

Chapter 9

Molecular Breeding for Resistance against *Phytophthora* in Soybean



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Abstract Soybean is a leading oilseed crop and contribute to a major part of the economy in many countries. However, soybean is affected by several diseases, reducing its productivity around the globe. The soilborne pathogen *Phytophthora sojae* is one of the most prevalent and deadly diseases affecting the soybean crop in Asia, Europe, and the United States. Scientists have developed numerous resistant varieties of soybean against *P. sojae*, but this fungal pathogen is continuously evolving and is still a serious threat to soybean production. Advances in molecular breeding coupled with sequencing techniques allowed breeders to map novel quantitative trait loci. The SNP-based mapping is an excellent tool to screen the resistant soybean cultivars and to identify new R-genes that can be used to develop resistant genotypes to cope with *P. sojae* infection. This chapter discusses the current knowledge on resistance against *P. sojae* in soybean. The current molecular breeding approaches as well as the identified genetic regions associated with *P. sojae* resistance were also highlighted.

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Keywords *Phytophthora* root rot (PRR) · *Phytophthora* stem rot (PSR) · Soybean · QTL · GWAS

9.1 Introduction

Phytophthora root rot (PRR) and *Phytophthora* stem rot (PSR) are caused by the oomycete *Phytophthora sojae*. This disease is soilborne and propagates through the air. In addition, this pathogen has been discovered and transmitted throughout the world over the last 60 years (Zhang et al. 2014). The PSR is more prevalent in the northern hemisphere due to the region's greater vulnerability to disease dissemination (Dorrance and Schmitthenner 2000). *P. sojae* can be found in every country that grows soybeans, including the United States, Europe, and Asia, and is considered as a major pest in the soybean industry (Schmitthenner 1999). The PSR was first reported in 1958 in Indiana (Kaufmann and Gerdemann 1958), and in 1977, PSR was discovered in the island of Hokkaido, Japan's northernmost island (Tsuchiya et al. 1978). It has been discovered that it exists in the prefectures of Shizuoka and Yamagata, as well as the cities of Saga, Niigata, and Hyogo, as well as other places around Japan (Sugimoto et al. 2006). Whenever a crop is infected with the *P. sojae* fungus, the stems of the plants turn reddish-brown color. As a result, plants begin to wilt and eventually die (Dorrance et al. 2003). As *P. sojae* develops infected tissue, it discharges zoospores which can accelerate further disease cycle (Gijzen and Qutob 2009). There is a possibility that zoospores will resurface and continue to spread disease (Schmitthenner 1985). Many oospores can survive in the soil for an extended period without finding a host, resulting in crop death in many cases (Kato 2010). If a plant is infected with *P. sojae*, it is more prone to contract other soilborne disease in the future. Due to environmental factors, PSR impacts areas of the United States that grow soybean, but disease outbreaks are more common in the northern United States (Dorrance and Schmitthenner 2000).

Several advanced breeding studies in soybean have been conducted to identify genomic regions that are associated with resistance to *P. sojae*. For example, there were three quantitative trait loci (QTL) for partial resistance to a midwestern US isolate that Tucker et al. (2010) found in a population of 298 F₁₁ individuals that came from a cross between 'V71-370' (a *G. max* cultivar with moderate partial resistance) and PI 407162 (a *G. soja* accession), which came from a cross between 'V71-370' and PI 407162. Some 22–42% of the variation in phenotypic traits came from one PI 407126 gene that was found at a significant QTL on MLG J in three separate trials. This QTL is the same with the previously identified in 'Conrad' gene on MLG J (Weng et al. 2007). It's not clear why the resistance gene was passed down by the weaker paternal line from the QTL. The locations of RGA018 and a

minor QTL gene from ‘V71-320’ that was mapped to MLG I (Chr 18) were both found to be near each other. These genes account for 7–12% of the phenotypic variance. Second, PI 407162 (susceptible) had another QTL that was linked to MLG G. The disease-associated EST-SSR marker SLP142 was linked to this QTL, which accounted for 9–11% of the variance in three studies. Tucker et al. (2010) found no reason why the more vulnerable parent, PI 407162, was able to pass on resistance genes to the MLG-J and G QTL. Even though these genetic regions were mapped, only a few were used in actual breeding programs.

In this chapter, we first introduce the system of infection on *P. sojae* in root and stem of soybean. Then, we briefly discuss the mechanism of infection in soybean plant. Lastly, we highlight molecular breeding approaches such as quantitative trait loci (QTL) mapping and genome wide associate studies (GWAS) that identified genetic regions associated with resistance to *P. sojae*.

9.2 Symptoms of Infection in Root and Stem Rot

The intensity of infection on soybean plants during the vegetative and reproductive stages of growth is connected to the plant’s resistance. For example, it is easier for *P. sojae* to enter plants after the invasion because it increases the number of nodes in the stems of plants that are susceptible to root colonization. As a result of this process, the roots and stems of a plant may become deeper in color. The plants turn yellow, and orange is in full swing at this point of infection, and as long as it is not on both sides of the plant, it will continue to develop and spread. The wilted leaves of a dying plant cling to the plant for as long as they can to keep it alive. Plants that are highly sensitive or vulnerable to the disease may succumb to the elements during the growing season. Stem rot is not a problem for plants that have a high level of tolerance or partial resistance. When roots expand yet remain a pale brown color, it is possible that the plants develop stunted growth. This could prevent them from reaching their full potential as a result of their circumstances. Those plants that have developed a high level of partial defense in the field do not show any signs of resistance as long as they do not reduce their yield. During the growing season, root and stem infections in soybeans can occur independent of the environmental conditions present and can be transmitted via oospores. The oospores are the most common type of pathogen inoculum used in pathogen inoculation. Because not all the oospores germinate at the same time, infection with *P. sojae* is classified as a monocyclic disease. In order for a growing season to be productive, only one successful infection cycle must be completed, and despite that, inoculum can spread from root to root and contribute to disease transmission. As soon as one plant begins to show signs of infection, it is normal to notice ten more healthy plants in proximity.

9.3 Seed Rot and Damping-Off

It is necessary to combat the threat of *P. sojae*, a fungus that causes seed degeneration in plants as well as damping-off. When the soil is both damp and hot, the chances of its growth increases. At the temperature of 25–30 °C, disease has the greatest chance of spreading. Replanting is commonly required in fields with significant seed rot and preemergence damping-off. Their roots appear brown and mushy because there is insufficient water in the soil. The roots and hypocotyls will very certainly die as the plant grows and develops. *P. sojae* has been identified as a host-specific pathogen; several lupine (*Lupinus* spp.) species have been implicated in the transmission of disease. Despite the fact that it can live the entire year and generate oospores at any time of day or night, *P. sojae* is a fungus that can cause damage to plants at any stage of development (Dorrance 2018). Seed degeneration and seedling damping down are the first signs of an infected soybean plant, and they are the most severe (Schmitthenner 1985). The appearance of root rot and brown stem lesions will occur as soon as the plant is in its primary stage. As soon as the plants' leaves begin to turn yellow, they begin to degrade and eventually die. A smaller number of seeds and plants will germinate as a result (Schmitthenner 1985). The disease *P. sojae*, which is a monocyclic, can survive for an extended period. It can thrive in cold and damp environments, where it can grow in soil and plant waste (Schmitthenner 1985). For *P. sojae*, the soil must be moist and warm for oospores to develop into mycelia and spread throughout the plant. Mycelia are then released into the environment because of this process. The pathogens sporangia and zoospores are two of the most frequent infections. This occurs during the development of the mycelia. As mycelia mature, they produce an increasing number of sporangia and zoospores. There are two isoflavones found in soybeans that can form connections with the roots of plants that include them, namely, genistein and daidzein. Genistein is an isoflavone that is found in soybeans that can form connections with the roots of plants that contain it (Morris and Ward 1992). During the growing season, the zoospores form new plants around the roots of soybeans and penetrate the cell membrane of the root cells (Morris and Ward 1992). Fungi are creatures that live in and on the roots and stems of plants. It is the environment in which fungus can generate oospores and thrive (Schmitthenner 1985).

9.4 Advanced Molecular Breeding Approaches

Advanced breeding technologies have been employed to gain resistance against pathotypes at molecular level. The development of resistant cultivars through molecular breeding approaches is well demonstrated among major crops such as rice, wheat, and maize (Angeles-Shim et al. 2020; Gill et al. 2011; Yang et al. 2017). Resistance can be classified as (i) complete or (ii) partial resistance. Single dominant resistance genes (*Rps*) provide the complete resistance but are not effective for

numerous *P. sojae* pathotypes, whereas resistance provided by multiple genes is incomplete and allows some pathogens to reproduce (Mideros et al. 2007). Multiple genes at numerous loci controlled partial resistance and represented it as a quantitative trait; each locus has a minor effect, or a few have moderate effect (Kou and Wang 2010; St. Clair 2010). Components of defensive signal transduction have been implicated in this pathosystem. According to mechanistic investigations, plant physiology is regulated by pathways including the deposition of suberin in *P. sojae* resistance (Wang et al. 2012b). An in-depth analysis of the genomic areas is required to effectively exploit partial resistance.

A considerable number of low-cost genome-wide SNPs have resulted from recent improvements in high-throughput genotyping-by-sequencing processes. The generated SNP markers from these high-throughput sequencing technologies have been widely used for genomics studies, QTL mapping, and marker-assisted breeding (Scheben et al. 2017; Wallace and Mitchell 2017; Reyes et al. 2021; Kitony et al. 2021). These next-generation sequencing breakthroughs have also improved transcriptome profiling through RNA sequencing, enabling for the investigation of differentially expressed genes within QTL, which is an important validation tool for candidate genes. The Williams82 soybean genome has been sequenced, assembled, and annotated, allowing for the identification of SNPs using whole-genome sequencing (Song et al. 2016). Furthermore, QTL sequencing is a new approach that combines next-generation sequencing with analysis of bulk segregant to find markers related to specific traits (Terauchi et al. 2015). Another approach is the RNA sequencing which is an alternative technique focusing on protein coding regions as a genotyping tool (Scheben et al. 2017). Several studies which used molecular markers have identified genetic regions associated with of *P. sojae* and soybean infection; some of these are the restriction site-associated DNA sequencing (RAD-seq), SSRs, and chip-based genotyping platform (Sun et al. 2014a; Li et al. 2016; Rolling et al. 2020; Van et al. 2020).

9.5 R-Gene-Mediated Resistance

Resistance mediated through R-genes is a commonly used approach for PRR. Domestic soybean cultivars have shown positive responses to a few isolates of *P. sojae* and the development of single dominant resistance genes (*Rps*) has been documented for controlling PRR (Sugimoto et al. 2012). PRR-resistant cultivars for *P. sojae* are an effective way for sustainable development of crops. Resistance through *Rps* genes is race specific, and it is effective against a small number of *P. sojae* isolates. The *P. sojae* isolates may have avirulence (*Avr*) genes in their genomes, which correspond to the *Rps* genes identified in soybean. One or more dominant resistance genes influence resistance mediated by R-genes (*Rps*). It confers total resistance, although the *Rps2* gene, in particular, has been discovered to confer partial resistance and cause root lesions (Mideros et al. 2007; Wang et al. 2010). Complete and partial resistance are the two major types of resistance to PRR

that has been identified and handled by the *Rps* genes and multiple genes, respectively (Sugimoto et al. 2012). The first *Rps* gene was found in 1950s (Bernard et al. 1957), and there are now more than 30 *Rps* genes that have been found so far, on nine soybean chromosomes located on 21 loci (Zhang et al. 2013; Sun et al. 2014a, b; Sahoo et al. 2017; Zhong et al. 2018a, b). The *Rps* genes code for receptors that identify *P. sojae* effectors and elicit effector-triggered immunity (Dong et al. 2011). The expression of defense responses in infected plants was determined using the interaction between the *Rps* genes encoded protein and avirulence genes encoded effector proteins.

A study has been conducted in which plant breeders crossed the *P. sojae*-resistant and *P. sojae*-susceptible cultivars to identify a novel *Rps* gene. The novel gene is found in a gene-rich genomic area that also contains multiple nucleotide binding site leucine-rich repeats. The novel *Rps* gene is expected to be located in the chromosomal region, proximal between *Rps4* and *Rps6* and distal between *Rps5* and *Rps6*. Resistance gene *Rps12* is the name given to this putative *Rps* gene, which is likely to be very useful to *Phytophthora* resistance in soybeans (Sahoo et al. 2017).

Resistance locus *RpsHN* has been mapped in soybean using two mapping populations, initial and secondary population, with SSR markers. The markers SSRSOYN-25 and SSRSOYN-44 flanked the resistance gene on chromosome 3 (Niu et al. 2017). The *P. sojae* resistance locus, *RpsQ*, a single dominant resistant gene, has been localized to a 118-kb region on soybean chromosome 3. Qichadou 1, a Chinese soybean cultivar, displayed broad-spectrum resistance to *RpsQ* when inoculated with 36 Chinese *P. sojae* isolates. The gene induced by infection is Glyma.03 g27200, the best candidate gene of *RpsQ*. According to phenotypic analysis, *RpsQ* and *Rps9* are apparently the same genes that confer resistance to *P. sojae* (Li et al. 2017).

Zhong et al. (2018b) finely mapped a new *Phytophthora* resistance gene, *RpsZS18*, on chromosome 2 by using SSR markers in soybean cultivar. Quantitative real-time PCR analysis identified putative candidate resistance genes of *P. sojae* (Glyma.02g245700, Glyma.02g245800, and Glyma.02g246300). A combination of genetic mapping and QTL sequencing has employed to identify *Rps* genes in soybean. Researchers discovered a new *Rps* gene, *RpsHC18*, on chromosome 3 in soybean cultivars by using QTL-seq and genetic mapping methods (Zhong et al. 2018a). They also discovered *RpsX* in soybean cultivar by using the combination of QTL and genetic mapping that confer resistance to a large number of *P. sojae* isolates (Zhong et al. 2019).

Jiang et al. (2020) used a mapping population obtained from a hybrid of resistant and susceptible cultivars to identify a PRR resistance gene, *RpsGZ*, on chromosome 3. Genetic linkage map was used to explore the candidate genes with an average distance of 0.81 cM. Quantitative real-time PCR analysis identified putative candidate resistance gene Glyma.03 g05300 of *P. sojae*.

Previously, *Rps12* was identified (Sahoo et al. 2017), but recently, a new *Rps* that linked to the *Rps12* locus with a distance of 4 cM has been localized, named as *Rps13*. In soybeans, the tightly linked loci on the same chromosome, *Rps12* and *Rps13*, give broad-spectrum *Phytophthora sojae* resistance. Although both *Rps* have

a different race specificity to *P. sojae* isolates, it still shows effective results. The resistance locus *Rps13* gives resistance to isolate V13, which is pathogenic to recombinants lacking *Rps13* but containing *Rps12* (Sahoo et al. 2021).

According to a hybrid population derived from PI 340,029 and a susceptible cultivar, resistance to *P. sojae* race 1 is conferred by a single gene, *Rps14*. The *Rps14* resistance locus was localized to a 4.5 cM region on chromosome 3, which was then narrowed to a 1.48 cM flanked by tightly linked markers, InDel4033 and InDel4263. Further, broad-spectrum analysis characterized the resistance pattern of locus *Rps14* against *P. sojae*. For precise selection and deployment of *Rps14* for soybean protection, it would be critical to isolate the gene (Chen et al. 2021). These findings suggested that single genes influence the specificities of various *Rps* and will be used to drive cloning, gene transfer, and breeding of *P. sojae*-resistant soybean cultivars. Recently, Ping et al. (2016) identified the *Rps11* gene which confers greater resistance against *P. sojae*. SNP-based genotyping and SSR markers were used to genotype the mapping population of *Rps11* gene that can be used for marker-assisted selection in soybean.

The *P. sojae* population's virulence changes quickly, and a single race can develop many pathotypes that is capable of overcoming the resistance obtained through *Rps* genes (Wu et al. 2017). Furthermore, *P. sojae* populations have to face severe selection pressure after the deployment of *Rps* genes. In result, *P. sojae* adopt resistance to *Rps* genes and may acquire virulence to the point where these genes have no control on infection. *Rps* genes are only effective for 8–20 years, lowering their durability due to the adaptability of resistance induced by the novel *P. sojae* pathotypes (Dorrance et al. 2016). Therefore, breeders must continue their search for new *Rps* genes.

9.6 QTL Mapping

Partial or incomplete resistance has shown to be more durable and effective than R-gene-mediated resistance against a wide range of pathotypes. This sort of resistance results in less selection pressure, enhancing the durability of PRR management (Kou and Wang 2010). When compared to *Rps* gene resistance to *P. sojae*, partial resistance is conferred by multiple genes and provides a longer-lasting defense against the disease (Schneider et al. 2016). The main technique for identifying QTL that contributes to partial resistance to *P. sojae* is through QTL mapping using biparental mapping populations arising from a cross between parental lines with variable resistance patterns to *P. sojae*. The soybean cultivar 'Conrad' has been widely investigated by QTL analysis with many biparental populations and demonstrated highly significant partial resistance (Li et al. 2010; Stasko et al. 2016).

Multiple plant species have been studied using the QTL sequencing approach to map qualitative and quantitative traits of genes. Interactions between previously known genes and new candidate genes can be included to existing models to help researchers better understand the genetic and metabolic pathways that control these

traits. Directly measurable attributes can only reveal a part of the information about a biological pathway; hence, pleiotropic effects must be discovered to acquire a better biological understanding of the phenotype.

Quantitative trait loci sequencing (QTL-seq) has been used to develop partial resistance in soybeans, and it has proven to be more successful than *Rps* genes, resulting in identification of more than 70 QTL for partial resistance to *P. sojae* (Nguyen et al. 2012; Lee et al. 2013a; Scott et al. 2019; de Ronne et al. 2020).

Mutual response to *P. sojae* may occur upon inoculation of specific isolates. For example, after the crossing of soybean cultivars ‘Conrad’ and ‘Sloan’, similar QTL were found against three isolates of *P. sojae*. The expression analysis of candidate genes identified hormonal defense pathways, signal transmission, and *Rps* genes that were no longer effective, all linked to high level of partial resistance (Wang et al. 2012a). Multiple isolates found two loci on chromosome 19 to be highly effective (Stasko et al. 2016). The QTL of cultivar Conrad (Stasko et al. 2016), Hefeng25 (Han et al. 2017), and PIs from South Korea (Jang et al. 2020) have been extensively studied for partial resistance. Although the majority of QTL have little variance, some were discovered to account for more than 20% of phenotypic variance (Lee et al. 2014).

A single QTL has been found on chromosome 5 and chromosome 11 from a cross of cultivar PI399036 and AR3 line (Abeysekara et al. 2016) and a cross between Conrad and Hefeng25 cultivars (Li et al. 2010), respectively. The identified QTL has contribution between 1.9 and 35% of the phenotypic variance (PVE). In a population derived from a hybrid of PI 427105B and OX20-8, a QTL with the highest phenotypic diversity of 45% was discovered on Chr 18 (Lee et al. 2014).

Some weak *Rps* genes may play a role in high levels of partial resistance, as some plant introductions (PIs) lack any *Rps* gene that was effective against the *P. sojae* isolates. In two PIs, 398841 and 407861A, a few partial resistance QTL have been found near known *Rps* loci and have high levels of partial resistance to *P. sojae*. The *Rps* loci were located on chromosome 3 and 13 at variable regions in these PIs (Lee et al. 2013a, b)

Previously, five QTL have been identified in ‘Hefeng 25’ and thought to have similar tolerance pattern to ‘Conard’ (Li et al. 2010). Han et al. (2017) discovered nine more QTL in ‘Hefeng 25’ through two populations (HD and HM) that underlie PRR tolerance against *P. sojae*. A total of nine QTL contributed wherein four QTL were from HD population (‘Hefeng 25’ and ‘Dongnong 93046’) and five QTL from HM population (‘Hefeng 25’ and ‘Maple Arrow’), and the phenotypic variance (PVE) ranged from 1.27% to 12.65%. These QTL had a stronger additive effect and persist across multiple circumstances and genetic origins. In addition, multiple studies have discovered that genetic influences such as additive and epistatic effects play a significant part in soybean disease resistance. However, these genetic impacts were poorly investigated. de Ronne et al. (2020) identified two QTL from an inbred line population of PI 449459 and Misty that have resistance to *P. sojae*. The QTL were discovered on chromosomes 13 and 19, with phenotypic variances of 17.6% and 13.1%, respectively.

de Ronne et al. (2021) discovered a new resistance QTL using hydroponic inoculation method. The novel QTL significantly increased resistance to a wide variety of *P. sojae* pathotypes. The QTL, which extends around 500 kb on chromosome 15, does not coincide with previously discovered QTL for resistance. Breeders combined the phenotypic characterization with hydroponic assay through whole genome sequencing. Plants with this QTL were 60% more resistant to *P. sojae*, and *Glyma.15G217100* was found to be a candidate gene.

Although this technique has been proven to be effective, it does have certain drawbacks, such as restricted allelic variation among the mapping population. It is critical to investigate a broader spectrum of common resistance alleles within the diversity of QTL leading to partial resistance to a variety of *P. sojae* pathotypes.

9.7 Genome-Wide Association Studies

The use of genome-wide association studies, which are carried out on soybean accessions, is relatively a new technique for *P. sojae* resistance. The interaction between a phenotype and genetic variants spread across the genome is investigated in GWAS analysis. Because of the advancement of next-generation sequencing technologies, the whole strategy has profited from the production of a significantly larger number of markers (Ballard et al. 2020). Plant scientists have frequently conducted GWAS analysis in agricultural species, including soybean cultivars. Because of developments in high-throughput sequencing technologies, rapid, economical, and accurate whole-genome sequencing of a large number of species is now possible (Kersey 2019). Prior to GWAS, marker data availability and the advent of new statistical approaches have provided incredible chances to grow and learn from old data and fill in gaps (Bandillo et al. 2017; Zhang et al. 2017). This allows for the collection of a considerably broader range of QTL and alleles, as well as a much greater level of precision in determining the genomic region where a QTL appears.

Gene mapping has been widely used to assess complex traits in various agricultural crops using high-density genotyping with SNP markers (Li et al. 2016). Large datasets of SNP markers have increased the likelihood of wrong marker-trait association. This then necessitates the application of many complex statistical models to discover the QTL (Huang et al. 2019; Kaler et al. 2020). The phenotyping of a germplasm sample with efficient method is critical for identification of favorable genes that contribute to resistance to *P. sojae* for GWAS success. Using high-density SNP markers, genome-wide association mapping has successfully examined complex trait variation in soybean to evaluate alleles for disease resistance and agronomic traits (Li et al. 2016).

Li et al. (2016) used 59,854 high-quality SNPs in a GWAS analysis of soybean to find quality markers and genes linked to *P. sojae* resistance. The findings could help researchers construct more durable resistance based on genes, as well as to gain a better understanding of the genetic basis of partial resistance to *P. sojae*. Genome-wide association studies have discovered more than 70 QTL related to

soybean partial resistance against *P. sojae*. However, a majority of them have a minimal impact on resistance levels or are restricted to a single phenotypic trait, limiting their application in breeding programs.

Ludke et al. (2019) used 3807 high-quality SNPs in a GWAS analysis to find markers and genes linked to *P. sojae* resistance. Multiple linear models were used to conduct genome-wide association analysis. Two QTL on each, chromosomes 3 and 15, were found to be effective. The use of these markers could improve the efficiency of breeding programs for *P. sojae*-resistant soybean varieties.

9.8 Conclusion

Resistance to plant root and rot (PRR) will remain a priority in many breeding projects as *P. sojae* has established itself in several soybean-producing regions throughout the world. Despite the fact that resistance obtained from *Rps* genes has been beneficial, breeders have also discovered the benefit of partial resistance, more durable and broader resistance than a single gene resistance. Molecular markers such as SNPs and SSRs could be used in marker-assisted selection (MAS) to swiftly identify seedlings carrying the resistance gene. Resistance by some *Rps* genes and QTL has provided adequate protection in regions where *Phytophthora*-resistant cultivars have been established.

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