transient expression, virus-induced gene silencing (VIGS), and transgenic plants with RNAi constructs it was proved that HIGS could be an effective tool to study the role of fungal genes in pathogenesis and it has the potential of disease control against biotrophic fungal pathogens (Fig. 16.2). Using VIGS the genes that are expressed in haustorial cells were silenced efficiently in *Puccinia striiformis* f. sp. *tritici* rather than the genes that are constitutively expressed in whole pathogen, probably pointing towards the fact that tissue which remains in intimate contact with host will receive more silencing-RNAs (Yin et al. 2011). More experiments with other systems are needed to standardize this technology before engineering at mass level and

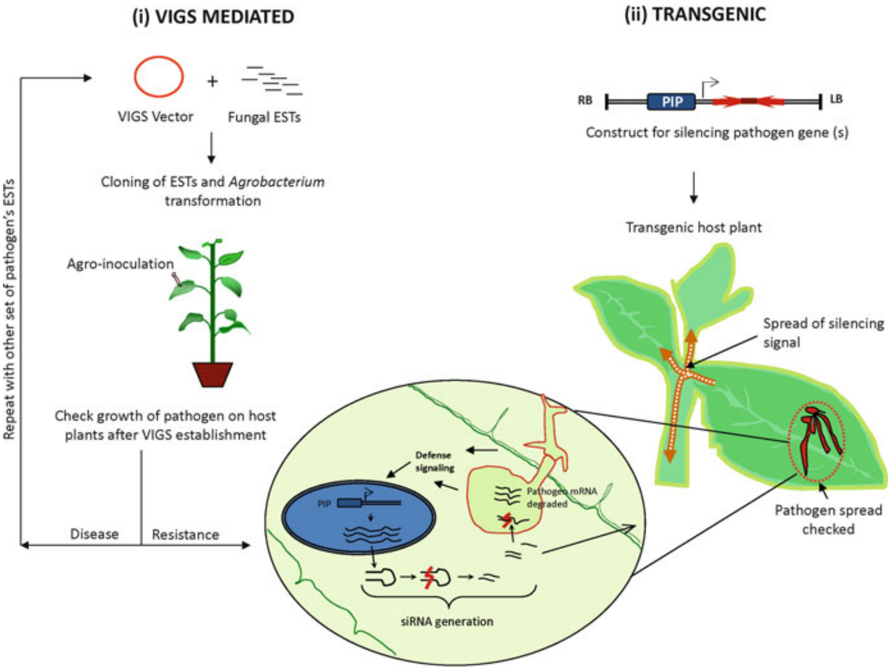

Fig. 16.2 Host-induced gene silencing (HIGS). Genes essential for pathogen growth on host plants can be downregulated by RNAi approach to limit the pathogen growth. (*i*) High-throughput approaches like virus-induced gene silencing (VIGS) can be used to identify the genes involved in pathogen growth and reproduction on host plants and (*ii*) the pathogen inducible promoter (PIP) can be used to generate transgenic plants having RNAi constructs against the gene/or genes of a pathogen

also the questions regarding the silencing of genes in hemibiotrophs and necrotrophs need to be answered. The usefulness of fungal inducible promoters to drive the RNAi constructs should help but the most important thing is to check for RNAi constructs off-targets and avoid it inside the plant cell. Overall the HIGS technology holds promise for generating fungal-tolerant crops leading to higher grain yield and it is believed that in future a common terminology of HIGS will be followed to make scientific literature retrieval easy regarding this type of silencing.

5 Conclusions and Future Prospects

We have come a long way in crop improvement from traditional elite variety selection to the development molecular breeding and transgenic crops. But our demand of food supply still needs rapid progress with growing population and nemesis of adverse environmental conditions. Also the increase in demand for biofuels will add more pressure on arable land. In this decade a great deal of information has been achieved about molecular aspects of plant–pathogen interactions. The technological advancements have certainly played a major role in this regard. Now, every aspect of plant–pathogen interaction is studied and sequencing of many crop plants and their pathogens will help in pyramiding various genes through marker-assisted selection especially against notorious pests and necrotrophic fungi where resistance is governed by many QTLs. Contrary to the biosafety-related opinions raised regarding GM crops, molecular plant biologists are optimistic about the need to incorporate GM crops in our crop improvement chain as it can be applied to all the crops outside the limits of species. Already more that 20% of arable land is under the GM crops in countries like USA, Brazil, and Argentina, which dictates the success story of GM crops.

We still need to study and effectively use the nonhost resistance components for high yielding disease-tolerant crops. In case of GM crops effective regulatory mechanisms and safeguards need to be installed to avoid any biosafety-related problem in future and the fields should be monitored regularly for the evolution of new pathogens against resistant crops. The need for translational of basic research to the field crops is more from public sector as investments are more in this sector. The areas where still we can improve for production of stress tolerance crops need to be evaluated and programs need to be implemented especially in developing countries.

Acknowledgements This work is supported partially by research grant provided by Department of Biotechnology, Government of India and National Institute of Plant Genome Research, New Delhi. We acknowledge Dr. K. D. Srivastava, Indian Agricultural Research Institute, New Delhi for valuable suggestions and critically editing the manuscript. K.K. acknowledges NIPGR for postdoctoral fellowship.

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