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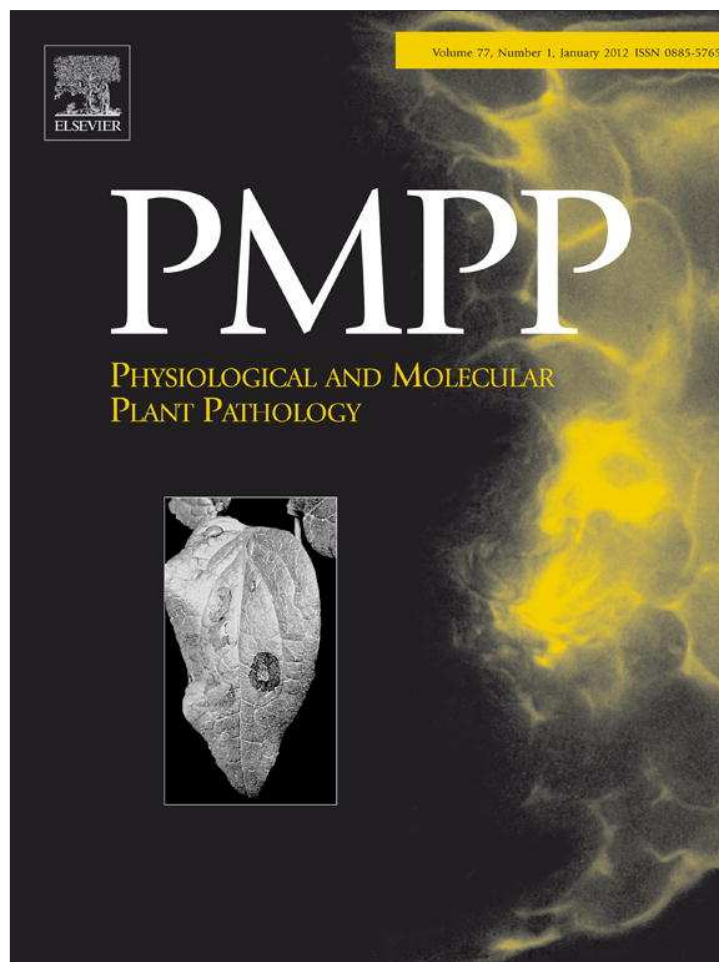
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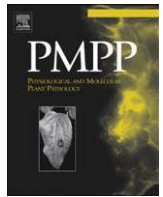
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Plant disease resistance genes: Current status and future directions

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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

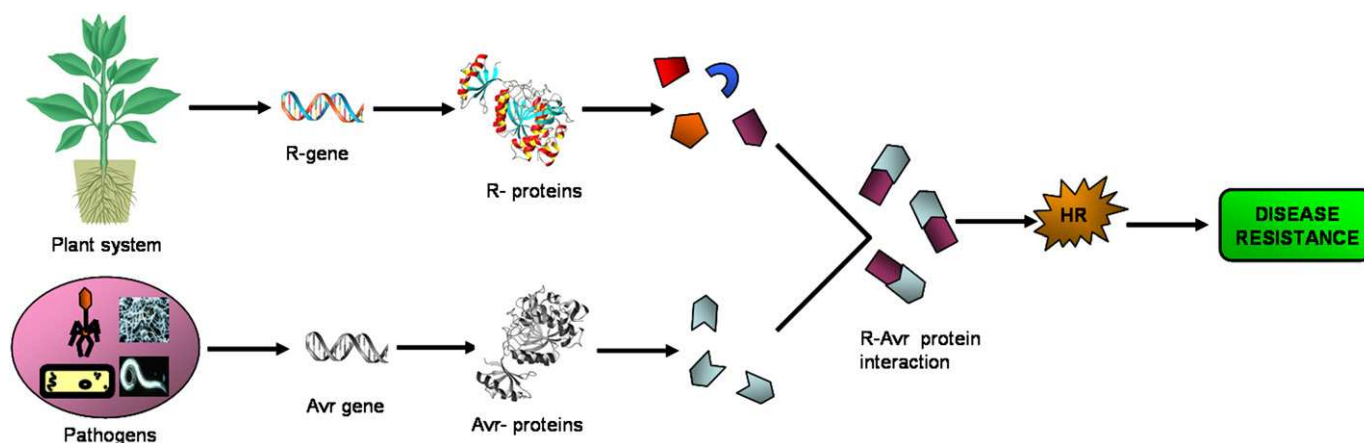


Fig. 1. Plant pathogen interaction and development of disease resistance.

order to create an appropriate environment. Resistance is initiated when the R protein detects an attack of its guard 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 (guard) 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 (guard) 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

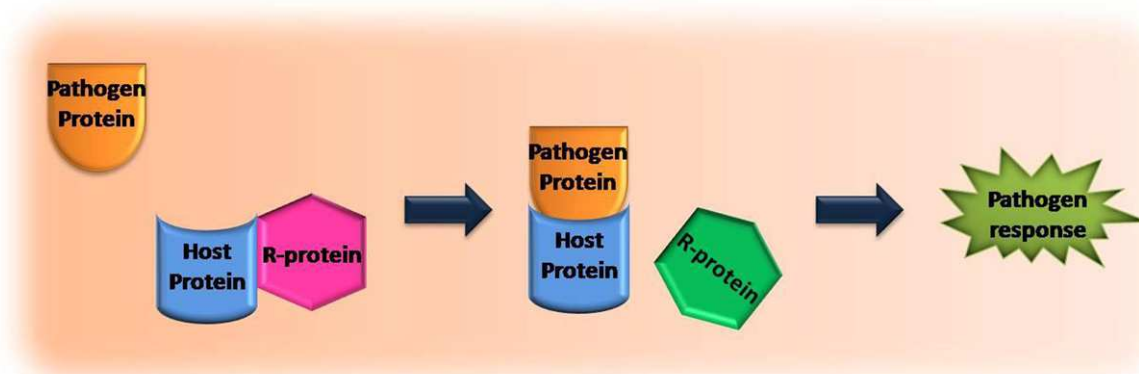


Fig. 2. Guard hypothesis – the plant R proteins (guard) are associated with the endogenous host protein (guard) which are common target proteins for the pathogens. The interaction of effector pathogen proteins with the host proteins, causes a change in their structure which is then recognized by the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

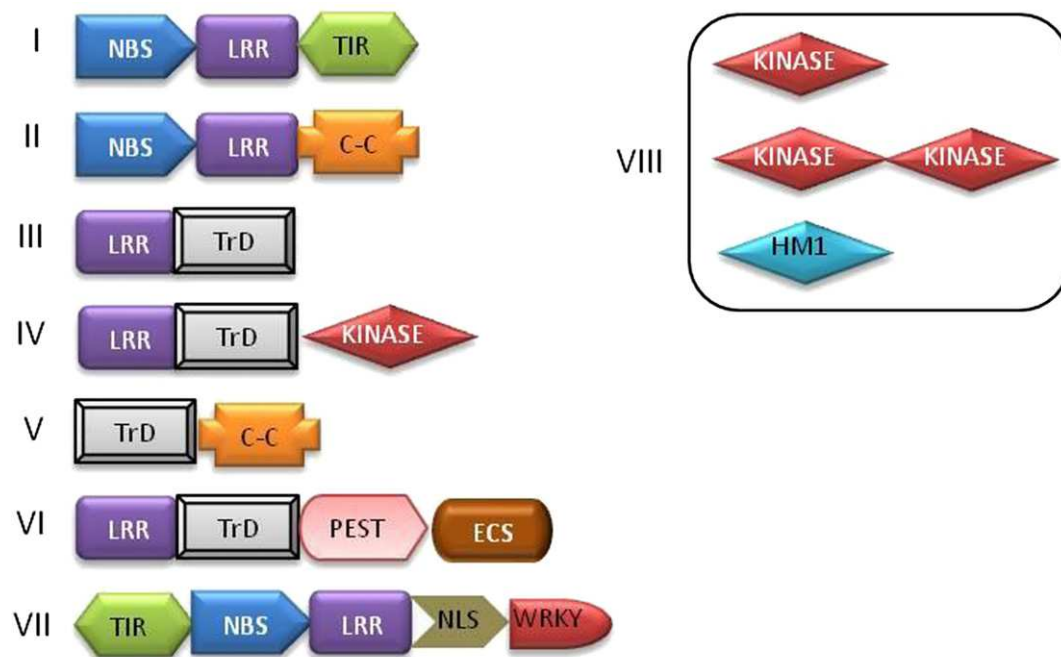


Fig. 3. Major classes of plant resistance (R) genes based on the arrangement of the functional domains. LRR – Leucine rich repeats; NBS – Nucleotide-binding site; TIR/Toll/Interleukin-1- receptors; C-C – Coiled coil; TrD – Transmembrane domain; PEST – Protein degradation domain (proline-glycine-serine-threonine); 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	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 AvrL567 genes, whose products are recognized by the L5, L6, and L7	N	
<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>Perenospora 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>	Ipi0, Ipi1, 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-04*) [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>Lycopersicum 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>	<i>Beta vulgaris</i>	–	HS1pro-1	[33]
<i>Heterodera avenae</i>	<i>Triticum spp.</i>	–	Cre3	[144,238]
<i>Meloidogyne incognita</i>	<i>Capsicum annuum</i>	–	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 *Lycopersicum 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 *Lycopersicum 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</i> protein	[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-elf4E1 (cum1)</i> <i>At-elf4G (cum2)</i>	[72,320]
<i>Lettuce mosaic virus (LMV)</i>	<i>Lettuce (Lactuca sativa)</i>	<i>3'half of genome</i>	<i>mo1(1), mo1(2)</i>	[183,211]
<i>Pea seed borne mosaic virus</i>	<i>Pea (Pisum sativum)</i>	<i>Vpg</i>	<i>sbm1</i>	[73,133]
		<i>P3 and 6K1 cistron</i>	<i>sbm2</i>	[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>elF(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>Arabidopsis thaliana</i>	<i>VPg</i>	<i>At-elf(iso)4E</i>	[311]
<i>Turnip mosaic virus</i>	<i>Brassica napus</i>	<i>TuRBO1,</i> <i>TuRBO1b,</i> <i>TuRBO3,</i> <i>TuRBO4,</i> <i>TuRBO5,</i> <i>TuMV P3</i>	<i>Cl</i>	[109–111]
<i>Turnip mosaic virus</i>	<i>Capsicum annumm</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 devectora*) 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>Lycopersicon esculentum</i>	–	<i>Mi</i>	[226]
<i>Nasanova ribisnigri</i>	<i>Lactuca sativa</i>	–	<i>Nr</i>	[285]
<i>Dysaphis devectora</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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References

- [1] Abramovitch RB, Kim YJ, Chen S, Dickman MB, Martin GB. Pseudomonas type III effector *AvrPtoB* induces plant disease susceptibility by inhibition of host programmed cell death. *EMBO J* 2003;22:60–9.
- [2] Acciarri N, Rotino GL, Tamiotti G, Valentino D, Voltattorni S, Sabatini E. Molecular markers for *Ve1* and *Ve2* Verticillium resistance genes from Italian tomato germplasm. *Plant Breed* 2007;126:617–21.
- [3] Albar L, Bangratz-Reyser M, Hebrard E, Ndjiondjop MN, Jones M, Ghesquiere A. Mutations in the eIF (iso)4G translation initiation factor confer high resistance of rice to Rice yellow mottle virus. *Plant J* 2006;47:417–26.
- [4] Alfano JR, Collmer A. Bacterial pathogens in plants: life up against the wall. *Plant Cell* 1996;8:1683–98.
- [5] Allen RL, Bittner-Eddy PD, Grenville-Briggs LJ, Meitz JC, Rehmany AP, Rose LE, et al. Host–parasite co-evolutionary conflict between *Arabidopsis* and downy mildew. *Science* 2004;306:1957–60.
- [6] Armstrong MR, Whisson SC, Pritchard L, Bos JIB, Venter E, Avrova AO, et al. An ancestral oomycete locus contains late blight avirulence gene *Avr3a*, encoding a protein that is recognized in the host cytoplasm. *Proc Natl Acad Sci USA* 2005;102:7766–71.
- [7] Austin MJ, Muskett P, Kahn K, Feys BJ, Jones JD, Parker JE. Regulatory role of *SGT1* in early R-gene-mediated plant defenses. *Science* 2002;295(5562):2032–3.
- [8] Baker CM, Chitrakar R, Obulareddy N, Panchal S, Williams P, Melotto M. Molecular battles between plant and pathogenic bacteria in the phyllosphere. *Braz J Med Biol Res* 2010;43:698–704.
- [9] Baldauf SL, Roger AJ, Wenk-Siefert I, Doolittle WF. A kingdom-level phylogeny of eukaryotes based on combined protein data. *Science* 2000;290:972–7.
- [10] Ballvora A, Ercolano MR, Weiß J, Meksem K, Bormann C, Oberhagemann P, et al. The *R1* gene for potato resistance to late blight (*Phytophthora infestans*) belongs to the leucine zipper/NBS/LRR class of plant resistance genes. *Plant J* 2002;30:361–71.
- [11] Bar-Joseph M, Marcus R, Lee A. The continuous challenge of citrus tristeza virus control. *Annu Rev Phytopathol* 1989;27:291–316.
- [12] Belfanti E, Silfverberg-Dilworth E, Tartarini S, Patocchi A, Barbieri M, Zhu J, et al. The *HcrVf2* gene from a wild apple confers scab resistance to a transgenic cultivated variety. *Proc Natl Acad Sci USA* 2004;101:886–90.
- [13] Belkadir Y, Subramaniam R, Dangl JL. Plant disease resistance protein signaling: NBS- LRR proteins and their partners. *Curr Opin Plant Biol* 2004;7:391–9.
- [14] Bendahmane A, Kanyuka K, Rouppe van der Voort J, Van der Vossen E, Baulcombe DC. A high resolution molecular map around the Rx locus of potato: analysis of a complex locus in a tetraploid background. *Theor Appl Genet* 1999;98:679–89.
- [15] Bendahmane A, Kohm B, Dedi C, Baulcombe D. The coat protein of potato virus X is a strain-specific elicitor of Rx-mediated virus resistance in potato. *Plant J* 1995;8:933–41.
- [16] Bendahmane A, Querci M, Kanyuka K, Baulcombe DC. *Agrobacterium* transient expression system as a tool for disease resistance genes isolation: application to Rx2 locus in potato. *Plant J* 2000;21(1):73–81.
- [17] Bent AF, Kunkel BN, Dahlbeck D, Brown KL, Schmidt R, Giraudat J, et al. RPS2 of *Arabidopsis thaliana*: a leucine-rich repeat class of plant disease resistance genes. *Science* 1994;265:1856–60.
- [18] Bent AF. Plant disease resistance: function meets structure. *Plant Cell* 1996;8:1757–71.
- [19] Bent AF, Mackey D. Elicitors, effectors, and R genes: the new paradigm and a lifetime supply of questions. *Annu Rev Phytopathol* 2007;45:399–436.
- [20] Berzal-Herranz A, de la Cruz A, Tenllado F, Diaz-Ruiz JR, Lopez L, Sanz AI, et al. The Capsicum *L3* gene-mediated resistance against the tobamoviruses is elicited by the coat protein. *Virology* 1995;209:498–505.
- [21] Bhaskar PB, Raasch JA, Kramer LC, Neumann P, Wielgus SM, Austin-Phillips S, et al. SGT1, but not Rar1, is essential for the RB-mediated broad-spectrum resistance to potato late blight. *BMC Plant Biol* 2008;8:8.
- [22] Bhattarai KK, Li Q, Liu Y, Dinesh-Kumar SP, Kaloshian I. The *Mi-1*-mediated pest resistance requires Hsp90 and SGT1. *Plant Physiol* 2007;144:312–23.
- [23] Bittner-Eddy PD, Crute IR, Holub EB, Beynon JL. RPP13 is a simple locus in *Arabidopsis thaliana* for alleles that specify downy mildew resistance to different avirulence determinants in *Peronospora parasitica*. *Plant J* 2000;21:177–88.
- [24] Bos JL, Kanneganti TD, Young C, Cakir C, Huitema E, Win J, et al. The C-terminal half of *Phytophthora infestans* RXLR effector AVR3a is sufficient to trigger R3a-mediated hypersensitivity and suppress INF1-induced cell death in *Nicotiana benthamiana*. *Plant J* 2006;48:165–76.
- [25] Botella MA, Parker JE, Frost LN, Bittner-Eddy PD, Beynon JL, Daniels MJ, et al. Three genes of the *Arabidopsis* RPP1 complex resistance locus recognize distinct *Peronospora parasitica* avirulence determinants. *Plant Cell* 1998;10:1847–60.
- [26] Branch C, Hwang CF, Navarre DA, Williamson VM. Salicylic acid is part of the Mi-1- mediated defense response to root-knot nematode in tomato. *Mol Plant-Microbe Int* 2004;17:351–6.
- [27] Brande BH, Wulff H, Thomas CM, Smoker M, Grant M, Jones JDG. Domain swapping and gene shuffling identify sequences required for induction of an Avr-dependent hypersensitive response by the tomato Cf-4 and Cf-9 Proteins. *The Plant Cell* 2001;13:255–72.
- [28] Brommonschenkel SH, Frary A, Tanksley SD. The broad-spectrum tospovirus resistance gene Sw-5 of tomato is a homolog of root-knot nematode resistance gene *Mi*. *Mol Plant-Microbe Int* 2000;13:1130–8.
- [29] Brommonschenkel SH, Frary A, Tanksley SD. The broad-spectrum tospovirus. *Annu Rev Phytopathol* 2000;43:581–621.
- [30] Brotman Y, Silberstein I, Kovalski I, Périn C, Dogimont C, Pitrat M, et al. Resistance gene homologues in melon are linked to genetic loci conferring disease and pest resistance. *Theor Appl Genet* 2002;104:1055–63.
- [31] Brueggeman R, Rostoks N, Kudrna D, Kilian A, Han F, Chen J, et al. The barley stem rust- resistance gene Rpg1 is a novel disease-resistance gene with homology to receptor kinases. *Proc Natl Acad Sci USA* 2002;99:9328–33.
- [32] Büschges R, Hollricher K, Panstruga R, Simons G, Wolter M, Frijters A, et al. The barley *Mlo* gene: a novel control element of plant pathogen resistance. *Cell* 1997;88:695–705.
- [33] Cai D, Kleine M, Kifle S, Harloff HJ, Sandal NN, Marcker KA, et al. Positional cloning of a gene for nematode resistance in sugar beet. *Science* 1997;275:832–4.
- [34] Cavalier-Smith T, Chao EE. Phylogeny and megasystematics of phagotrophic heterokonts (kingdom Chromista). *J Mol Evol* 2006;62:388–420.
- [35] Cavalier-Smith T. Membrane heredity and early chloroplast evolution. *Trends Plant Sci* 2000;5:174–82.
- [36] Champouret N, Bouwmeester K, Rietman H, van der Lee T, Maliepaard C, Heupink A, et al. *Phytophthora infestans* isolates lacking class I ipiO variants are virulent on Rpi-blb1 potato. *Mol Plant-Microbe Int* 2009;22:1535–45.
- [37] Chen RG, Li HX, Zhang LY, Zhang JH, Xiao JH, Ye ZB. CaMi, a root-knot nematode resistance gene from hot pepper (*Capsicum annuum* L.) confers nematode resistance in tomato. *Plant Cell Rep* 2007;26:895–905.
- [38] Chen W, Provart NJ, Glazebrook J, Katagiri F, Chang HS, Eulgem T, et al. Expression profile matrix of *Arabidopsis* transcription factor genes suggests their putative functions in response to environmental stresses. *Plant Cell* 2002;14:559–74.
- [39] Chern MS, Fitzgerald HA, Yadav RC, Canlas PE, Dong X, Ronald PC. Evidence for a disease-resistance pathway in rice similar to the NPR1-mediated signaling pathway in *Arabidopsis*. *Plant J* 2001;27:101–13.

- [40] Chisholm ST, Coaker G, Day B, Staskawicz BJ. Host-microbe interactions: shaping the evolution of the plant immune response. *Cell* 2006;124:803–14.
- [41] Chisholm ST, Mahajan SK, Whitham SA, Yamamoto ML, Carrington JC. Cloning of the *Arabidopsis* RTM1 gene, which controls restriction of longdistance movement of Tobacco etch virus. *Proc Natl Acad Sci USA* 2000;97:489–94.
- [42] Chu Z, Yuan M, Yao J, Ge X, Yuan B, Xu C, et al. Promoter mutations of an essential gene for pollen development result in disease resistance in rice. *Gene Dev* 2006;20:1250–5.
- [43] Collins N, Drake J, Ayliffe M, Sun Q, Ellis J, Hulbert S, et al. Molecular characterization of the maize Rp1-D rust resistance haplotype and its mutants. *Plant Cell* 1999;11:1365–76.
- [44] Collmer A. Determinants of pathogenicity and avirulence in plant pathogenic bacteria. *Curr Opin Plant Biol* 1998;1:329–35.
- [45] Cooley MB, Pathirana S, Wu HJ, Kachroo P, Klessig DF. Members of the *Arabidopsis* HRT/RPP8 family of resistance genes confer resistance to both viral and oomycete pathogens. *Plant Cell* 2000;12:663–76.
- [46] Couldridge C, Newbury HJ, Ford-Lloyd B, Bale J, Pritchard J. Exploring plant responses to aphid feeding using a full *Arabidopsis* microarray reveals a small number of genes with significantly altered expression. *Bull Entomol Res* 2007;97:523–32.
- [47] Dangl JL, Dietrich RA, Richberg MH. Death don't have no mercy: cell death programs in plant-microbe interactions. *Plant Cell* 1996;8:1793–807.
- [48] de la Cruz A, Lopez L, Tenllado F, Diaz- Ruiz JR, Sanz AI, Vaquero C, et al. The coat protein is required for the elicitation of the Capsicum L2gene-mediated resistance against the tobamoviruses. *Mol Plant Microbe Interact* 1997;10: 107–13.
- [49] de Wit PJGM. Molecular characterization of gene-for-gene systems in plant-fungus interactions and application of avirulence genes in control of plant pathogens. *Ann Rev Phytopathol* 1992;30:391–418.
- [50] Debener T, Lehnackers H, Arnold M, Dangl JL. Identification and molecular mapping of a single *Arabidopsis thaliana* locus determining resistance to a phytopathogenic *Pseudomonas syringae* isolate. *Plant J* 1991;1:289–302.
- [51] Dempsey DA, Silva H, Klessig DF. Engineering disease and pest resistance in plants. *Trends Microbiol* 1998;6:54–61.
- [52] Deslandes L, Olivier J, Peeters N, Feng DX, Khounlotham M, Boucher C, et al. Physical interaction between RRS1-R, a protein conferring resistance to bacterial wilt, and PopP2, a type III effector targeted to the plant nucleus. *Proc Natl Acad Sci USA* 2003;100:8024–9.
- [53] Deslandes L, Olivier J, Soulieres F, Hirsch J, Feng DX, Bittner-Eddy P, et al. Resistance to *Ralstonia solanacearum* in *Arabidopsis thaliana* is conferred by the recessive RRS1-R gene, a member of a novel family of resistance genes. *Proc Natl Acad Sci USA* 2002;99:2404–9.
- [54] Desvaux M, Parham NJ, Scott-Tucker A, Henderson IR. The general secretory pathway: a general misnomer? *Trends Microbiol* 2004;12:306–9.
- [55] Dixon MS, Hatzixanthis K, Jones DA, Harrison K, Jones JDG. The tomato Cf-5 disease resistance gene and six homologs show pronounced allelic variation in leucine-rich repeat copy number. *Plant Cell* 1998;10:1915–25.
- [56] Dodds PN, Lawrence GJ, Catanzariti AM, Teh T, Wang CIA, Ayliffe MA, et al. Direct protein interaction underlies gene-for-gene specificity and coevolution of the flax resistance genes and flax rust avirulence genes. *Proc Natl Acad Sci USA* 2006;103(23):8888–93.
- [57] Dodds PN, Lawrence GJ, Ellis JG. Contrasting modes of evolution acting on the complex N locus for rust resistance in flax. *Plant J* 2001;27:439–53.
- [58] Dong S, Qutob D, Tedman-Jones J, Kuflu K, Wang Y, Tyler BM. The *Phytophthora sojae* avirulence locus Avr3c encodes a multi-copy RXLR effector with sequence polymorphisms among pathogen strains. *PLoS One* 2009; 4(5):e5556.
- [59] Dou D, Kale SD, Wang X, Chen Y, Wang Q, Wang X, et al. Conserved C-terminal motifs required for avirulence and suppression of cell death by *Phytophthora sojae* effector Avr1b. *Plant Cell* 2008;20:1118–33.
- [60] Dropkin VH. The necrotic reaction tomato and other hosts resistant to *Meloidogyne*: reversal by temperature. *Phytopathology* 1969;59:1632–7.
- [61] Dropkin VH, Helgesonj P, Upper CD. The hypersensitivity reaction of tomatoes resistant to *Meloidogyne incoqnita*: reversal by cytokinins. *J Nematol* 1969;1:55–61.
- [62] Dunwell JM. Transgenic approaches to crop improvement. *J Exp Bot* 2000;51: 487–96.
- [63] Dweikat I, Ohm H, Patterson F, Cambron S. Identification of RAPD markers for 11 Hessian fly resistance genes in wheat. *Theor Appl Genet* 1997;94:419–23.
- [64] Eggenburger AL, Hill JH. Analysis of resistance-breaking determinants of soybean mosaic virus (Astr.). *Phytopathology* 1997;87:27.
- [65] Ellis J, Jones D. Structure and function of proteins controlling strain-specific pathogen resistance in plants. *Curr Opin Plant Biol* 1998;1:288–93.
- [66] Ernst K, Kumar A, Krisleit D, Kloos DU, Phillips MS, Ganai MW, et al. Broad-spectrum potato cyst nematode-resistance gene (Hero) from tomato is the only member of a large gene family of NBS LRR-genes with an unusual amino acid repeat in the LRR region. *Plant J* 2002;31:127–36.
- [67] Flor HH. Current status of the gene-for-gene concept. *Annu Rev Phytopathol* 1971;9:275–98.
- [68] Fradin EF, Zhang Z, Ayala JC, Castroverde CDM, Nazar RN, Robb J, et al. Genetic dissection of *Verticillium* wilt resistance mediated by tomato Ve1. *Plant Physiol* 2009;150:320–32.
- [69] Freeman BC, Beattie GA. An Overview of plant defenses against pathogens and herbivores. *The Plant Health Instructor*; 2008. doi:10.1094/PHI-I-2008-0226-01.
- [70] Friedman AR, Baker BJ. The evolution of resistance genes in multi-protein plant resistance systems. *Curr Opin Genet Dev* 2007;17:493–9.
- [71] Galan JE, Collmer A. Type III secretion machines: bacterial devices for protein delivery into host cells. *Science* 1999;284:1322–8.
- [72] Gallois JL, Charron C, Sánchez F, Pagny G, Houvenaghel MC, Moretti A, et al. Single amino acid changes in the turnip mosaic virus viral genome-linked protein (VPg) confer virulence towards *Arabidopsis thaliana* mutants knocked out for eukaryotic initiation factors *elF(iso)4E* and *elF(iso)4G*. *J Gen Virol* 2010;91:288–93.
- [73] Gao Z, Johansen E, Eyers S, Thomas CL, Noel Ellis TH, Maule AJ. The potyvirus recessive resistance gene, *sbm1*, identifies a novel role for translation initiation factor *elF4E* in cell-to-cell trafficking. *Plant J* 2004;40: 376–85.
- [74] Garnsey SM, Lee RF, Tristeza. In: Whiteside JO, Garnsey SM, Timmer LW, editors. Compendium of citrus diseases. Amer Phytopath Soc Press; 1998. p. 48–50.
- [75] Garnsey SM, Barrett HC, Hutchinson DJ. Identification of citrus tristeza virus resistance in citrus relatives and potential applications. *Phytophylactica* 1987;19:187–91.
- [76] Garrido-Ramirez ER, Sudarshana MR, Lucas WJ, Gilbertson RL. Bean dwarf mosaic virus BV1 protein is a determinant of the hypersensitive response and avirulence in *Phaseolus vulgaris*. *Mol Plant Microbe Interact* 2000;13: 1184–94.
- [77] Gassmann W, Hinsch ME, Staskawicz B. The *Arabidopsis* RPS4 bacterial-resistance gene is a member of the TIR-NBSLRR family of disease-resistance genes. *Plant J* 1999;20:265–77.
- [78] Gilardi P, Garcia-Luque I, Serra MT. Pepper mild mottle virus coat protein alone can elicit the Capsicum spp. L gene-mediated resistance. *Mol Plant Microbe Interact* 1998;11:1253–7.
- [79] Gilbert JC, McGuire DC. Inheritance of resistance to severe root-knot from *Meloidogyne incognita* in commercial-type tomatoes. *Proc Am Soc Hort Sci* 1956;68:437–42.
- [80] Gmitter FG, Xiao SY, Huang S, Hu XL, Garnsey SM, Deng Z. A localized linkage map of citrus tristeza virus resistance gene region. *Theor Appl Genet* 1996; 92:688–95.
- [81] Govers F, Gijzen M. Phytophthora genomics: the plant destroyers' genome decoded. *Mol Plant-Microbe Int* 2006;19:1295–301.
- [82] Grant MR, Godiard L, Straube E, Ashfield T, Lewald J, Sattler A, et al. Structure of the *Arabidopsis* RPM1 gene enabling dual specificity disease resistance. *Science* 1995;269:843–6.
- [83] Grouffaud S, Stephen C, Whisson P, Birch RJ, van West P. Towards an understanding on how RxLR-effector proteins are translocated from oomycetes into host cells. *Fungal Biol Rev* 2010;24:27–36.
- [84] Grover PBJ. Hypersensitive response of wheat to the Hessian fly. *Entomol Exp Appl* 1995;74:283–94.
- [85] Gu K, Yang B, Tian D, Wu L, Wang D, Sreekala C, et al. R-gene expression induced by a type-III effector triggers disease resistance in rice. *Nature* 2005; 435:1122–5.
- [86] Hall TJ. Resistance at the *Tm-2* locus in the tomato to tomato mosaic virus. *Euphytica* 1980;29:189–97.
- [87] Halterman DA, Chen Y, Sopee J, Berduo-Sandoval J, Sánchez-Pérez A. Competition between *Phytophthora infestans* effectors leads to increased aggressiveness on plants containing broad-spectrum late blight resistance. *PLoS ONE* 2010;5(5):e10536.
- [88] Halterman DA, Fusheng W, Wise RP. Powdery mildew-Induced *Mla* mRNAs are alternatively spliced and contain multiple upstream open reading frames. *Plant Physiol* 2003;131:558–67.
- [89] Hammond-Kosack KE, Jones JDG. Inducible plant defense mechanisms and resistance gene function. *Plant Cell* 1996;8:1773–91.
- [90] Hammond-Kosack KE, Tang SJ, Harrison K, Jones JDG. The tomato Cf-9 disease resistance gene functions in tobacco and potato to confer responsiveness to the fungal avirulence gene product Avr9. *Plant Cell* 1998;10: 1251–66.
- [91] Hammond-Kosack KE, Kanyuka K. Resistance genes (R genes) in plants. *eLS*; 2007.
- [92] Hatchett JH, Gallun RL. Genetics of the ability of the Hessian fly, *Mayetiola destructor*, to survive on wheat having different genes for resistance. *Ann Entomol Soc Am* 1970;63:1400–7.
- [93] Hatchett JH, Sears RG, Cox TH. Inheritance of resistance to Hessian fly in rye and in wheat-rye translocation lines. *Crop Sci* 1993;33:730–4.
- [94] He SY. Type III protein secretion systems in plant and animal pathogenic bacteria. *Annu Rev Phytopathol* 1998;36:363–92.
- [95] Heath MC. Nonhost resistance and nonspecific plant defenses. *Curr Opin Plant Biol* 2000;3:315–9.
- [96] Heath MC. Hypersensitive response-related death. *Plant Mol Biol* 2000;44: 321–34.
- [97] Heath MC. Evolution of plant resistance and susceptibility to fungal invaders. *Can J Plant Pathol* 1987;9:389–97.
- [98] Heath MC. Nonhost resistance in plants to microbial pathogens. In: Ezekowitz RAB, Hoffmann JA, editors. Infectious disease: innate immunity. Totowa, NJ: Humana Press; 2002. p. 47–57.
- [99] Hein I, Barciszewska-Pacak M, Hrubikova K, Williamson S, Dinesen M, Soenderby IE, et al. Virus-induced gene silencing-based functional characterization of genes associated with powdery mildew resistance in barley. *Plant Physiol* 2005;138:2155–64.

- [100] Hébrard E, Poulicard N, Gérard C, Traoré O, Wu HC, Albar L, et al. Direct interaction between the Rice yellow mottle virus (RYMV) VPg and the central domain of the rice eIF(iso)4G1 factor correlates with rice susceptibility and RYMV virulence. *Mol Plant Microbe Interact* 2010;23(11): 1506–13.
- [101] Hinsch M, Staskawicz BJ. Identification of a new *Arabidopsis* disease resistance locus, RPS4, and cloning of the corresponding avirulence gene, AvrRps4, from *Pseudomonas syringae* pv. pisi. *Mol Plant-Microbe Int* 1996;9: 55–61.
- [102] Hoffman T, Schmidt JS, Zheng X, Bent AF. Isolation of ethylene-insensitive soybean mutants that are altered in pathogen susceptibility and gene-for-gene disease resistance. *Plant Physiol* 1999;119:935–50.
- [103] Horvath H, Rostoks N, Brueggeman R, Steffenson B, von Wettstein Diter, Kleinhofs A. Genetically engineered stem rust resistance in barley using the Rpg1 gene. *Proc Natl Acad Sci USA* 2003;100:364–9.
- [104] Huang S, van der Vossen EA, Kuang H, Vleeshouwers VG, Borm TJ, van Eck HJ, et al. Comparative genomics enabled the isolation of blight resistance gene in potato. *Plant J* 2005;42:251–61.
- [105] Hubert DA, Tornero P, Belkhadir Y, Krishna P, Takahashi A, Shirasu K, et al. Cytosolic HSP90 associates with and modulates the *Arabidopsis* RPM1 disease resistance protein. *EMBO J* 2003;22:5679–89.
- [106] Iyer AS, McCouch SR. The rice bacterial blight resistance gene xa5 encodes a novel form of disease resistance. *Mol Plant Microbe Interact* 2004;17: 1348–54.
- [107] Jena KK, Pasalu IC, Rao YK, Varalaxmi Y, Krishnaiah K, Khush GS, et al. Molecular tagging of a gene for resistance to brown planthopper in rice (*Oryza sativa* L.). *Euphytica* 2002;129:81–8.
- [108] Jenner C, Hitchin E, Mansfield J, Walters K, Betteridge P, Taylor J. Gene-for-gene interactions between *Pseudomonas syringae* pv. phaseolicola and Phaseolus. *Mol Plant Microbe Interact* 1991;4:553–62.
- [109] Jenner CE, Sanchez F, Nettleship SB, Foster GD, Ponz F, Walsh JA. The cylindrical inclusion gene of Turnip mosaic virus encodes a pathogenic determinant to the Brassica resistance gene TuRB01. *Mol Plant Microbe Interact* 2000;13:1102–8.
- [110] Jenner CE, Tomimura K, Ohshima K, Hughes SL, Walsh JA. Mutations in Turnip mosaic virus P3 and cylindrical inclusion proteins are separately required to overcome two Brassica napus resistance genes. *Virology* 2002; 300:50–9.
- [111] Jenner CE, Wang X, Tomimura K, Ohshima K, Ponz F, Walsh JA. The dual role of the potyvirus P3 protein of Turnip mosaic virus as a symptom and avirulence determinant in Brassicas. *Mol. Plant Microbe Interact* 2003;16: 777–84.
- [112] Jeong RD, Chandra Shekara AC, Kachroo A, Klessig DF, Kachroo P. HRT-mediated hypersensitive response and resistance to turnip crinkle virus in *Arabidopsis* does not require the function of TIP, the presumed guard cell protein. *Mol Plant-Microbe Int* 2008;21:1316–24.
- [113] Jia Y, McAdams SA, Bryan GT, Hershey HP, Valent B. Direct interaction of resistance gene and avirulence gene products confers rice blast resistance. *EMBO J* 2000;19:4004–14.
- [114] Jiang RH, Weide R, van de Vondervoort PJ, Govers F. Amplification generates modular diversity at an avirulence locus in the pathogen *Phytophthora*. *Genome Res* 2006;16:827–40.
- [115] Jiang RHY, Tripathy S, Govers F, Tyler BM. RXLR effector reservoir in two *Phytophthora* species is dominated by a single rapidly evolving superfamily with more than 700 members. *Proc Natl Acad Sci USA* 2008;105: 4874–9.
- [116] Jiang GH, Xia ZH, Zhou YL, Wan J, Li DY, Chen RS, et al. Testifying the rice bacterial blight resistance gene xa5 by genetic complementation and further analyzing xa5 (Xa5) in comparison with its homolog TFL1Agamma1. *Mol Genet Genomics* 2006;275:354–66.
- [117] Johal GS, Briggs SP. Reductase activity encoded by the HM1 disease resistance gene in maize. *Science* 1992;258:985–7.
- [118] Johansen IE, Lund OS, Hjulsgaard CK, Laursen J. Recessive resistance in *Pisum sativum* and potyvirus pathotype resolved in a gene-for-cistron correspondence between host and virus. *J Virol* 2001;75:6609–14.
- [119] Jones DA, Jones JDG. The role of leucine rich repeat proteins in plant defenses. *Adv Bot Res Inc Adv Plant Pathol* 1997;24:120–7.
- [120] Jones DA, Thomas CM, Hammond-Kosack KE, Balint-Kurti PJ, Jones JDG. Isolation of the tomato Cf-9 gene for resistance to *Cladosporium fulvum* by transposon tagging. *Science* 1994;266:789–93.
- [121] Jones JD. Putting knowledge of plant disease resistance genes to work. *Curr Opin Plant Biol* 2001;4:281–7.
- [122] Jones JDG, Dangl JL. The plant immune system. *Nature* 2006;444:323–9.
- [123] Joosten MH, Cozijnsen TJ, De Wit PJ. Host resistance to a fungal tomato pathogen lost by a single base-pair change in an avirulence gene. *Nature* 1994;367:384–6.
- [124] Jung C, Cai D, Kleine M. Engineering nematode resistance in crop species. *Trends Plant Sci* 1998;3:266–71.
- [125] Jung C. A singular R-gene doubles up pest resistance. *Nat Biotechnol* 1998; 16:1315–6.
- [126] Kaloshian I. Gene of gene disease resistance: breeding insect pest and pathogen defense. *J Chem Ecol* 2004;30:2419–38.
- [127] Kaloshian I, Kinsey MG, Williamson VM, Ullman DE. Mi-mediated resistance against the potato aphid *Macrosiphum euphorbiae* (Hemiptera: aphididae) limits sieve element ingestion. *Environ Entomol* 2000;29:690–5.
- [128] Kamoun S. A catalogue of the effector secretome of plant pathogenic oomycetes. *Annu Rev Phytopathol* 2006;44:41–60.
- [129] Kang BC, Yeam I, Frantz JD, Murphy JF, Jahn MM. The pvr1 locus in pepper encodes a translation initiation factor eIF4E that interacts with Tobacco etch virus VPg. *Plant J* 2005;42:392–405.
- [130] Kang BC, Yeam I, Jahn MM. Genetics of plant virus resistance. *Annu Rev Phytopathol* 2005;43:581–621.
- [131] Kawchuk LM, Hachey J, Lynch DR, Kulcsar F, van Rooijen G, Waterer DR, et al. Tomato Ve disease resistance genes encode cell surface-like receptors. *Proc Natl Acad Sci USA* 2001;98:6511–5.
- [132] Keen NT. Gene-for-gene complementarity in plant-pathogen interactions. *Annu Rev Genet* 1990;24:447–63.
- [133] Keller KE, Johansen IE, Martin RR, Hampton RO. Potyvirus genomelinked protein (VPg) determines Pea seedborne mosaic virus pathotype-specific virulence in *Pisum sativum*. *Mol Plant Microbe Interact* 1998;11:124–30.
- [134] Khang CH, Park SY, Lee YH, Valent B, Kang S. Genome organization and evolution of the AVR-Pita avirulence gene family in the *Magnaporthe grisea* Species complex. *Mol Plant-Microbe Int* 2008;21:658–70.
- [135] Kim Y, Lin N, Martin G. Two distinct *Pseudomonas* effector proteins interact with the Pto kinase and activate plant immunity. *Cell* 2002;109:589–98.
- [136] Kleinhofs A, Brueggeman R, Nirmala J, Zhang L, Mirolohi A, Druka A, et al. Barley stem rust resistance genes: structure and function. *The Plant Genome* 2009;2:109–20.
- [137] Klingler J, Powell G, Thompson GA, Isaacs R. Phloem specific aphid resistance in *Cucumis melo* line AR5: effects on feeding behavior and performance of *Aphis gossypii*. *Entomol Exp Appl* 1998;86:79–88.
- [138] Klingler J, Ramakrishnan MN, Edwards OR, Singh KB. A single gene, AIN in *Medicago truncatula* mediates a hypersensitive response to both blue-green aphid and pea aphid, but confers resistance only to blue-green aphid. *J Exp Bot* 2009;60:4115–27.
- [139] Klingler J, Kovalski I, Silberstein L, Thompson GA, Perl-Treves R. Mapping of cotton-melon aphid resistance in melon. *J Am Soc Hort Sci* 2001;126:56–63.
- [140] Knogge W. Funga1 infection of plants. *Plant Cell* 1996;8:1711–22.
- [141] Korbel JO, Kim PM, Chen X, Urban AE, Weissman S, Snyder M, et al. The current excitement about copy-number variation: how it relates to gene duplications and protein families. *Curr Opin Struct Biol* 2008;18:366–74.
- [142] Kuang H, Woo SS, Meyers BC, Nevo E, Michelmore RW. Multiple genetic processes result in heterogeneous rates of evolution within the major cluster disease resistance genes in lettuce. *Plant Cell* 2004;16:2870–94.
- [143] Kusnierczyk A, Winge P, Jorstad TS, Troczynska J, Rossiter JT, Bones AM. Towards global understanding of plant defense against aphids-timing and dynamics of early *Arabidopsis* defense responses to cabbage aphid (*Brevicoryne brassicae*) attack. *Plant Cell Environ* 2008;31:1097–115.
- [144] Lagudah E, Moulet O, Appels R. Map-based cloning of a gene sequence encoding a nucleotide binding domain and a leucine rich region at the Cre3 nematode resistance locus of wheat. *Genome* 1997;40:659–65.
- [145] Lanfermeijer FC, Dijkhuis J, Sturte MJG, Haan P, Hille J. Cloning and characterization of the durable Tomato mosaic virus resistance gene Tm-22 from *Lycopersicon esculentum*. *Plant Mol Biol* 2003;52:1039–51.
- [146] Lawrence JG, Finnegan EJ, Ayliffe MA, Ellisai JG. The L6 gene for flax rust resistance 1s related to the *Arabidopsis* bacterial resistance gene RPS4 and the tobacco virA1 resistance gene N. *Plant Cell* 1995;7:1195–206.
- [147] Leach JE, Shah J. Future prospects for developing disease resistant plants: review. *Transgenic Res* 2002;11:597–8.
- [148] Li Q, Xie QG, Smith-Becker J, Navarre D, Kaloshian I. Mi-1-mediated aphid resistance involves salicylic acid and mitogen-activated protein kinase signaling pathways. *Mol Plant Microbe Interact* 2006;19:655–64.
- [149] Li X, Eck HJ, Rouppe van der Voort JNAM, Huigen DJ, Stam P, Jacobsen E. Autotetraploids and genetic mapping using common AFLP markers: the R2 allele conferring resistance to *Phytophthora infestans* mapped on potato chromosome 4. *Theor Appl Genet* 1998;96:1121–8.
- [150] Lin X, Derdeyn CA, Blumenthal R, West J, Hunter E. Progressive truncations C terminal to the membrane-spanning domain of simian immunodeficiency virus Env reduce fusogenicity and increase concentration dependence of Env for fusion. *J Virol* 2003;77:7067–77.
- [151] Litzenberger SC. Nature of susceptibility to *Helminthosporium victoriae* and resistance to *Puccinia coronata* in Victoria oats. *Phytopathology* 1949;39: 300–18.
- [152] Liu T, Wenwu Y, Yanyan R, Xinyu Y, Biao G, Kai T, et al. Two host cytoplasmic effectors are required for pathogenesis of *Phytophthora sojae* by suppression of host defenses. *Plant Physiol* 2011;155:490–501.
- [153] Liu X, Smith C, Gill B, Tolmay V. Microsatellite markers linked to six Russian wheat aphid resistance genes in wheat. *Theor Appl Genet* 2001;102: 504–10.
- [154] Liu Y, Burch-Smith T, Schiff M, Feng S, Dinesh-Kumar SP. Molecular chaperone Hsp90 associates with resistance protein N and its signaling proteins SGT1 and Rar1 to modulate an innate immune response in plants. *J Biol Chem* 2004;279:2101–8.
- [155] Liu Y, Schiff M, Marathe R, Dinesh-Kumar SP. Tobacco Rar1, EDS1 and NPR1/NIM1 like genes are required for N-mediated resistance to tobacco mosaic virus. *Plant J* 2002;30:415–29.
- [156] Lokossou AA, Park TH, van Arkel G, Arens M, Ruyter-Spira C, Morales J, et al. Exploiting knowledge of R/Avr genes to rapidly clone a new LZ-NBS-LRR family of late blight resistance genes from potato linkage group IV. *MPMI* 2009;22:630–41.

- [157] Luderer R, Takken FLW, De Wit PJGM, Joosten MHAJ. *Cladosporium fulvum* overcomes Cf-2-mediated resistance by producing truncated AVR2 elicitor proteins. *Mol Microbiol* 2002;45:875–84.
- [158] Mackey D, Holt BF, Wiig A, Dangl JL. RIN4 interacts with *Pseudomonas syringae* type III effector molecules and is required for RPM1-mediated resistance in *Arabidopsis*. *Cell* 2002;108:743–54.
- [159] Malnoy M, Xu M, Borejsza-Wysocka E, Korban SS, Aldwinckle HS. Two receptor-like genes, Vfa1 and Vfa2, confer resistance to the fungal pathogen *Venturia inaequalis* inciting apple scab disease. *Mol Plant Microbe Interact* 2008;21:448–58.
- [160] Mao Y, Tyler BM. The *Phytophthora sojae* genome contains tandem repeat sequences which vary from strain to strain. *Fungal Genet Biol* 1996;20:43–51.
- [161] Martin GB, Brommonschenke SH, Chunwongse J, Frary A, Ganal MW, Spivey R, et al. Map-based cloning of a protein kinase gene conferring disease resistance in tomato. *Science* 1993;26:1432–6.
- [162] Martin GB. Functional analysis of plant disease resistance genes and their downstream effectors. *Curr Opin Plant Biol* 1999;2:273–9.
- [163] Martinez de I, Nombela O, Hwang G, Williamson CF, Muniz VM, Kaloshian MI. Rme1 is necessary for Mi-1-mediated resistance and acts early in the resistance pathway. *Mol Plant Microbe Interact* 2004;17:55–61.
- [164] Martinez F, Niks RE, Singh RP, Rubiales D. Characterization of *Lr46*, a gene conferring partial resistance to wheat leaf rust. *Hereditas* 2001;135:111–4.
- [165] McDowell JM, Woffenden BJ. Plant disease resistance genes: recent insights and potential applications. *Trends Biotechnol* 2003;21(4):178–83.
- [166] McDowell JM, Dhandaydham M, Long TA, Aarts MGM, Goff S, Holub EB, et al. Intragenic recombination and diversifying selection contribute to the evolution of downy mildew resistance at the RPP8 locus of *Arabidopsis*. *Plant Cell* 1998;10:1861–74.
- [167] McHale L, Tan X, Koehl P, Michelmore RW. Plant NBS-LRR proteins: adaptable guards. *Genome Biol* 2006;7:212.
- [168] Meateos-Hernandez M, Singh RP, Hulbert SH, Borden RL, Huerta-Espino J, Gill BS, et al. Targeted mapping of ESTs linked to the adult plant resistance gene *Lr46* in wheat using synteny with rice. *Funct Integr Genomics* 2006;6:122–31.
- [169] Meehan F, Murphy HC. A new *Helminthosporium* blight of oats. *Science* 1946;104:413–4.
- [170] Mestre P, Brignetti G, Baulcombe DC. An R_y-mediated resistance response in potato requires the intact active site of the Nla proteinase from potato virus Y. *Plant J* 2000;23:653–61.
- [171] Mestre PF, Asinini MJ, Carbonell EA, Navarro L. New gene(s) involved in the resistance of *Poncirus trifoliata* (L.) Raf to citrus tristeza virus. *Theor Appl Genet* 1997;95:691–5.
- [172] Meyers BC, Chin DB, Shen KA, Sivaramakrishnan S, Lavelle DO, Zhang Z, et al. The major resistance gene cluster in lettuce is highly duplicated and spans several megabases. *Plant Cell* 1998;10:1817–32.
- [173] Meyers BC, Shen KA, Rohani P, Gaut BS, Michelmore RW. Receptor like genes in the major resistance locus of lettuce are subject to divergent selection. *Plant Cell* 1998;10:1833–46.
- [174] Michelmore R, Wong J. Classical and molecular genetics of *Bremia lactucae*, cause of lettuce downy mildew. *Eur J Plant Pathol* 2008;122:19–30.
- [175] Milligan SB, Bodeau J, Yaghoobi J, Kaloshian I, Zabel P, Williamson VM. The root-knot nematode resistance gene Mi from tomato is a member of leucine zipper, nucleotide binding, leucine-rich repeat family of plant genes. *Plant Cell* 1998;10:1307–19.
- [176] Mindrinos M, Katagiri F, Yu GL, Ausubel FM. The *Arabidopsis thaliana* disease resistance gene RPS2 encodes a protein containing a nucleotide-binding site and leucine-rich repeats. *Cell* 1994;78:1089–99.
- [177] Minsavage GV, Dahlbeck D, Whalen MC, Kearney B, Bonas U, Staskawicz BJ, et al. Gene-for-gene relationships specifying disease resistance in *Xanthomonas campestris* pv *vesicatoria* – pepper interactions. *Mol Plant-Microbe Interact* 1990;3:41–7.
- [178] Misas-Villamil JC, van der Hoorn RA. Enzyme–inhibitor interactions at the plant–pathogen interface. *Curr Opin Plant Biol* 2008;11:380–8.
- [179] Morel J, Dangl J. The hypersensitive response and the induction of cell death in plants. *Cell Death Differ* 1997;4:671–83.
- [180] Moury B, Morel C, Johansen E, Guilbaud L, Souche S, Ayme V, et al. Mutations in Potato virus Y genome-linked protein determine virulence toward recessive resistances in *Capsicum annuum* and *Lycopersicon hirsutum*. *Mol Plant Microbe Interact* 2004;17:322–9.
- [181] Mudgett MB. New insights to the function of phytopathogenic bacterial type III effectors in plants. *Annu Rev Plant Biol* 2005;56:509–31.
- [182] Muskett PR, Kahn K, Austin MJ, Moisan LJ, Sadanandom A, Shirasu K, et al. *Arabidopsis* RAR1 exerts rate-limiting control of R-gene-mediated defenses against multiple pathogens. *Plant Cell* 2002;14:979–92.
- [183] Nicaise V, German-Retana S, Sanjuan R, Dubrana MP, Mazier M, Maisonneuve B, et al. The eukaryotic translation initiation factor 4E controls lettuce susceptibility to the potyvirus Lettuce mosaic virus. *Plant Physiol* 2003;132:1272–82.
- [184] Niirnberger T, Nennstiel D, Jabs T, Sacks WR, Hahlbrock K, Scheel D. High-affinity binding of a fungal oligopeptide elicitor to parsley plasma membranes triggers multiple defense responses. *Cell* 1994;78:449–60.
- [185] Nimchuk Z, Eulgem T, Holt BF, Dangl JL. Recognition and response in the plant immune system. *Annu Rev Genet* 2003;37:579–609.
- [186] Nombela G, Williamson VM, Muñiz M. The root-knot nematode resistance gene Mi-1.2 of tomato is responsible for resistance against the whitefly *Bemisia tabaci*. *Mol Plant Microbe Interact* 2003;16:645–9.
- [187] Niirnberger T, Brunner F, Kemmerling B, Piater L. Innate immunity in plants and animals: striking similarities and obvious differences. *Immunol Rev* 2004;198:249–66.
- [188] Oerke EC, Dehne HW. Safeguarding production-losses in major crops and the role of crop protection. *Crop Prot* 2004;23:275–85.
- [189] Ori N, Eshed Y, Paran I, Presting G, Aviv D, Tanksley S, et al. The I2C family from the wilt disease resistance locus I2 belongs to the nucleotide binding, leucine-rich repeat superfamily of plant resistance genes. *Plant Cell* 1997;9:521–32.
- [190] Paal J, Henselewski H, Muth J, Meksem K, Menendez CM, Salamini, et al. Molecular cloning of the potato Gro1-4 gene conferring resistance to pathotype Ro1 of the root cyst nematode *Globodera rostochiensis*, based on a candidate gene approach. *Plant J* 2004;38:285–97.
- [191] Panda N, Khush GS. Host plant resistance to insects. Wallingford, UK: CAB Int; 1995. p. 431.
- [192] Pauquet J, Burget E, Hagen L, Chovelon V, Le Menn A, Valot N, et al. Map-based cloning of the Vat gene from melon conferring resistance to both aphid colonization and aphid transmission to several viruses. In: Lebeda A, Paris HS, editors. Proceedings of the 8th EUCARPIA meeting on cucurbit genetics and breeding: *Cucurbitaceae*; 2004. p. 307–12.
- [193] Park TH, Vleeshouwers VGAA, Huigen DJ, van der Vossen EAG, van Eck HJ, Visser RGF. Characterization and high-resolution mapping of a late blight resistance locus similar to R2 in potato. *Theor Appl Genet* 2005;111:591–7.
- [194] Park TH, Vleeshouwers VGAA, Hutten RCB, van Eck HJ, van der Vossen E, Jacobsen E, et al. High-resolution mapping and analysis of the resistance locus Rpi-abpt against *Phytophthora infestans* in potato. *Mol Breed* 2005;16:33–43.
- [195] Park T, Gros J, Sikkema A, Vleeshouwers VGAA, Muskens M, Allefs S, et al. The late blight resistance locus Rpi-blb3 from *Solanum bulbocastanum* belongs to a major late blight R gene cluster on chromosome 4 of potato. *Mol Plant-Microbe Interact* 2005;18:722–9.
- [196] Parker JE, Coleman MJ, Szabó V, Frost LN, Schmidt R, Van der Biezen, et al. The *Arabidopsis* downy mildew resistance gene RPP5 shares similarity to the toll and interleukin-1 receptors with N and L6. *Plant Cell* 1997;9:879–94.
- [197] Parker JE, Holub EB, Frost LN, Falk A, Gunn ND, Daniels MJ. Characterization of eds1, a mutation in *Arabidopsis* suppressing resistance to *Peronospora parasitica* specified by several different RPP genes. *Plant Cell* 1996;8:2033–46.
- [198] Peart JR, Lu R, Sadanandom A, Malcuit I, Moffett P, Brice DC, et al. Ubiquitin ligase-associated protein SGT1 is required for host and nonhost disease resistance in plants. *Proc Natl Acad Sci USA* 2002;99:10865–9.
- [199] Peart JR, Mestre P, Lu R, Malcuit I, Baulcombe DC. NRG1, a CC-NB-LRR protein together with N, a TIR-NB-LRR protein mediates resistance against tobacco mosaic virus. *Curr Biol* 2005;15:968–73.
- [200] Pegadaraju V, Knepper C, Reese J, Shah J. Premature leaf senescence modulated by the *Arabidopsis* phytoalexin deficient4 gene is associated with defense against the phloem-feeding green peach aphid. *Plant Physiol* 2005;139:1927–34.
- [201] Pegadaraju V, Louis J, Singh V, Reese JC, Bautor J, Feys BJ. Phloem-based resistance to green peach aphid is controlled by *Arabidopsis* phytoalexin deficient4 without its signaling partner enhanced disease susceptibility1. *Plant J* 2007;52:332–41.
- [202] Pelham J. Resistance in tomato to tobacco mosaic virus. *Euphytica* 1966;15:258–67.
- [203] Pieterse CMJ, Derksen AMCE, Folders J, Govers F. Expression of the *Phytophthora infestans* *ipiB* and *ipiO* genes in planta and in vitro. *Mol Gen Genet* 1994;244:269–77.
- [204] Piron F, Nicolai M, Minoia S, Piednoir E, Moretti A, Salgues A, et al. An induced mutation in tomato eIF4E leads to immunity to two Potyviruses. *PLoS ONE* 2010;5(6):e11313.
- [205] Querci M, Baulcombe DC, Goldbach RW, Salazar LF. Analysis of the resistance-breaking determinants of Potato Virus X (PVX) Strain HB on different potato genotypes expressing extreme resistance to PVX. *Phytopathol* 1995;85:1003–10.
- [206] Quisenberry SS, Clement SL. Conservation and use of global plant genetic resources for insect resistance. *Aust J Agric Res* 2002;53:865–72.
- [207] Qutob D, Tedman-Jones J, Dong S, Kufu K, Pham H, Wang Y, et al. Copy number variation and transcriptional polymorphisms of *Phytophthora sojae* RXLR effector genes Avr1a and Avr3a. *PLoS ONE* 2009;4:e5066.
- [208] Qutob D, Tedman-Jones J, Gijzen M. Effector-triggered immunity by the plant pathogen *Phytophthora*. *Trends Microbiol* 2006;14:470–3.
- [209] Rai M. Refinement of the Citrus tristeza virus resistance gene (Ctv) positional map in *Poncirus trifoliata* and generation of transgenic grapefruit (*Citrus paradisi*) plant lines with candidate resistance genes in this region. *Plant Mol Biol* 2006;61:399–414.
- [210] Ramonell KM, Somerville S. The genomics parade of defense responses: to infinity and beyond. *Curr Opin Plant Biol* 2002;5:291–4.
- [211] Redondo E, Krause-Sakate R, Yang SJ, Lot H, Le Gall O, Candresse T. Lettuce mosaic virus pathogenicity determinants in susceptible and tolerant lettuce cultivars map to different regions of the viral genome. *Mol Plant Microbe Interact* 2001;14:804–10.
- [212] Rehmany AP, Gordon A, Rose LE, Allen RL, Armstrong MR, Whisson SC, et al. Differential recognition of highly divergent downy mildew avirulence gene alleles by RPP1 resistance genes from two *Arabidopsis* lines. *Plant Cell* 2005;17:1839–50.

- [213] Reinink K, Dieleman FL. Comparison of sources of resistance to leaf aphids in lettuce (*L. sativa* L.). *Euphytica* 1989;40:21–9.
- [214] Ren T, Qu F, Morris TJ. HRT gene function requires interaction between a NAC protein and viral capsid protein to confer resistance to turnip crinkle virus. *Plant Cell* 2000;12:1917–26.
- [215] Ren T, Qu F, Morris TJ. The nuclear localization of the *Arabidopsis* transcription factor TIP is blocked by its interaction with the coat protein of Turnip crinkle virus. *Virology* 2005;331:316–24.
- [216] Richards TA, Talbot NJ. Plant parasitic oomycetes such as *Phytophthora* species contain genes derived from three eukaryotic lineages. *Plant Signaling Behav* 2007;2(2):112–4.
- [217] Robaglia C, Caranta C. Translation initiation factors: a weak link in plant RNA virus infection. *Trends Plant Sci* 2006;11:40–5.
- [218] Roberts PA, Thomason IJ. A review of variability in four *Meloidogyne* spp. measured by reproduction on several hosts including *Lycopersicon*. *Agri Zool Rev* 1989;3:225–52.
- [219] Roche PA, Alston FH, Maliepaard CA, Evans KM, Vrieling R, Dunemann F, et al. RFLP and RAPD markers linked to the rosy leaf curling aphid resistance gene (*Sd1*) in apple. *Theor Appl Genet* 1996;94:528–33.
- [220] Romeis T, Piedras P, Jones JDG. Resistance gene-dependent activation of a calcium-dependent protein kinase in the plant defense response. *Plant Cell* 2000;12:803–16.
- [221] Romeis T, Piedras P, Zhang S, Klessig DF, Hirt H, Jones JDG. Rapid Avr9- and Cf-9-dependent activation of MAP kinases in tobacco cell cultures and leaves: convergence of resistance gene, elicitor, wound, and salicylate responses. *Plant Cell* 1999;11:273–87.
- [222] Ron M, Avni A. The receptor for the fungal elicitor ethylene-inducing xylanase is a member of a resistance-like gene family in tomato. *Plant Cell* 2004;16:1604–15.
- [223] Ronald PC, Salmeron JM, Carland FM, Staskawicz BJ. The cloned avirulence gene *AvrPto* induces disease resistance in tomato cultivars containing the *Pto* resistance gene. *J Bacteriol* 1992;174:1604–11.
- [224] Rooney HC, Van't Klooster JW, van der Hoorn RA, Joosten MH, Jones JD, de Wit PJ. *Cladosporium* Avr2 inhibits tomato Rcr3 protease required for Cf-2-dependent disease resistance. *Science* 2005;308:1783–6.
- [225] Rosello S, Diez MJ, Nuez F. Genetics of tomato spotted wilt virus resistance coming from *Lycopersicon peruvianum*. *Eur J Plant Pathol* 1998;104:499–509.
- [226] Rossi M, Goggin FL, Milligan SB, Kaloshian I, Ullman DE, Williamson VM. The nematode resistance gene *Mi* of tomato confers resistance against the potato aphid. *Proc Natl Acad Sci USA* 1998;95:9750–4.
- [227] Rouppe van der Voort JR, Kanyuka K, van der Vossen E, Bendahmane A, Mooijman P, Klein-Lankhorst R, et al. Tight physical linkage of the nematode resistance gene *Gpa2* and the virus resistance gene *Rx* on a single segment introgressed from the wild species *Solanum tuberosum* subsp. *andigena* CPC1673 into cultivated potato. *Mol Plant-Microbe Int* 1999;12:197–206.
- [228] Ruffel S, Dussault MH, Palloix A, Moury B, Bendahmane A, Robaglia C, et al. A natural recessive resistance gene against potato virus Y in pepper corresponds to the eukaryotic initiation factor 4E (eIF4E). *Plant J* 2002;32:1067–75.
- [229] Ruffel S, Gallois JL, Lesage ML, Caranta C. The recessive potyvirus resistance gene *pot-1* is the tomato orthologue of the pepper *pvr2-eIF4E* gene. *Mol Genet Genomics* 2005;274:346–53.
- [230] Rushton PJ, Reinstädler A, Lipka V, Lippok B, Somssich IE. Synthetic plant promoters containing defined regulatory elements provide novel insights into pathogen- and wound induced signaling. *Plant Cell* 2002;14:479–762.
- [231] Salmeron JM, Oldroyd GE, Rommens CM, Scofield SR, Kim HS, Lavelle DT, et al. Tomato Prf is a member of the leucine-rich repeat class of plant disease resistance genes and lies embedded within the *Pto* kinase gene cluster. *Cell* 1996;86:123–33.
- [232] Sanseverino W, Roma G, Simone MD, Faino L, Melito S, Stupka E, et al. PRGdb: a bioinformatics platform for plant resistance gene analysis. *Nucleic Acids Res* 2010;38. Database issue.
- [233] Scheel D. Resistance response physiology and signal transduction. *Curr Opin Plant Biol* 1998;1:305–10.
- [234] Schornack S, Ballvora A, Gurlebeck D, Peart J, Baulcombe DC, Ganai M, et al. The tomato resistance protein Bs4 is a predicted non-nuclear TIR-NB-LRR protein that mediates defense responses to severely truncated derivatives of *AvrBs4* and overexpressed *AvrBs3*. *Plant J* 2004;37:46–60.
- [235] Schulze-Lefert P, Panstruga R. Establishment of biotrophy by parasitic fungi and reprogramming of host cells for disease resistance. *Annu Rev Phytopathol* 2003;41:641–67.
- [236] Schwessinger B, Zipfel C. News from the frontline: recent insights into PAMP-triggered immunity in plants. *Curr Opin Plant Biol* 2008;11:389–95.
- [237] Scofield SR, Huang L, Brandt AS, Gill BS. Development of a virus-induced gene-silencing system for hexaploid wheat and its use in functional analysis of the Lr21-mediated leaf rust resistance pathway. *Plant Physiol* 2005;138:2165–73.
- [238] Seah S, Sivasithamparan K, Karakousis A, Lagudah E. Cloning and characterization of a family of disease resistance gene analogs from wheat and barley. *Theor Appl Genet* 1998;97:937–45.
- [239] Seah S, Yaghoobi J, Rossi M, Gleason CA, Williamson VM. The nematode-resistance gene, *Mi-1*, is associated with an inverted chromosomal segment in susceptible compared to resistant tomato. *Theor Appl Genet* 2004;108:1635–42.
- [240] Seo YS, Rojas MR, Lee JY, Lee SW, Jeon JS, Ronald P, et al. A viral resistance gene from common bean functions across plant families and is up-regulated in a non-virus-specific manner. *Proc Natl Acad Sci USA* 2006;103:11856–61.
- [241] Shan WX, Cao M, Dan LU, Tyler BM. The *Avr1b* locus of *Phytophthora sojae* encodes an elicitor and a regulator required for avirulence on soybean plants carrying resistance gene *Rps1b*. *Mol Plant-Microbe Int* 2004;17:394–403.
- [242] Shao F, Golstein C, Ade J, Stoutemyer M, Dixon JE, Innes EWL. Cleavage of *Arabidopsis* PBS1 by a bacterial type III effector. *Science* 2003;301:1230–3.
- [243] Shao F, Merritt PM, Bao Z, Innes RW, Dixon JE. A Yersinia effector and a *Pseudomonas* avirulence protein define a family of cysteine proteases functioning in bacterial pathogenesis. *Cell* 2002;109:575–88.
- [244] Shen KA, Chin DB, Arroyo-Garcia R, Ochoa OE, Lavelle DO, Wroblewski T, et al. *Dm3* is one member of a large constitutively-expressed family of NBS-LRR encoding genes. *Mol Plant-Microbe Int* 2002;15:251–61.
- [245] Shen KA, Meyers BC, Islam-Faridi MN, Chin DB, Stelly DM, Michelmore RW. Resistance gene candidates identified using PCR with degenerate primers map to resistance genes clusters in lettuce. *Mol Plant-Microbe Int* 1998;11:815–23.
- [246] Shirasu K, Lahaye T, Tan MW, Zhou F, Azevedo C, Schulze-Lefert P. A novel class of eukaryotic zinc-binding proteins is required for disease resistance signaling in barley and development in *C. elegans*. *Cell* 1999;99:355–66.
- [247] Silue D, Nottenghem JL, Tharreau D. Evidence for a gene-for-gene relationship in the *Oryza sativa*-*Magnaporthe oryzae* pathosystem. *Phytopathology* 1992;82:577–80.
- [248] Simons G, Groenendijk J, Wijbrandi J, Reijmans M, Groenen J, Diergaarde P, et al. Dissection of the *Fusarium* 12 gene cluster in tomato reveals six homologs and one active gene copy. *Plant Cell* 1998;10:1055–68.
- [249] Smith PG. Embryo culture of a tomato species hybrid. *Proc Am Soc Hortic Sci* 1944;44:413–6.
- [250] Song J, Bradeen JM, Naess SK, Raasch JA, Wielgus SM, Haberlach GT, et al. Gene *RB* cloned from *Solanum bulbocastanum* confers broad spectrum resistance to potato late blight. *Proc Natl Acad Sci USA* 2003;100:9128–33.
- [251] Song J, Win J, Tian M, Schornack S, Kaschani F, Ilyas M, et al. Apoplastic effectors secreted by two unrelated eukaryotic plant pathogens target the tomato defense protease Rcr3. *Proc Natl Acad Sci USA* 2009;106:1654–9.
- [252] Song WY, Wang GL, Chen LL, Kim HS, Pi LY, Holsten T, et al. A receptor kinase-like protein encoded by the rice disease resistance gene, *Xa21*. *Science*; 1995:1804–6.
- [253] Soosaar JLM, Burch-Smith, Dinesh-Kumar SP. Mechanisms of plant resistance to viruses. *Nat Rev Microbiol* 2005;10:789–98.
- [254] Staskawicz BJ, Ausubel FM, Baker BJ, Ellis JG, Jones JD. Molecular genetics of plant disease resistance. *Science* 1995;268:661–7.
- [255] Stebbins CE, Galan JE. Maintenance of an unfolded polypeptide by a cognate chaperone in bacterial type III secretion. *Nature* 2001;414:77–81.
- [256] Stotz HU, Bishop JG, Bergmann CW, Koch M, Albersheim P, Darvill AG, et al. Identification of target amino acids that affect interactions of fungal polygalacturonases and their plant inhibitors. *Physiol Mol Plant Pathol* 2000;56:117–30.
- [257] Swiderski MR, Innes RW. The *Arabidopsis* PBS1 resistance gene encodes a member of a novel protein kinase subfamily. *Plant J* 2001;26:101–12.
- [258] Tagu D, Klingler JP, Moya A, Simon JC. Early progress in aphid genomics and Consequences for plant-aphid interactions studies. *Am Phytopathol Soc* 2008;21(6):701–8.
- [259] Tai TH, Dahlbeck D, Clark ET, Gajiwala P, Pasion R, Whalen MC, et al. Expression of the Bs2 pepper gene confers resistance to bacterial spot disease in tomato. *Proc Natl Acad Sci USA* 1999;96(141):53–8.
- [260] Takahashi A, Casais C, Ichimura K, Shirasu K. HSP90 interacts with RAR1 and SG1 and is essential for RPS2-mediated disease resistance in *Arabidopsis*. *Proc Natl Acad Sci USA* 2003;100(117):77–82.
- [261] Takahashi H, Miller J, Nozaki Y, Takeda M, Shah J, Hase S, et al. RCY1, an *Arabidopsis thaliana* RPP8/HRT family resistance gene, conferring resistance to cucumber mosaic virus requires salicylic acid, ethylene and a novel signal transduction mechanism. *Plant J* 2002;32:655–67.
- [262] Takahashi H, Suzuki M, Natsuaki K, Shigyo T, Hino K, Teraoka T, et al. Mapping the virus and host genes involved in the resistance response in cucumber mosaic virus infected *Arabidopsis thaliana*. *Plant Cell Physiol* 2001;42:340–7.
- [263] Tamaki S, Dahlbeck D, Staskawicz B, Keen NT. Characterization and expression of two avirulence genes cloned from *Pseudomonas syringae* pv. *Glycinia*. *J Bacteriol* 1988;170:4846–54.
- [264] Tameling WIL, Elzinga SDP, Darmin PS, Vossen JH, Takken FLW, Haring MA, et al. The tomato R gene products I-2 and Mi-1 are functional ATP binding proteins with ATPase activity. *Plant Cell*. 2002;14(11):2929–39.
- [265] Tan GX, Weng QM, Ren X, Huang Z, Zhu LL, He GC. Two whitebacked planthopper resistance genes in rice share the same loci with those for brown planthopper resistance. *Heredity* 2004;92:212–7.
- [266] Tang X, Frederick RD, Zhou J, Halterman DA, Jia Y, Martin GB. Physical interaction of *AvrPto* and the *Pto* kinase defines a recognition event involved in plant disease resistance. *Science* 1996;274:2060–3.
- [267] Tang X, Xie M, Kim Y, Zhou J, Klessig DF, Martin GB. Overexpression of *Pto* activates defense responses and confers broad resistance. *Plant Cell* 1999;11:15–29.
- [268] Thines M, Kamoun S. Oomycete-plant coevolution: recent advances and future prospects. *Curr Opin Plant Biol* 2010;13:1–7.
- [269] Thomas CM, Jones DA, Parniske M, Harrison K, BalintKurti PJ, Hatzixanthos K, et al. Characterization of the tomato Cf-4 gene for resistance to *Cladosporium*

- fulvum* identifies sequences that determine recognitional specificity in Cf-4 and Cf-9. *Plant Cell* 1997;9:2209–24.
- [270] Thomma BP, Nürnberger T, Joosten MH. Of PAMPs and effectors: the blurred PTI-ETI dichotomy. *Plant Cell*. 2011;23:4–15.
- [271] Tian M, Huitema E, da Cunha L, Torto-Alalibo T, Kamoun S. A Kazal-like extracellular serine protease inhibitor from *Phytophthora infestans* targets the tomato pathogenesis related protease P69B. *J Biol Chem* 2004;279:26370–7.
- [272] Tian M, Win J, Song J, van der Hoorn R, van der Knaap E, Kamoun S. A *Phytophthora infestans* cystatin-like protein targets a novel tomato papain-like apoplastic protease. *Plant Physiol* 2007;143:364–77.
- [273] Tian M, Benedetti B, Kamoun S. A second Kazal-like protease inhibitor from *Phytophthora infestans* inhibits and interacts with the apoplastic pathogenesis-related P69B of tomato. *Plant Physiol* 2005;138:1785–93.
- [274] Torp J, Jorgensen JH. Modification of the powdery mildew resistance gene *Mla12* by induced mutation. *Can J Genet Cytol* 1986;28:725–31.
- [275] Torto-Alalibo T, Candace W, Collmer MGG, Lindeberg M, Meng S, Chibucos MC, et al. Unifying Themes in microbial associations with animal and plant hosts described using the gene ontology. *Microbiol Mol Biol Rev* December 2010;74(4):479–503.
- [276] Trudgill DL. Resistance to and tolerance of plant parasitic nematodes in plants. *Annu Rev Phytopathol* 1991;29:167–93.
- [277] Tyler BM, Tripathy S, Zhang XM, Dehal P, Jiang RHY, Aerts A, et al. *Phytophthora* genome sequences uncover evolutionary origins and mechanisms of pathogenesis. *Science* 2006;313:1261–6.
- [278] Valent B, Farrall L, Chumley FG. *Magnaporthe grisea* genes for pathogenicity and virulence identified through a series of backcrosses. *Genetics* 1991;127:87–101.
- [279] Van den Ackerveken GF, Van Kan JA, De Wit PJGM. Molecular analysis of the avirulence gene *Avr9* of the fungal tomato pathogen *Cladosporium fulvum* fully supports the gene-for-gene hypothesis. *Plant J* 1992;2:359–66.
- [280] van der Biezen EA, Freddie CT, Kahn K, Parker JE, Jones JDG. *Arabidopsis* RPP4 is a member of the RPP5 multigene family of TIR-NBLRR-genes and confers downy mildew resistance through multiple signaling components. *Plant J* 2002;29:439–51.
- [281] Van der Biezen EA, Jones JDG. Plant disease-resistance proteins and the gene-for-gene concept. *Trends Biochem Sci* 1998;12:454–6.
- [282] van der Vossen EA, Sikkema A, Hekkert BTL, Gros J, Stevens P, Muskens, et al. An ancient R-gene from the wild species *Solanum bulbocastanum* confers broad-spectrum resistance to *Phytophthora infestans* in cultivated potato and tomato. *Plant J* 2003;36:867–82.
- [283] van der Vossen EAG, van der Voort J, Kanyuka K, Bendahmane A, Sandbrink H, Baulcombe DC, et al. Homologues of a single resistance-gene cluster in potato confer resistance to distinct pathogens: a virus and a nematode. *Plant J* 2000;23:567–76.
- [284] Van Esse HP, van't Klooster, Bolton MD, Yadeta KA, van Baarlen P, Boeren S, et al. The *Cladosporium fulvum* virulence protein *Avr2* inhibits host proteases required for basal defense. *Plant Cell* 2008;20:1948–63.
- [285] Van Helden M, Tjallingii WF, Dieleman FL. The resistance of lettuce (*Lactuca sativa* L.) to *Nasonovia ribisnigri*: bionomics of *N. ribisnigri* on near isogenic lettuce lines. *Entomol Exp Appl* 1993;66:3–58.
- [286] Van Poppel P, Guo J, de Vondervoort P, Jung MWM, Birch PRJ, Whisson SC, et al. The *Phytophthora infestans* avirulence gene *Avr4* encodes an RXLR-DEER effector. *Mol Plant Microbe Interact* 2008;21:1460–70.
- [287] van West P, de Jong AJ, Judelson HS, Emons AMC, Govers F. The *ipiO* gene of *Phytophthora infestans* is highly expressed in invading hyphae during infection. *Fungal Genet Biol* 1998;23:126–38.
- [288] Venter V, Botha AM. Development of markers linked to *Diuraphis noxia* resistance in wheat using a novel PCR-RFLP approach. *Theor Appl Genet* 2000;100:965–70.
- [289] Veremis JC, Roberts PA. Identification of resistance to *Meloidogyne javanica* in the *Lycopersicon peruvianum* complex. *Theor Appl Genet* 1996;93:894–901.
- [290] Veronese P, Ruiz MT, Coca MA, Hernandez-Lopez A, Lee H, Ibeas JI, et al. In defense against pathogens. Both plant sentinels and foot soldiers need to know the enemy. *Plant Physiol* 2003;131:1580–90.
- [291] Vidal S, Cabrera H, Andersson RA, Frederiksson A, Valkonen JP. Potato gene *Y-1* is an N gene homolog that confers cell death upon infection with potato virus Y. *Mol Plant Microbe Interact* 2002;15:717–27.
- [292] Vinatzer BA, Patocchi A, Gianfranceschi L, Tartarini S, Zhang HB, Gessler C, et al. Apple contains receptor-like genes homologous to the *Cladosporium fulvum* resistance gene family of tomato with a cluster of genes cosegregating with Vf apple scab resistance. *Mol Plant Microbe Interact* 2001;14:508–15.
- [293] Vining K, Davis T. Isolation of a Ve homolog, mVe1, and its relationship to *verticillium* wilt resistance in *Mentha longifolia* (L.) Huds. *Mol Genet Genomics* 2009;282:173–84.
- [294] Vleeshouwers VG, Rietman H, Krenek P, Champouret N, Young C, Oh SK, et al. Effector genomics accelerates discovery and functional profiling of potato disease resistance and *Phytophthora infestans* avirulence genes. *PLoS ONE* 2008;3:e2875.
- [295] Vos P, Simons G, Jesse T, Wijbrandi J, Heinen L, Hogers R, et al. The tomato *Mi-1* gene confers resistance to both root-knot nematodes and potato aphids. *Nat Biotechnol* 1998;16:1365–9.
- [296] Vossen EAGV, Gros J, Sikkema A, Muskens M, Wouters D, Wolters P, et al. The *Rpi-blb2* gene from *Solanum bulbocastanum* is an *Mi-1* gene homolog conferring broad-spectrum late blight resistance in potato. *Plant J* 2005;44:208–22.
- [297] Vossen EAGV, Rouppé van der Voort JNAM, Kanyuka K, Bendahmane A, Sandbrink S, Baulcombe DC, et al. Homologues of a single resistance-gene cluster in potato confer resistance to distinct pathogens: a virus and a nematode. *Plant J* 2000;23:567–76.
- [298] Walton JD. Host-selective toxins: agents of compatibility. *Plant Cell* 1996;8:1723–33.
- [299] Wang W, Wen Y, Berkey R, Xiao S. Specific targeting of the *Arabidopsis* resistance protein RPW8.2 to the interfacial membrane encasing the fungal haustorium renders broad-spectrum resistance to powdery mildew. *Plant Cell* 2009;21:2898–913.
- [300] Wani SH. Inducing fungus-resistance into plants through biotechnology. *Not Sci Biol* 2010;2(2):14–21.
- [301] Warren FR, Merritt PM, Holub E, Innes RW. Identification of three putative signal transduction genes involved in R-gene-specified disease resistance in *Arabidopsis*. *Genetics* 1999;152:401–12.
- [302] Watts VM. The use of *Lycopersicon peruvianum* as a source nematode resistance in tomatoes. *Proc Am Soc Hort Sci* 1947;49:233–4.
- [303] Weng Q, Li Z, Xing J, Dong Z, Dong J. Cloning and structure analysis of an NBS-LRR disease-resistant gene from *Setaria italica* Beauv. *Front Agric China* 2009;3:240–6.
- [304] Whalen MC, Innes RW, Bent AF, Staskawicz BJ. Identification of *Pseudomonas syringae* pathogens of *Arabidopsis* and a bacterial locus determining avirulence on both *Arabidopsis* and soybean. *Plant Cell* 1991;3:49–59.
- [305] Whitham S, DineshKumar SP, Choi D, Hehl R, Corr C, Baker B. The product of the tobacco mosaic virus resistance gene *N*: similarity to Toll and the interleukin-1 receptor. *Cell* 1994;78:1101–15.
- [306] Whitham S, McCormick S, Baker B. The *N* gene of tobacco confers resistance to tobacco mosaic virus in transgenic tomato. *Proc Natl Acad Sci USA* 1996;93:8776–81.
- [307] Whitham SA, Anderberg RJ, Chisholm ST, Carrington JC. *Arabidopsis* RTM2 gene is necessary for specific restriction of tobacco etch virus and encodes an unusual small heat shock-like protein. *Plant Cell* 2000;12:569–82.
- [308] Williams CE, Collier CC, Nemacheck JA, Liang CZ, Cambron SE. A lectin-like wheat gene responds systemically to attempted feeding by avirulent first-instar Hessian fly larvae. *J Chem Ecol* 2002;28:1411–28.
- [309] Williamson VM, Hussey RS. Nematode pathogenesis and resistance in plants. *Plant Cell* 1996;8:1735–45.
- [310] Williamson VM, Kumar A. Nematode resistance in plants: the battle underground. *Trends Genet* 2006;22:396–403.
- [311] Wittmann S, Chatel H, Fortin MG, Laliberté JF. Interaction of the viral protein genome linked of turnip mosaic potyvirus with the translational eukaryotic initiation factor (iso) 4E of *Arabidopsis thaliana* using the yeast two-hybrid system. *Virology* 1997;234:84–92.
- [312] Wolpert TJ, Dunkle LD, Ciufoletti LM. Host-selective toxins and avirulence determinants. What's in a name? *Annu Rev Phytopathol* 2002;40:251–85.
- [313] Wroblewski T, Piskurewicz U, Tomczak A, Ochoa O, Michelmore RW. Silencing of the major family of NBS-LRR-encoding genes in lettuce results in the loss of multiple resistance specificities. *Plant J* 2007;51:803–18.
- [314] Xiao S, Ellwood S, Calis O, Patrick E, Li T, Coleman M, et al. Broad-spectrum mildew resistance in *Arabidopsis thaliana* mediated by RPW8. *Science* 2001;291:118–20.
- [315] Xu ML, Korban SS. A cluster of four receptor like genes resides in the Vf locus that confers resistance to apple scab disease. *Genetics* 2002;162:1995–2006.
- [316] Yaghoobi J, Kaloshian I, Wen Y, Williamson VM. Mapping a new nematode resistance locus in *Lycopersicon peruvianum*. *Theor Appl Genet* 1995;91:457–64.
- [317] Yang X, Wang W, Coleman M, Orgil U, Feng J, Ma X, et al. *Arabidopsis* 14-3-3 lambda is a positive regulator of RPW8-mediated disease resistance. *Plant J* 2009;60(3):539–50.
- [318] Yang Y, Shah J, Klessig DF. Signal perception and transduction in plant defense responses. *Genes Dev* 1997;11:621–39.
- [319] Yencho GC, Cohen MB, Byrne PF. Applications of tagging and mapping insect resistance loci in plants. *Annu Rev* 2000;5:393–422.
- [320] Yoshii M, Nishikiori M, Tomita K, Yoshioka N, Kozuka R, Naito S, et al. The *Arabidopsis* Cucumovirus multiplication 1 and 2 loci encode translation initiation factors 4E and 4G. *J Virol* 2004;78:6102–11.
- [321] Yoshimura S, Yamanouchi U, Katayose Y, Toki S, Wang ZX, Kono I, et al. Expression of *Xa1*, a bacterial blight-resistance gene in rice, is induced by bacterial inoculation. *Proc Natl Acad Sci USA* 1998;95:1663–8.
- [322] Zhai XG, Zhao T, Liu YH, Long H, Deng GB, Pan ZF, et al. Characterization and expression profiling of a novel cereal cyst nematode resistance gene analog in wheat. *Mol Biol* 2008;42:960–5.
- [323] Zhao B, Lin X, Poland J, Trick H, Leach J, Hulbert S. A maize resistance gene functions against bacterial streak disease in rice. *Proc Natl Acad Sci USA* 2005;102(43):15383–8.
- [324] Zhou FS, Kurth JC, Wei F, Elliott C, Vale G, Yahiaoui N, et al. Cell-autonomous expression of barley *Mla1* confers race-specific resistance to the powdery mildew fungus via a *Rar1*-independent signaling pathway. *Plant Cell* 2001;13:337–50.
- [325] Zipfel C. Pattern-recognition receptors in plant innate immunity. *Curr Opin Immunol* 2008;20:10–6.