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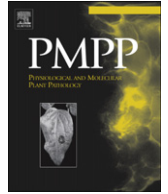
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Plant disease resistance genes: Current status and future directions

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ABSTRACT

Plant diseases can drastically abate the crop yields as the degree of disease outbreak is getting severe around the world. Therefore, plant disease management has always been one of the main objectives of any crop improvement program. Plant disease resistance (R) genes have the ability to detect a pathogen attack and facilitate a counter attack against the pathogen. Numerous plant R-genes have been used with varying degree of success in crop improvement programs in the past and many of them are being continuously exploited. With the onset of recent genomic, bioinformatics and molecular biology techniques, it is quite possible to tame the R-genes for efficiently controlling the plant diseases caused by pathogens. This review summarizes the recent applications and future potential of R-genes in crop disease management.

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1. Introduction

Plant pathogen interaction is a well understood mechanism which involves the activation of signals sometimes resulting in a rapid defense response against an array of plant pathogens. This response helps the host plant to avoid further infection of the disease. Induction of plant defense signaling involves the recognition of specific pathogen effectors by the products of specialized host genes called R-genes [13]. Numerous individual plant resistance (R) genes have already been characterized and are being efficiently used in crop improvement research programs. Using plant resistance genes for developing disease-resistant varieties is a convenient alternative to other measures like pesticides or other chemical control methods employed to protect crops from diseases. Benefits of using the plant resistance genes in resistance breeding programs include the efficient reduction of pathogen growth, minimal damage to the host plant, zero input of pesticides from the farmers and most importantly the environment friendly nature of

such crops. However, in case of conventional breeding for resistance, the introgression of resistance genes from one species into the gene pool of another by repeated backcrossing is a long-term process which usually takes many hybrid generations before the backcrossing occurs. It is assumed that the complete functional studies, cloning, characterization and genetic transformation of plant resistance genes could help the researchers to overcome these problems in near future.

Efficient and sustained control of pathogens such as bacteria, fungi, oomycetes, viruses, nematodes and insects is an exigency for all agricultural systems. In spite of the continued release of new resistant cultivars, the global yield losses caused by pathogens are substantial [8,188]. Plant pathogens not only decrease the crop yields, they also lower the crop quality by releasing toxins that affect human health. Moreover, pathogens are constantly becoming resistant to existing resistance genes and pesticides. This situation therefore demands some alternate methods of disease control. Crop improvement programs based on plant disease resistance genes are being optimized by incorporating molecular marker techniques and biotechnology. Therefore, plant resistance genes need to be studied extensively to alleviate the existing problem of pest and diseases apart from the abiotic challenges [147]. Facing selective pressure imposed by the pathogens, plants have evolved post invasion resistance mechanisms, often controlled by dominant resistance genes, whose products directly or indirectly detect specific pathogen effectors and trigger effective defense responses [40,122]. R protein-triggered resistance to various pathogens is

Abbreviations: Avr, Avirulence; CC, Coiled coil; HR, Hypersensitive reaction; LRR, Leucine rich repeats; NBS, Nucleotide-binding site; Pto, *Pseudomonas* tomato resistance; R, Resistance; RPP5, Resistance to *Peronospora parasitica* 5; RPS2, Resistance to *Pseudomonas syringae* 2; TIR, Toll/interleukin-1-receptor homology region.

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normally race-specific and only effective against pathogen strains expressing the cognate effector protein (Avr protein) recognized by the R protein. This resistance is often associated with a hypersensitive response (HR), which is manifested as rapid death of the invaded cell and in some cases a few surrounding cells [89,96,179,260]. The structural and functional analysis of plant resistance genes and R-gene loci is relevant for assembling various resistance sources effectively and for engineering new strategies for disease resistance in agriculture. Apart from that, it is highly desirable to understand the plant–pathogen interaction in order to achieve the said goals. These aspects have been discussed in detail later in the present review which would be beneficial for researchers engaged in plant disease control based projects. The present article also highlights the concernment of many recent investigations regarding the plant resistance genes and their dispensation in the field of plant disease management strategies.

2. Plant basal disease resistance

Plants possess two major types of disease resistance, basal defense and R-gene mediated defense (Fig. 1). Basal defense, which can be a constituent of both non-host and host resistance, provides first line of defense to the infection by a wide range of pathogens. Often, the plant disease resistance is cultivar or accession specific which is referred as host resistance whereas non-host resistance is the resistance against pathogens throughout all members of a plant species [95,97,254] that is expressed when a plant comes into contact with a pathogen which is incapable of provoking any disease [98]. Elicitors of basal defense can be plant cell wall-derived components released by hydrolytic activity of enzymes secreted by invading pathogens, but also common features of the pathogen, referred as pathogen-associated molecular patterns (PAMPs), such as lipopolysaccharides, chitins, glucans and flagellins [187,222,236,325]. Non-pathogens as well as pathogens can trigger a basal resistance in plants due to the widespread presence of these molecular components in their cells [69]. However, adapted microbes express a suite of effector proteins that often act to suppress these defenses. Subsequently, plants have evolved other receptors (R proteins) that detect these pathogen effectors and activate strong defenses [19].

3. R-gene mediated pathogen resistance

Phytopathogens produce certain molecules called ‘effectors’, encoded by *Avr* (avirulence) genes, which are delivered directly into the plant cells during initial stage of infection. These effectors either

change the physiological state of host plant in order to benefit pathogen colonization or are used to interrupt the activation of host plant defenses [44,91]. However, plants have subsequently developed a form of immunity that is based on perception of these proteins [185] by host resistance proteins called R-gene mediated pathogen resistance.

In gene-for-gene relationships, a plant carrying a resistance gene resists pathogen races with the corresponding effectors [67,132,281]. The effectors found in bacteria, virus, nematodes, fungus, oomycetes and insects cause a plant pathogen to elicit a resistance response in a host plant (Fig. 1). The effector genes are defined by corresponding resistance genes of which a relatively large number have now been cloned [162]. This resistance response is appended with another reaction called hypersensitive reaction (HR) which is a form of programmed cell death. The signaling cascade behind the HR is triggered either when an appropriate disease resistance gene recognizes an effector or by an elicitor of plant defense responses recognized by a specific receptor [177,184]. Either of these signals accompanied by other factors like influx of Ca^{2+} ions from the extracellular space and/or anion flux results in an oxidative burst producing reactive oxygen intermediates (ROIs) and defense gene activation, finally resulting in development of local and systemic disease resistance [233,316,318].

A well characterized example of HR elicitation through gene-for-gene interaction is provided by the tomato (*Solanum lycopersicon*) *Cf-9* gene, which confers resistance to races of the fungus *Cladosporium fulvum* expressing the *Avr9* gene [279]. Treatment of leaves of *Cf-9* tomato or transgenic *Cf-9* tobacco (*Nicotiana tabacum*) with the *Avr9* peptide induces HR [90] and *Avr9*-treated *Cf-9* tobacco cell cultures showed rapid production of ROS and activation of MAP (Mitogen Activated Protein) kinases and calcium-dependent protein kinases [220,221]. The interaction between rice (*Oryza sativa*) and the fungal pathogen *Magnaporthe grisea* (Hebert) Barr (anamorph *Pyricularia grisea* Sacc.) causing the devastating rice blast disease is another example of well documented gene-for-gene system [134,247,278]. *M. grisea* has the *Avr-Pita* gene containing the C-terminal 176 amino acids which functions as an elicitor molecule that directly binds the *Pita* protein of rice and triggers a signal cascade leading to resistance [113].

Despite several studies and intense efforts with numerous sets of R and Avr proteins [113,266], the interaction between R and Avr proteins remained inexplicit and the insufficiency of verifiable R-Avr interactions led to the formulation of the ‘guard hypothesis’ [165,270,279,280]. According to this model, the R proteins activate resistance when they interact with another plant protein known as guard protein that is targeted and modified by the pathogen in

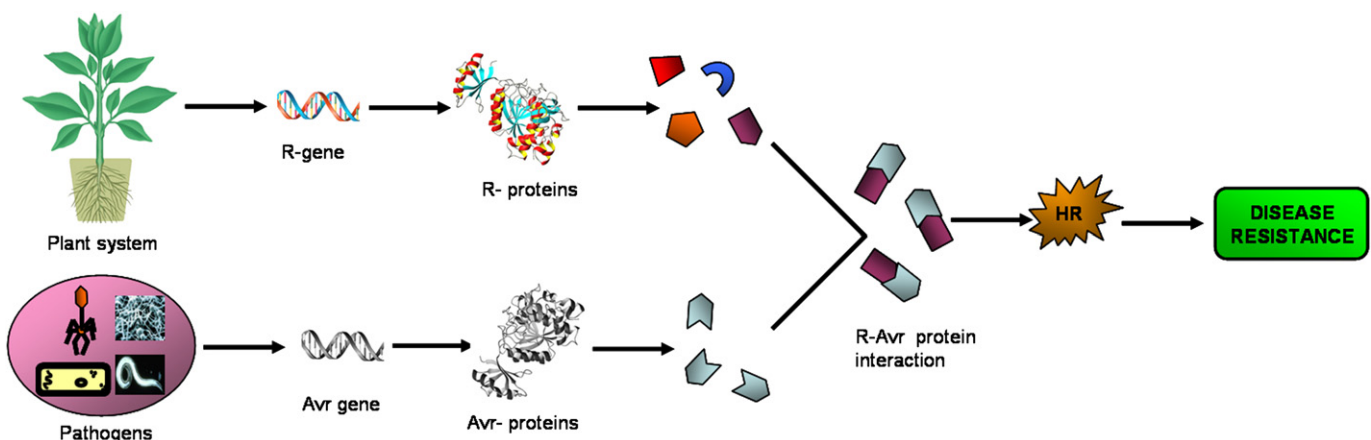


Fig. 1. Plant pathogen interaction and development of disease resistance.

order to create an appropriate environment. Resistance is initiated when the R protein detects an attack of its guardee or, in some cases when the R protein recognizes the product of the pathogen attack [244], which might not necessarily involve direct interaction between the R and Avr proteins [165], (Fig. 2). To date, the most convincing evidence for the guard hypothesis has been found in *Arabidopsis thaliana* bacterial R-Avr systems [158] where RIN4 (RPM1-interacting protein 4) was identified as a cellular protein that is required for the resistance to *Pseudomonas syringae* pv. tomato mediated by *RPM1* and *RPS2*. The RIN4 (guardee) is modified in various ways, depending on the Avr that it associates with, and these modifications then serve to activate the corresponding R protein (guard). Another example is the cleavage of the *A. thaliana* kinase PBS1 (guardee) by the cysteine protease AvrPphB from *P. syringae* pv. tomato, which results in activation of RPS5 (guard)-mediated resistance [244]. Recently, it was shown that AvrPphB, a cysteine protease, binds PBS1 and cleaves it, which triggers RPS5-mediated resistance, indicating that RPS5 might sense the integrity of PBS1 [242,243].

Several genes have been implicated in the regulation of resistance gene function; of these, *Rar1* and *Sgt1* are among the most extensively studied genes. It has been reported that *Rar1* and *Sgt1* are required in multiple R-gene mediated and non-host resistance responses to a variety of pathogens [198,199,234]. A notable example is in barley where the regulation of *Mla* transcript accumulation is not constitutive and that induction is coordinately controlled by recognition-specific factors [88]. *Rar1* from barley has been identified as a required component for resistance against powdery mildew (*Blumeria graminis* f. sp. *Hordei*) mediated by *Mla12* [274] which is required for a subset of R-gene mediated resistance responses in monocot and dicot plant species [155,182,237,246]. *Sgt1* interacts with *Rar1*, and contributes to R-gene mediated resistance [7,154,155] although recently, Bhaskar et al. [21] demonstrated that *Sgt1*, but not *Rar1*, is essential for the RB-mediated broad-spectrum resistance to potato late blight. Similarly, Hein et al. [99] reported that Hsp90 (heat shock protein 90), a molecular chaperone and one of the most abundant proteins expressed in cells was found as a required component for *Mla13*-mediated race-specific resistance.

4. Major classes of R proteins

Plant resistance genes can be broadly divided into eight groups based on their amino acid motif organization and their membrane

spanning domains (Fig. 3, Table 1). The LRRs (Leucine rich repeats) represents the components having an important role for recognition specificity and these domains are present in the majority of R proteins [121].

First major class of R-genes include the genes encoding for cytoplasm proteins with a nucleotide-binding site (NBS), a C-terminal leucine rich repeat (LRR) and a putative coiled coil domain (CC) at the N-terminus. The examples of this class of resistance genes include the *P. syringae* *RPS2* and *RPM1* resistance genes of *Arabidopsis* and the tomato *Fusarium oxysporum* resistance gene *I2*. The second class of resistance genes consists of cytoplasmic proteins which possess LRR and NBS motifs and an N-terminal domain with homology to the mammalian toll-interleukin-1-receptor (TIR) domain. The tobacco *N* gene, flax *L6* gene and *RPP5* gene are a few examples categorized under this class [146]. Third major class of resistance genes family devoid of NBS motif consists of extra cytoplasmic leucine rich repeats (eLRR), attached to a transmembrane domain (TrD). eLRRs are known to play an important role for certain defense proteins such as, polygalacturonase inhibiting proteins (PGIPs) [119] even though they are not directly involved in pathogen recognition and activation of defense genes [121,256]. The *C. fulvum* resistance genes (*Cf-9*, *Cf-4* and *Cf-2*) having an extracellular LRR (eLRR), a membrane spanning domain, and a short cytoplasmic C terminus [150] are some examples of this class of resistance genes. The rice *Xa21* resistance gene for *Xanthomonas* is an example of the fourth class of resistance genes which consists of an extracellular LRR domain, a transmembrane domain (TrD) and an intracellular serine-threonine kinase (KIN) domain [252].

The fifth class of resistance genes contain the putative extracellular LRRs, along with a PEST (Pro-Glu-Ser-Thr) domain for protein degradation (found only in *Ve2*, and not *Ve1*), and short proteins motifs (ECS) that might target the protein for receptor mediated endocytosis (e.g. tomato *Ve1* and *Ve2* genes) However, these *Ve1* and *Ve2* proteins have recently been proposed as PAMP receptors [270].

The *Arabidopsis* RPW8 protein is an example of the sixth major class of resistance genes which contains a membrane protein domain (TrD), fused to a putative coiled coil domain (CC) [299] whereas, the seventh major class of resistance genes includes the *Arabidopsis* *RRS1-R* gene conferring resistance to the bacterial phytopathogen *Ralstonia solanacearum*, and it is a new member of the TIR–NBS–LRR R protein class. *RRS1-R* has a C-terminal extension with a putative nuclear localization signal (NLS) and a WRKY

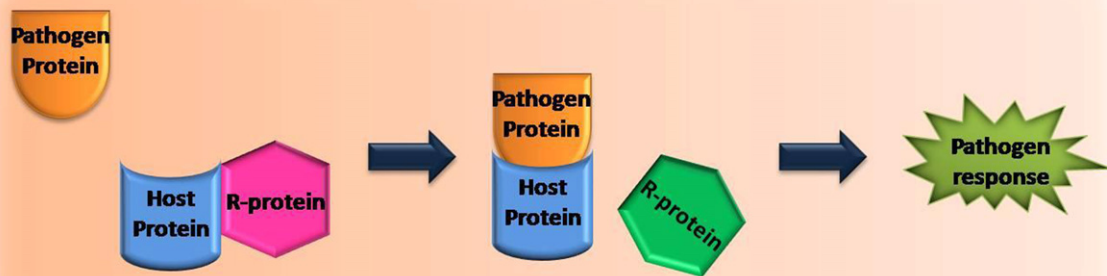


Fig. 2. Guard hypothesis – the plant R proteins (guard) are associated with the endogenous host protein (guardee) which are common target proteins for the pathogens. The interaction of effector pathogen proteins with the host proteins, causes a change in their structure which is then recognized by the guard proteins. As a result, a pathogen response signaling cascade is triggered against the microbial evasion.

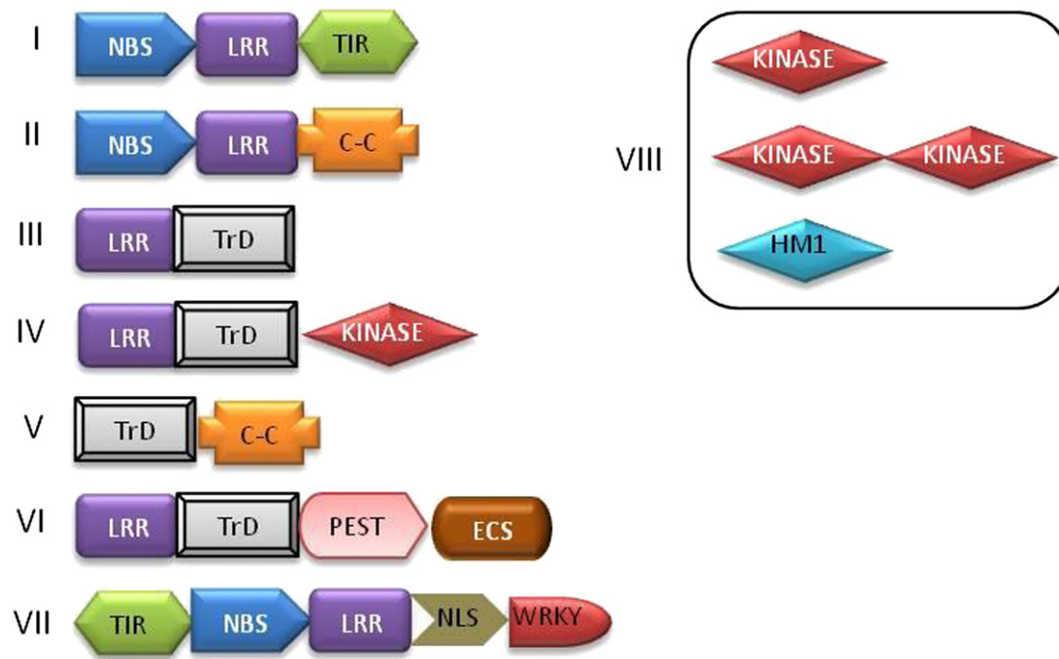


Fig. 3. Major classes of plant resistance (R) genes based on the arrangement of the functional domains. LRR – Leucine rich repeats; NBS – Nucleotide-binding site; TIR/Toll/Interleukin-1- receptors; C-C – Coiled coil; TrD – Transmembrane domain; PEST – Protein degradation domain (proline-glycine-serine-threonine); ECS – Endocytosis cell signaling domain; NLS – Nuclear localization signal; WRKY – Amino acid domain; HM1 – *Helminthosporium carbonum* toxin reductase enzyme.

domain [52,53]. The WRKY domain is a 60 amino acid region that is defined by the conserved amino acid sequence WRKYGQK at its N-terminal end, together with a novel zinc-finger-like motif.

The eighth major class of resistance genes includes the enzymatic R-genes which contain neither LRR nor NBS groups. For example the maize *Hm1* gene which provides protection against southern corn leaf blight caused by the fungal pathogen *Cochliobolus carbonum* [117]. Unlike other resistance genes, *Hm1* encodes the enzyme HC toxin reductase, which detoxifies a specific cyclic tetrapeptide toxin produced by the fungus (HC toxin) that is essential for pathogenicity. Therefore, cereal resistance genes like *Hm1* can be seen to encode a range of different proteins that in some cases have obviously very different functions. Another notable example, Pto protein in *P. syringae* contains a Ser-Thr kinase domain without LRRs [161] whereas, the *Rpg1* gene of barley which confers resistance to stem rust encodes a receptor kinase-like protein with two tandem protein kinase (kinase–kinase) domains and does not contain a strong membrane-targeting motif and known receptor sequences [31].

Though most of the resistance genes show dominant inheritance, recessive resistance is fairly common in viral systems [130], (Section 4.5) Recessive resistance genes in bacterial and fungal plant pathogen interactions have also been reported, such as barley *mlo* [32], *Arabidopsis* RRS1-R [53], rice *xa13* [42], and *xa5* [106,116].

With the onset of functional genomics approaches and complete genome sequencing of some important crop plants, the identification and deployment of R-genes has become easier. Numerous resistance genes conferring resistance against a range of pathogens have been successfully used in development of transgenic crops. Therefore, the possibility of discerning some novel classes of resistance genes in near future cannot be ruled out.

4.1. Bacterial resistance genes

A number of plant resistance genes conferring resistance against bacterial attack have been studied so far (Table 2) and for the majority of plant diseases, the genetics of susceptibility are less tangible. It has been known that bacterial pathogens of both plants

Table 1
Major classes of plant resistance genes – LRR – Leucine rich repeats; NBS – Nucleotide-binding site; TIR – Toll/Interleukin-1- receptors; CC – Coiled coil; TrD – Transmembrane domain; PEST – Amino acid domain; ECS – Endocytosis cell signaling domain; NLS – Nuclear localization signal; WRKY – Amino acid domain; HC toxin reductase – *Helminthosporium carbonum* toxin reductase enzyme.

S. no	Major R-gene classes	Domains										Example
		LRR	NBS	TIR	Kinase	CC	TrD	PEST	ECS	NLS	WRKY	
I	NBS–LRR–TIR	✓	✓	✓	X	X	X	X	X	X	X	<i>N, L6, RPP5</i>
II	NBS–LRR–CC	✓	✓	X	X	✓	X	X	X	X	X	<i>I2, RPS2, RPM1</i>
III	LRR–TrD	✓	X	X	X	X	✓	X	X	X	X	<i>Cf-9, Cf-4, Cf-2</i>
IV	LRR–TrD–Kinase	✓	X	X	✓	X	✓	X	X	X	X	<i>Xa21</i>
V	TrD–CC	X	X	X	X	✓	✓	X	X	X	X	<i>RPW8</i>
VI	TIR–NBS–LRR–NLS–WRKY	✓	✓	✓	X	X	X	X	✓	✓	✓	<i>RRS1R</i>
VII	LRR–TrD–PEST–ECS	✓	X	X	X	X	✓	✓	✓	X	X	<i>Ve1, Ve2</i>
VIII	Enzymatic R-genes	X	X	X	✓	X	X	X	X	X	X	<i>Pto, Rpg1</i>
		X	X	X	X	X	X	X	X	X	X	<i>Hm1</i>

✓ = present.

X = absent.

Table 2
Bacterial pathogens and interacting Avr-genes and R-genes.

Pathogen	Host	Avr-gene	R-gene	Reference
<i>Xanthomonas campestris</i>	<i>Capsicum annum</i>	Avr-Bs2	Bs2	[177,259]
<i>Xanthomonas oryzae</i>	<i>Oryza sativa</i>	—	NPR1	[39]
		Avr-Xa1	Xa1	[321]
		Avr-Xa21	Xa21	[252]
<i>Pseudomonas syringae</i> pv <i>tomato</i>	<i>Lycopersicum esculentum</i>	Avr-Pto, Avr-PtoB	Pto	[1,135,161,223]
<i>P. syringae</i>	<i>Arabidopsis thaliana</i>	AvrRpm1, AvrB	RPM1	[50,82,105,263]
		AvrRpt2	RPS2	[17,102,176,304]
		AvrPphB	RPS5	[108,257,301]
		AvrRps4	RPS4	[77,101]

and animals deliver virulence proteins into the host cytoplasm via the type-III secretion system (T3SS), also called injectisome [54] which enables Gram negative bacteria to secrete and inject pathogenicity proteins into the cytosol of eukaryotic host cells [71,94]. The T3SS is encoded by *hrp* (HR and pathogenicity) and *hrc* (HR and conserved) genes, whose mutations eliminate bacterial pathogenicity in susceptible host plants and the ability to elicit HR in non-host or cultivar-specific resistant plants. Many of the T3SS effector proteins have been shown to be dependent on molecular chaperones, which keep the effector in a partially unfolded form in the bacterial cytoplasm [255]. The emergent results on their role in pathogenesis have indicated that they act as molecular double agents betraying the pathogen to plant defenses in some interactions and suppressing host defenses in others [181].

In rice, resistance and susceptible alleles of *Xa27* encode identical proteins however, expression of only the resistance allele occurs when a rice plant is challenged by bacteria harboring *AvrXa27*, whose product is a nuclear localized T3SS effector. Induction of *Xa27* occurs only in the immediate vicinity of infected tissue, whereas ectopic expression of *Xa27* results in resistance to otherwise compatible strains of the pathogen. The *Xa27* specificity

toward incompatible pathogens involves the differential expression of the resistance gene in presence of the *AvrXa27* effector [85]. A dominant rice gene *Os8N3* is an exception as it is up-regulated by a bacterial type-III effector protein, and that confers gene-for-gene-specified disease susceptibility [126].

Some bacterial resistant plant resistance genes may confer resistance against unrelated or distantly related pathogens. Zhao et al. [323] demonstrated the feasibility of non-host resistance gene transfer between two cereal crops maize and rice. They proposed that a maize non-host resistance gene *Rxo1* recognizes a rice pathogen, *Xanthomonas oryzae* pv. *oryzicola* and causes bacterial streak disease. Interestingly, *Rxo1* was also found to confer resistance to the unrelated pathogen *Burkholderia andropogonis*, known to cause bacterial stripe of sorghum and maize indicating that the same gene controls resistance to both pathogens and non-pathogens of maize. The function of *Rxo1* in rice thus demonstrates that an NBS-LRR type of resistance gene can be effectively transferred between distantly related cereals [323].

4.2. Fungal resistance genes

Fungal diseases are rated either the most important or second most important factor contributing to yield losses in almost all the major crops [300]. So far, several fungal resistance genes (Table 3) have been reported and used in crop improvement programs. However, the sequence variation occurring within the central LRR domain and the variation in LRR copy number of the gene plays an important role in determining recognition specificity [27,141]. For example, the sequence variations in tomato *Cf-4* and *Cf-9* genes play an important role in determining recognition specificity, which confer resistance to biotrophic leaf mold pathogen *Cladosporium* and induce a hypersensitive response (HR) upon recognition of the fungus-encoded *Avr4* and *Avr9* peptides [27]. In tomato, *Ve* is involved in race-specific resistance to infection by *Verticillium* species [126]. The *Ve1*-mediated resistance signaling only partially overlaps with signaling mediated by *Cf*- proteins [191]. Recently, a virus induced gene silencing approach for the characterization of

Table 3
Fungal pathogens and interacting R-genes.

Pathogen	Host	Avr-gene	R-gene	Reference
<i>Blumeria graminis</i>	<i>Hordeum vulgare</i>	AvrMla	Mla	[324]
		—	Mlo	[32]
<i>Cochliobolus carbonum</i>	<i>Zea mays</i>	—	Hm1	[117]
<i>Cladosporium fulvum</i>	<i>Lycopersicum esculentum</i>	Avr2	Cf-2	[157,224,251,284]
		Avr4	Cf-4	[27,123,269]
		Avr5	Cf-5	[55]
		Avr9	Cf-9d	[120]
<i>Erysiphe orontii</i> , <i>E. cichoracearum</i> and <i>Oidium lycopersici</i>	<i>Arabidopsis thaliana</i>	—	RPW8.1, RPW8.2	[299,314,317]
<i>Fusarium oxysporium</i>	<i>Lycopersicum esculentum</i>	Avr1	I2	[189,248]
<i>Melampsora lini</i>	<i>Linum usitatissimum</i>	AyrL	L	[56,57,146]
		AvrM	M	
		AvrN	N	
		AvrL567 genes, whose products are recognized by the L5, L6, and L7		
<i>Magnaporthe grisea</i>	<i>Oryza sativa</i>	Avr-Pita	Pi-ta	[113,134]
<i>Puccinia sorghi</i>	<i>Zea mays</i>	AvrRP-I-D	Rp1	[43]
<i>Puccinia triticina</i>	<i>Triticum aestivum</i>	—	Lr46	[164,168]
<i>Puccinia graminis</i> f. sp. <i>tritici</i>	<i>Hordeum vulgare</i>	Avr-Rpg1	Rpg1, Rpg4, Rpg5	[31,103,136]
<i>Verticillium albo-atrum</i>	<i>Lycopersicum esculentum</i>	—	Ve1, Ve2	[2,131,293]
	<i>Mentha arvensis</i>		mVe1	
	<i>Mentha longifolia</i>			
<i>Verticillium dahliae</i>	<i>Lycopersicum esculentum</i>	—	Ve1	[68]

Ve mediated signaling revealed that signaling cascade downstream of *Ve1* requires two genes *EDS1* (Enhanced Disease Susceptibility 1) and *NDR1* (non race-specific disease resistance 1). Moreover, the results showed that the locus *Ve* consists of two closely linked inversely oriented genes, *Ve1* and *Ve2* encoding cell surface receptor proteins of the extracellular LRR receptor-like protein. Out of them, only *Ve1* provides resistance in tomato against race 1 strains of *Verticillium dahliae* and *Verticillium albo-atrum* and not against race 2 strain. Based on the sequence analysis and the expression study, *Ve1* and *Ve2* expression is induced in resistant as well as susceptible tomato genotypes and that no single mutation in the CDS of *Ve2* discriminates resistant and susceptible tomato genotypes. However, a single point mutation in *Ve1*, resulting in a premature stop codon, was found in all susceptible genotypes and was absent in all resistant genotypes. This suggested that *Ve1*, but not *Ve2*, governs *Verticillium* resistance in tomato [68].

A disease epidemic broke out in oats in the 1940's due to the extensive planting of "Victoria-type" oats carrying the *Pc-2* gene for resistance against the rust fungus, *Puccinia coronata*. Oats carrying *Pc-2* were highly susceptible to another disease, Victoria blight, caused by a fungus *Cochliobolus victoriae* [151,169]. Pathogenicity of *C. victoriae* is dependent on the production of a toxin called victorin, and in oats, both toxin sensitivity and Victoria blight disease susceptibility are conferred by the dominant *Vb* gene. Despite extensive efforts, rust resistance (*Pc-2*) and Victoria blight susceptibility (*Vb*) have not been genetically separated and are suspected to share identity [298,312] thus suggesting an unexpected relationship between plant disease resistance and susceptibility.

Stem rust-susceptible barley cv. Golden Promise was transformed into a highly resistant one to pathotype Pgt-MCC of the stem rust fungus *Puccinia graminis* f. sp. tritici by *Agrobacterium*-mediated transformation with the dominant *Rpg1* gene. A single copy of *Rpg1* against stem rust, and progenies from several transformants segregated in a 3:1 ratio for resistance: susceptibility as expected for Mendelian inheritance and unequivocally demonstrated that the DNA segment isolated by map-based cloning is the functional *Rpg1* gene for resistance to stem rust and the transformants exhibited a higher level of resistance than the original sources of *Rpg1* like cvs. Chevron and Peatland [103]. Another fungal resistance plant resistance gene *RUS1* from *Setaria italica* Beauv. cv. Shilixiang resistant to *Uromyces S. italica*, was cloned and it was found to contain an NB-ARC (nucleotide-binding adapter shared by APAF-1, R proteins, and CED-4) domain as well as three conserved motifs P-loop, kinase 2, and kinase 3, having the characteristics of NBS-LRR type resistance gene of plant [303].

Another notable example of fungal resistance genes is the broad-spectrum mildew resistance gene *RPW8.2* from *Arabidopsis thaliana* which is induced by powdery mildew [299] and is assumed to be involved in enhancing the formation of a callosic encasement of the haustorial complex (EHC) with onsite accumulation of H₂O₂, in order to constrain the haustorium while reducing oxidative damage to the host cell. Targeting of *RPW8.2* to the EHM (Extra haustorial membrane) requires normal function of the actin cytoskeleton while microtubules are not involved in the process. Despite its critical role for the defense function, SA signaling is dispensable for targeting *RPW8.2* to the EHM and both EHM localization and defense activation are required for *RPW8.2* to induce resistance against powdery mildew [314].

The majority of resistance genes reside in clusters, and the frequency of recombination between clustered genes can vary remarkably, even within a single cluster. The Apple *Vf* locus, derived from the crab apple species *Malus floribunda*, confers resistance to five races of the apple scab fungus *Venturia inaequalis*. The *Vf* locus comprises a cluster of four *RLP* genes, *HcrVfa1* to *HcrVfa4* (for

homolog of the *C. fulvum* resistance genes of the *Vf* region), of which *HcrVfa1*, *HcrVfa2* and *HcrVfa4* encode typical RLPs while *HcrVfa3* contains an insertion at the end of the LRR motif, resulting in truncated transcripts [292,315]. Only expression of *HcrVfa1* or *HcrVfa2* in susceptible apple cultivars provided resistance against *V. inaequalis* strains [12,159].

4.3. Oomycetes resistance genes

Phytopathogenic oomycetes are responsible for economically important diseases, such as late blight of potato and sudden oak death caused by *Phytophthora infestans* and *Phytophthora ramorum* respectively. The oomycetes (Pseudofungi) have been classified within the phylum Heterokontophyta comprising a number of microbial lineages with phenotypic similarities to true fungi [216]. It was only with the use of molecular phylogenetic methods starting with small subunit rDNA analysis [34,35] followed by multiple concatenated gene phylogenies [9] that the oomycetes were demonstrated to group within the heterokont radiation [216].

Several functional resistance genes from potato conferring resistance to late blight have been cloned and all of them belong to the NBS-LRR class of plant resistance genes [10,14–16,104,190,250,282,283]. In addition to the resistance to *P. infestans* genes *Rpi-blb1* (RB) and *Rpi-blb2*, *Solanum bulbocastanum* appears to harbor *Rpi-blb3* located at a major late blight resistance locus on LG IV, which also harbors *Rpi-abpt*, *R2*, *R2*-like, and *Rpi-mcd1* in other *Solanum* spp [156]. Vleeshouwers et al. [294] used a candidate gene approach for the rapid cloning of *S. stoloniferum* *Rpi-sto1* and *S. papita* *Rpi-pta1*, which are functionally equivalent to *Rpi-blb1*. Cloning and functional analyses of four *Rpi* genes, *Rpi-blb3*, *Rpi-abpt*, *R2*, and *R2*-like revealed that these genes contain all signature sequences characteristic of leucine zipper nucleotide-binding site leucine rich repeat (LZ-NBS-LRR) proteins, and share 34.9% of amino acid sequences similar to *RPP13* from *A. thaliana* [149,193–195]. So far, a number of *Hyaloperonospora parasitica* resistance (RPP) genes against the downy mildew have been cloned from *Arabidopsis* which belong to the NBS-LRR class of resistance genes [119,264]. These resistance genes are distinguished by their N-terminal regions, showing homology to the TIR domain (*RPP1* and *RPP5* clusters) and leucine zipper motifs (*RPP8* cluster) [25,166,172]. Another example of oomycetes resistance genes with NBS-LRR motifs is downy mildew resistance gene, *Dm3* [45,244,245] in *Bremia lactucae* which is a member of the large RGC2 (Resistance Gene Candidate2) multigene family similar to the genes cloned from other species for resistance to downy mildews and other pathogens [167].

Several oomycete effector genes (Table 4) encoding products that are recognized by R proteins situated in the plant cytoplasm have been discovered which indicate toward a mechanism of transporting fungal and oomycete effectors into plant cells [5,241,271,273,294]. This mechanism has recently been characterized using gene ontology by Torto-Alalibo et al. [275] while the motifs in their amino acid sequence have already been identified in the past [8,13,16]. The identification of the first effectors from oomycetes, together with whole genome sequencing projects has revealed a special class of secreted effector proteins, RXLR that are delivered into host cells [4,6,81,83,212,277]. The RXLR effectors constitute large super families of rapidly evolving proteins in all oomycete genomes [58,115] and include *Avr1b-1*, *Avr1a* and *Avr3a* from *Phytophthora sojae* [207,241], *Avr3a*, *Avr4*, and *Avrblb1* from *P. infestans* [5,6,286,294], *ATR1* and *ATR13* from *Hyaloperonospora arabidopsidis* [5,212] and *IpiO* and *IpiB* from certain *Phytophthora* species including *P. infestans* [36,203,294]. While the majority of IPI-O proteins are recognized by *RB* gene to elicit host resistance,

Table 4
Oomycetes pathogens and interacting Avr-genes and R-genes.

Pathogen	Host	Avr-gene	R-gene	Reference
<i>Bremia lactucae</i>	<i>Lactuca sativa</i>	Avr3	Dm3	[173,174]
<i>Hyaloperonospora arabidopsis</i>	<i>Arabidopsis thaliana</i>	ATR1	RPP1-Nd/WsB	[212]
		ATR13	RPP13-Nd	[5,23]
<i>Peronospora parasitica</i>	<i>A. thaliana</i>	AvrB, AvrRPP1A, AvrRPP1B, AvrRPP1C, AvrRPP2, AvrRPP4, AvrRPP5, AvrRPP8	RPP1, RPP2 RPP4, RPP5, RPP8	[25,166,196,197,280]
<i>Phytophthora infestans</i>	<i>Solanum tuberosum</i>	Avr1	R1	[10]
<i>P. infestans</i>	<i>Solanum tuberosum</i>	Avr-blb1	Rpi-blb1	[294]
<i>P. infestans</i>	<i>Solanum tuberosum</i>	PiAvr2	Rpi	[156,296]
<i>P. infestans</i>	<i>Solanum demissum</i>	Avr3a	R3a	[6]
<i>P. infestans</i>	<i>Solanum bulbocastanum</i>	Ipio, IpiB, Ipi-o4	RB	[36,287]
<i>P. infestans</i>	<i>Solanum tuberosum</i>	Avr3b–Avr10–Avr11 locus,	R3b, R10, R11	[114]
<i>Phytophthora sojae</i>	<i>Glycine max</i>	Avr1a, Avr3a and Avr3c,	Rps1a Rps3a Rps3c	[58,160,207]

some variants exist that are able to elude detection (e.g. *Ipi-O4*) [87]. Intriguingly, few oomycete effectors that do not encode RXLR effectors have also been proposed, such as *Avr3b*, *Avr10* and *Avr11* in *P. infestans* [114,208] and *Avr1b-2* in *P. sojae* [241]. So far, the host targets of RXLR effectors have not been well described in the literature [268], while the target proteins of several oomycete apoplastic effectors have been determined [128,178,271,272].

P. sojae encodes numerous putative host cytoplasmic effectors [1,24,59] with conserved FLAK (F, Phe; L, Leu; A, Ala; and K, Lys) motifs following signal peptides, termed crinkling- and necrosis-inducing proteins (CRN) or Crinkler. Recently, the functional studies of CRN revealed that two functional genes, *PsCRN63* and *PsCRN115* encode proteins that induce contrasting responses when expressed in *Nicotiana benthamiana* and soybean (*Glycine max*). Silencing of the *PsCRN63* and *PsCRN115* genes in *P. sojae* stable transformants exhibited a reduction of virulence on soybean and a loss of ability to suppress host cell death and callose deposition on inoculated plants. These results suggested a role for CRN effectors in the suppression of host defense responses [152]. In future, more studies on oomycete effectors and their cognate host targets will undoubtedly explore novel plant immune pathways.

4.4. Nematode resistance genes

Plant parasitic nematodes are obligate parasites that obtain nutrition from the cytoplasm of living plant cells and comprise many species including ectoparasites and endoparasites. Nematode resistance genes are present in several crop species (Table 5) and form an important component in many breeding programs including those for tomato, potato, soybeans and cereals [276].

Table 5
Nematodes and interacting R-genes.

Pathogen	Host	Avr-gene	R-gene	Reference
<i>Meloidogyne incognita</i>	<i>Lycopersicon esculentum</i>	–	Mi	[175,239]
<i>Globodera pallida</i>	<i>Solanum tuberosum</i>	–	Hero, Gpa2	[66,227,297]
<i>Globodera rostochiensis</i>	<i>Solanum tuberosum</i>	–	Hero, Gro1–4	[310]
<i>Heterodera schachtii</i>	Beta vulgaris	–	HS1pro-1	[33]
<i>Heterodera avenae</i>	Triticum spp.	–	Cre3	[144,238]
<i>Meloidogyne incognita</i>	Capsicum annuum	–	CaMi	[37]

Numerous sources of nematode resistance have been identified and several of the responsible genes have been genetically mapped [125,276,289,309,316].

Resistance to root-knot nematode was first identified in *Lycopersicon peruvianum* Mill., a wild relative of cultivated tomato [302]. The single dominant *Mi* gene of tomato confers resistance to three major root-knot nematodes *Meloidogyne arenaria*, *Meloidogyne incognita* and *Meloidogyne javanica* [79] but it does not confer resistance to *Meloidogyne hapla*, a nematode present in overlapping geographic locations [218]. *Mi* gene encodes a protein with CC-NBS-LRR motifs [175] was introduced into cultivated tomato using embryo culture of an interspecific cross between *Lycopersicon esculentum* and *L. peruvianum* [249], followed by extensive backcrossing with *L. esculentum*. Later this gene was isolated by positional cloning approach [175]. *Mi-1* confers resistance to the root-knot nematodes. The mechanism of resistance to nematodes conferred by *Mi* appeared to involve a hypersensitive response on the part of the host [60,61]. *Mi-1* remains the only cloned root-knot nematode resistance gene [310] and the resistance mediated by *Mi-1* acts in a gene-for-gene manner.

Several common components that interact with R proteins or required for resistance gene function have been recently identified [235]. Bhattarai et al. [22] demonstrated the role of *Hsp90*, *Sgt1*, and *Rar1* in *Mi-1*-mediated aphid and nematode resistance. Studies with approaches however identified the requirement of *Rme1* gene for *Mi-1*-mediated resistance to nematodes, aphids, and whiteflies [22,163]. In addition to *Rme1*, *Mi-1* resistance requires the salicylic acid (SA) signaling pathway and mitogen activated protein kinase (MAPK) cascades [26,148]. The tomato MAPK kinases MKK2 and MAPKs LeMPK1, LeMPK2, and LeMPK3 are required for *Mi-1*-mediated aphid resistance [148]. However, their role in root-knot nematode resistance has not yet been identified.

The first nematode resistance gene to be cloned was *Hs1pro-1*, a gene from a wild relative of sugar beet conferring resistance against *Heterodera schachtii*, the beet cyst nematode [33]. *Hs1pro-1* cloned under the control of the CaMV35S promoter, was shown to confer nematode resistance to susceptible sugar beet roots transformed with *Agrobacterium rhizogenes* [65] however, the resistance mediated by *Hs1pro-1*, does not appear to involve a hypersensitive response [124]. Complementation analysis by stable potato transformation showed that the gene *Gro1-4* conferred resistance to *Globodera rostochiensis* pathotype *Ro1* and it encodes a protein of 1136 amino acids containing the TIR, NBS and LRR homology domains along with a C-terminal domain with unknown function [190]. The *Gpa2* gene that confers resistance against some isolates of the potato cyst nematode *Globodera pallida*, is a member of the

NBS-LRR-gene family and contains a possible LZ near its amino terminus. *Gpa2* is highly similar in predicted amino acid sequence to the *Rx1* gene which confers extreme resistance to *Potato Virus X* [227].

The *Cre3* gene confers a high level of resistance to the root endoparasitic nematode *Heterodera avenae* in wheat. As a result of map-based cloning of a disease resistance gene family at the *Cre3* locus, two genes related to members of the cytoplasmic NBS-LRR class of plant disease resistance genes have been analyzed. One encodes a polypeptide with a nucleotide-binding site (NBS) and a leucine rich region; this member of the disease resistance gene family is expressed in roots. The second *Cre3* gene sequence appears to be a pseudo gene, with a frame shift caused by a deletion event [144]. Based on the conserved regions of known resistance genes, an NBS-LRR-type CCN (cereal cyst nematode) resistance gene analog was isolated from the CCN resistant E-10 near isogenic lines (NILs) of wheat, designated as *CreZ*. The expression profiling of *CreZ* indicated that it was specifically expressed in the roots of resistant plants and expression levels drastically increased when the plants were inoculated with cereal cyst nematodes [322]. In addition, the wheat and barley resistance gene analogs (RGAs) contain other conserved motifs present in known resistance genes from other plants and share between 55 and 99% amino acid sequence identity to the NBS-LRR sequence at the *Cre3* locus and have been found to be associated with CCN and aphid resistance in barley [238].

In another example, a candidate root-knot nematode resistance gene (designated as *CaMi*) was isolated from the resistant pepper line PR 205 which was highly expressed in roots, leaves, and flowers, and at a lower level in stems, and not detectable at all in fruits. Transgenic plants expressing *CaMi* gene triggered a hypersensitive response (HR) as well as many necrotic cells around nematodes and thus conferred significant resistance to root-knot nematodes when compared to susceptible control plants [37].

4.5. Viral resistance genes

The majority of characterized viral resistance genes from plants fall into the NBS-LRR class of resistance genes, providing

monogenic dominant resistance (Table 6). Although, these R proteins appear to be similar, they confer resistance to highly divergent viruses. For example, *A. thaliana* *RCY1* (resistance to C strain Y1) and *HRT* (HR to turnip crinkle virus) are allelic, encode proteins that share 91% similarity [261] but confer resistance to unrelated viruses such as *cucumber mosaic virus* (CMV, a cucumovirus) and *turnip crinkle virus* (TCV, a carmovirus), respectively [253].

The viral R protein-Avr system that strongly justifies the guard hypothesis is the *HRT*-TCV pair. The TCV coat protein is the Avr determinant for *HRT*-mediated resistance responses and its interaction with a host transcription factor, TCV-interacting protein (TIP) is required for *HRT*-elicited defense responses [214]. Although, a direct interaction between *HRT* and TIP has not been reported, TCV coat protein inhibits the nuclear localization of TIP [215], however it is possible that *HRT* detects the altered cellular distribution of TIP which might therefore be the guard of the guard protein *HRT*. However knock out mutation studies [112] showed that loss of TIP does not alter HR or resistance to TCV. Moreover, the mutation in TIP neither impaired the salicylic acid-mediated induction of *HRT* expression nor the enhanced resistance conferred by overexpression of *HRT*. Noticeably, the mutation in TIP resulted in increased replication of TCV and *Cucumber mosaic virus*, suggesting that TIP may play a role in basal resistance but is not required for *HRT*-mediated signaling. Resistance to *Tomato Spotted Wilt Virus* (TSWV) in tomato is conferred by *Sw-5* gene which was introgressed from *Solanum peruvianum* into tomato, and has demonstrated broad and stable resistance [225]. The positional cloning of *Sw-5* locus was revealed that the resistance allele encodes a CC-NBS-LRR R protein and is remarkably similar to the tomato *Mi* gene for nematode resistance with the exception of four leucine zippers at the N terminus [29].

In cultivated tomato, *ToMV* (*Tomato mosaic virus*) infections are controlled by the introgressed *Tm-1*, *Tm-2* and *Tm-22* genes. The *Tm-22* resistance gene was shown to be strikingly durable [86,202] and it has been cloned and well characterized by Lanfermeijer et al. [145]. The susceptible tomato plants, which were transformed with the *Tm-22* gene, displayed resistance against *ToMV* infection and the resistance was conserved in all transgenic lines. Similarly, Rai [209],

Table 6
Viral pathogens and interacting R-genes.

Pathogen	Host	Avr-gene	R-gene	Reference
<i>Bean dwarf mosaic virus</i>	<i>Phaseolus vulgaris</i>	<i>Bdm</i>	<i>BV1 protein</i>	[76]
<i>Cucumber mosaic virus</i>	<i>Arabidopsis thaliana</i>	<i>Coat protein</i>	<i>RCY1</i>	[262]
<i>Cucumber mosaic virus</i>	<i>A. thaliana</i>	<i>Vpg (viral genome-linked protein)</i>	<i>At-eIF4E1 (cum1)</i> <i>At-eIF4G (cum2)</i>	[72,320]
<i>Lettuce mosaic virus (LMV)</i>	<i>Lettuce (Lactuca sativa)</i>	3'half of genome	<i>mo1(1), mo1(2)</i>	[183,211]
<i>Pea seed borne mosaic virus</i>	<i>Pea (Pisum sativum)</i>	<i>Vpg</i> <i>P3 and 6K1 cistron</i>	<i>sbm1</i> <i>sbm2</i>	[73,133] [118]
<i>Potato virus X</i>	<i>Solanum tuberosum</i>	<i>Coat protein</i>	<i>Rx1, Rx2</i>	[14,15,205]
<i>Potato virus Y</i>	<i>Capsicum annuum</i>	<i>VPg</i>	<i>pvr1, pvr12</i>	[129,180,228]
<i>Potato virus X</i>	<i>Solanum tuberosum</i>	<i>Nla protease</i>	<i>Ry</i>	[170]
<i>Potato virus Y</i>	<i>Solanum tuberosum</i>	–	<i>Y-1</i>	[291]
<i>Potato virus Y, Tobacco etch virus</i>	<i>Tomato (Lycopersicon spp.)</i>	<i>Vpg</i>	<i>pot-1</i>	[180]
<i>Rice yellow mottle virus</i>	<i>Oryza sativa</i>	<i>Vpg</i>	<i>eIF(iso)4G1</i>	[100]
<i>Soybean mosaic virus</i>	<i>Glycine max</i>	<i>Hc-Pro and P3 cistron</i>	<i>Rsv1</i>	[64]
<i>Tobacco etch virus</i>	<i>Arabidopsis thaliana</i>	–	<i>RTM1, RTM2</i>	[41,307]
<i>Tobacco mosaic virus</i>	<i>Solanum lycopersicon</i>	–	<i>N gene</i>	[305,306]
		<i>Replicase</i>	<i>Tm1</i>	[145]
		<i>30 kD movement protein</i>	<i>Tm2, Tm22</i>	
<i>Turnip mosaic virus,</i> <i>Turnip mosaic virus</i>	<i>Arabidopsis thaliana</i> <i>Brassica napus</i>	<i>VPg</i> <i>TuRBO1,</i> <i>TuRBO1b,</i> <i>TuRBO3,</i> <i>TuRBO4,</i> <i>TuRBO5,</i> <i>TuMV P3</i>	<i>At-eIF(iso)4E</i> <i>Cl</i>	[311] [109–111]
<i>Turnip mosaic virus</i>	<i>Capsicum annuum</i>	<i>Coat protein</i>	<i>P3</i> <i>P3</i> <i>Cl</i>	
			<i>L1, L2, L3</i>	[20,48,78]

cloned a single dominant gene *Ctv-R* present in the trifoliolate relative of Citrus, *Poncirus trifoliata* conferring broad-spectrum resistance against *Citrus tristeza virus* (CTV), a major pathogen of citrus [11,74,75,80,171,209]. Transgenic grapefruit plants carrying Citrus *Ctv-R* gene were developed and it was found that two of the candidate resistance genes, *R-2* and *R-3* were exclusively expressed resulting in either an absence of initiation of infection or its slow spread in *R-2* plant lines or an initial appearance of infection and its subsequent eradication in some *R-1* and *R-4* plant lines [209].

Seo et al. identified the TIR-NBS-LRR gene *RT4-4* involved in a viral resistance response in common bean (*Phaseolus vulgaris* cv. *Othello*) [240] which functions across two plant families. The functional analysis revealed that the *RT4-4* gene in transgenic *N. benthamiana* lines is up-regulated in a non-virus-specific manner, although *RT4-4* did not confer resistance to the reporter virus, it activated a resistance-like response (systemic necrosis) to *Cucumber Mosaic Virus* (CMV).

Recent molecular cloning of recessive resistance genes to potyviruses led to the identification of resistance genes corresponding to mutations in translation initiation factors, eukaryotic initiation factors 4E (eIF4E) and to a lesser extent, the eukaryotic initiation factor 4G (eIF4G) [204]. The *eIF4E* gene provides resistance to several Potyviridae family viruses and has been identified in the dicots, pepper (*pvr1*), pea (*sbm1*), lettuce (*mo1 (1)*, *mol (2)*), tomato (*pot1*), and melon (*nsv*) and in the monocot barley (*rym4/5*) [130,217,229]. Similarly, translation initiation factor *eIF4G* is responsible for resistance of rice to *Yellow mottle virus* [3] and in *Arabidopsis* to *Cucumber mosaic virus* and *Turnip crinkle virus* [320].

4.6. Insect resistance genes

Studies using the model plant *Arabidopsis* have contributed greatly to our understanding of R-gene mediated plant defense, especially against pathogens [103], as well as the basal defense mechanisms against aphid feeding [46,143,200,201]. Resistance to insects has been identified in various plant species since long back [18,51,62,191,206] and a number of single dominant R-genes have been mapped, and molecular markers linked to these loci have been identified [30,107,139,153,155,288,319]. The majority of these mapped genes (Table 7) are in staple crops like wheat and rice. In addition to these mapped genes, several single dominant aphid resistance genes have been identified that confer resistance to a single species of insects [213]. Cloning of number of insect resistance genes has been accelerated with the advent of high throughput molecular tools, such as genome mapping, sequencing, and gene cloning.

To date, only few insect resistance genes belonging to NBS-LRR group of plant resistance genes have been cloned and characterized. For example, The tomato *Mi-1* confers resistance to the potato aphid (*Macrosiphum euphorbiae*) and whitefly (*Bemisia tabaci*), Lettuce *Nr*-gene confers resistance to a single species of aphid

(*Nasanova ribisnigri*) [213], *Sd1* gene confers resistance rosy leaf curling aphid (*Dysaphis devecta*) in apple [219] and the melon *Vat* gene against the melon/cotton aphid *Aphis gossypii* [126,192].

Triticum aestivum resistance to Hessian fly, *Mayetiola destructor* (Say), has also been demonstrated to be a gene-for-gene mechanism [92], although no genes have been cloned yet, 26 resistance genes have been described as being effective against 13 biotypes of Hessian fly [63]. The occurrence of a hypersensitive response (HR) in case of an insect attack still remains dubious, since both presence and absence of HR have been reported in incompatible interactions between wheat and Hessian fly [84,93,308].

Recently, Klingler and co workers reported the presence of an HR response to bluegreen aphid and pea aphid in *Medicago truncatula* [138]. A single gene *AIN* was found responsible to trigger HR response against those two pathogens. However, it was also concluded that although the HR response is triggered in both cases, the resistance is conferred only to bluegreen aphid [138]. Irrespective of presence or absence of HR, a common mechanism of R-gene mediated resistance to piercing, sucking insects appears to be limited phloem-feeding [127,137,285]. A detailed description on plant–aphid interactions along with a summary of recent studies has recently been reviewed by Tagu et al. [258].

4.7. R-genes with broad range host resistance

A common strategy proposed to achieve broad-range host resistance is to modify the narrow pathogen specificity of R-gene mediated resistance. Therefore, elucidation of R protein domains that control recognition of specific pathogens and subsequent activation of the downstream defense response has been the subject of intense research [290]. The function of a particular resistance gene totally depends on the pathogen's genotype [4,47,49,132,140] but there are some resistance genes which confer resistance against a broad range of pathogens. For instance, the *Mi-1* gene in tomato confers resistance to root-knot nematodes (*Meloidogyne* spp.), potato aphid *M. euphorbiae* [175,226,239,295], whitefly *B. tabaci* [186], viruses [28], bacteria [231] and fungi [189,248]. Tomato *Pto*-overexpressing plants show resistance not only to *P. syringae* pv. tomato but also to *Xanthomonas campestris* pv. vesicatoria and to the fungal pathogen *C. fulvum* [267,314]. Similarly, the lettuce *Dm3* gene confers resistance to lettuce downy mildew (*B. lactucae*) as well as to lettuce root aphid [172]. Moreover, several other *Dm* specificities as well as resistance to lettuce root aphids have been shown to be conferred by members of the RGC2 family using RNAi approach [142,313].

5. Challenges and future directions

With the advent of high throughput techniques and efficient genomic approaches, researchers have managed to produce a large amount of experimental data in the form of ESTs, whole genome sequences, gene expression data etc. Still, the progress in understanding the functional mechanism of resistance genes has been moderate. For instance, little is known about the structural basis of pathogen recognition. Furthermore, there is still an inadequacy of a reference set of sequences to be used as model for resistance genes that usually cluster in genomic regions with a high number of homologs and pseudo genes. The difficulties in performing the plant–pathogen interaction studies pose another obstacle [70]. Nevertheless, efficacious applications are being continuously developed based on our rather finite knowledge base. For example, recently PRGdb, a web accessible open source database providing a comprehensive overview of resistance genes has been developed [232], which is definitely going to help filling some gaps in the models of the plant defense signal transduction network.

Table 7
Insects and interacting R-genes.

Pathogen	Host	Avr-gene	R-gene	Reference
<i>Macrosiphum euphorbiae</i>	<i>Lycopersicum esculentum</i>	–	<i>Mi</i>	[226]
<i>Nasanova ribisnigri</i>	<i>Lactuca sativa</i>	–	<i>Nr</i>	[285]
<i>Dysaphis devecta</i>	<i>Malus domestica</i>	–	<i>Sd1</i>	[219]
<i>Sogatella furcifera</i> , <i>Nilaparvata lugens</i>	<i>Oryza sativa</i>	–	<i>Qbp1</i> , <i>Qbp2</i>	[265]

The primary benefit of deploying resistance genes in transgenic technology is its ability to overcome the fertility restraints for the dispersal of genes originating from a different species; for example, *Bs2* resistance gene was identified originally in pepper and its resistance has been found durable in the field against isolates of *B. campestris* [259]. Another advantage of resistance genes usage in transgenic technology is that it allows introducing several different resistance gene alleles, each effective against a single pathogen species or race, into semi-elite and elite germplasm. Moreover, most resistance genes exhibit exquisite recognition specificity and to overcome this deficit, new resistance genes have been created in the laboratory through single point mutations, which are autoactivating [91]. Cloned resistance and effector genes can be used in combination to promote acquired resistance. The rapid activation of localized defense responses at the site of pathogen infection, often associated with an HR, is the most prevalent and effective mechanism used by plants to minimize pathogen attack. By combining R and Avr gene expression in a single plant genotype, it is possible to engineer a 'trigger' for HR [230].

Efficient application of functional genomics tools for disease resistance could not only help us better understand the plant defense signaling, it could reveal novel insights on the interactions between these signaling pathways and other plant processes [38,210]. Even though, the progress toward the overall plant defense mechanism studies is going on at a considerable pace, it would still be imprudent to expect a great breakthrough in impervious broad-spectrum resistance. However, it is judicious to anticipate an array of highly useful tools aided by other control measures providing adequate protection in certain contexts.

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