Recent Findings Unravel Genes and Genetic Factors Underlying *Leptosphaeria maculans* Resistance in *Brassica napus* and Its Relatives

Aldrin Y. Cantila, Nur Shuhadah Mohd Saad, Junrey C. Amas, David Edwards and Jacqueline Batley*

School of Biological Sciences, University of Western Australia, Perth, WA 6009, Australia; aldrin.cantila@research.uwa.edu.au (A.Y.C.); nur.mohdsaad@research.uwa.edu.au (N.S.M.S.); junrey.amas@research.uwa.edu.au (J.C.A.); dave.edwards@uwa.edu.au (D.E.)

* Correspondence: jacqueline.batley@uwa.edu.au; Tel.: +61-(0)8-6488-5929

**Abstract:** Among the *Brassica* oilseeds, canola (*Brassica napus*) is the most economically significant globally. However, its production can be limited by blackleg disease, caused by the fungal pathogen *Leptosphaeria maculans*. The deployment of resistance genes has been implemented as one of the key strategies to manage the disease. Genetic resistance against blackleg comes in two forms: qualitative resistance, controlled by a single, major resistance gene (*R* gene), and quantitative resistance (QR), controlled by numerous, small effect loci. *R*-gene-mediated blackleg resistance has been extensively studied, wherein several genomic regions harbouring *R* genes against *L. maculans* have been identified and three of these genes were cloned. These studies advance our understanding of the mechanism of *R* gene and pathogen avirulence (*Avr*) gene interaction. Notably, these studies revealed a more complex interaction than originally thought. Advances in genomics help unravel these complexities, providing insights into the genes and genetic factors towards improving blackleg resistance. Here, we aim to discuss the existing *R*-gene-mediated resistance, make a summary of candidate *R* genes against the disease, and emphasise the role of players involved in the pathogenicity and resistance. The comprehensive result will allow breeders to improve resistance to *L. maculans*, thereby increasing yield.

**Keywords:** *Brassica napus*; blackleg; resistance genes

1. **Introduction**

The Brassicaceae family consists of diverse members, comprised of 372 genera and 4060 species [1]. The members include, but are not limited to, domesticated and wild root vegetables like turnip (*Brassica rapa* ssp. *rapa*, ssp. *oleifera*), swede (*Brassica napus* var. *napobrassica*), kohlrabi (*Brassica oleracea* var. *gongylodes*), radish (*Raphanus sativus*), and leafy vegetables (*B. rapa* ssp. *chinensis*, *B. oleracea* var. *viridis*, var. *acephala*, *Eruca sativa*, *Diplotaxis tenuifolia*) like cabbages (*B. oleracea* var. *capitata*, *Brassica fruticulosa*, *C. monensis*), broccoli (*B. oleracea* var. *italica*), cauliflower (*B. oleracea* var. *botrytis*), Brussel sprouts (*B. oleracea* var. *gemmifera*), mustards (*Brassica juncea*, *Brassica nigra*, *Brassica carinata*, *Brassica elongata*, *Hirschfeldia incana*, *Sinapis arvensis*, *Sinapis alba*), oilseed crops (*B. napus*, *B. rapa*, *B. juncea*, *Camelina sativa*), and a model plant (*Arabidopsis thaliana*). Interspecific hybridisations between diploid *B. rapa* (AA, 2n = 20), *B. nigra* (BB, 2n = 16), and *B. oleracea* (CC, 2n = 18) resulted in allotetraploid *B. juncea* (AABB, 2n = 4x = 36), *B. napus* (AACC, 2n = 4x = 38), and *B. carinata* (BBCC, 2n = 4x = 34), as shown in the triangle of U [2]. These Brassicaceae plant species have gained economic importance as condiments, dyes, medicinal uses, scientific models, ornamentals, vegetables, and the profitable canola oilseed [3–8]. The International Food Standards identified canola oil as those with low-erucic acid varieties from polyploid *B. napus* and *B. juncea* or diploid *B. rapa* [9].

Oilseed *Brasses* are ranked second behind soybean in terms of worldwide production, with 75 million tonnes with an estimated value of 62.23 billion USD, cultivated over...
38 million hectares in 63 countries in 2018 [10]. The top five producing countries, Canada, China, India, France and Australia, share 68% and 72% of the total production and cultivation, respectively (Table 1) [10]. Canola oil is recommended by health experts due to the low levels of saturated fat and high levels of omega-3 and -6 [11,12]. The oil can also be used for the production of margarine and as an additive for biodiesel, feedstock, fertilizer, adhesives, plastics and lubricants. The world export rate for canola oil and derived products is expected to rise from 20% to 40% in the coming years [13].

Table 1. The top 10 producing countries for canola with corresponding area harvested and yield in 2018 [10].

| Country   | Production (Tonnes, 10^6) | Area Harvested (Ha, 10^6) | Yield (Tonnes Per Ha) |
|-----------|--------------------------|---------------------------|-----------------------|
| 1. Canada | 20.34                    | 9.12                      | 2.23                  |
| 2. China  | 13.28                    | 6.55                      | 2.03                  |
| 3. India  | 8.43                     | 6.70                      | 1.26                  |
| 4. France | 4.95                     | 1.62                      | 3.06                  |
| 5. Australia | 3.89                   | 3.17                      | 1.23                  |
| 6. Germany | 3.67                    | 1.22                      | 3.00                  |
| 7. Ukraine | 2.75                     | 1.04                      | 2.65                  |
| 8. Poland | 2.20                     | 0.84                      | 2.64                  |
| 9. USA    | 2.01                     | 0.79                      | 2.55                  |
| 10. Russia| 1.99                     | 1.50                      | 1.33                  |

Blackleg disease, caused by the fungal pathogen *Leptosphaeria maculans*, is considered as one the main constraints to *B. napus* production [14–16]. The pathogen inoculum is disseminated through air and rain splashes [17], and may remain in infected crop residues for many years through the production of fruiting bodies (pycnidia and pseudothecia) [18,19]. *L. maculans* is a highly adapted fungal pathogen, capable of infecting all parts of the canola plant. Initially, spores enter into leaf openings or wounds, where they initiate a biotrophic mode of infection and eventually transition to a necrotrophic lifestyle as they find their way into the stem, leading to stem canker development. This stem colonization disrupts the nutrient flow and affects metabolic processes, ultimately killing the plant [20–27].

The first reported blackleg outbreak in *Brassica* was documented in *B. oleracea* [28]. Significant losses in *B. napus* were later reported in 1961 and 1972 in Canada and Australia, respectively [29–31]. An average of 10 to 20% annual yield losses is associated with this disease across canola-growing regions [19,32–35]. In uncontrolled conditions, losses range between 30% and 50% [36], with severe loss correlated to early seedling stage infection, particularly in the four- to five-leaf stage [36,37]. One of the most damaging incidences was documented in the Eyre Peninsula of South Australia following the breakdown of resistance of the cultivar Surpass 400 in 2003. This outbreak resulted in 90% production loss, equating to approximately 7.3 million USD [38,39].

Plants protect themselves by providing non-specific barriers in physical forms, such as a rigid cell wall [40,41], and chemical systems, such as producing proteins, sugars, lipoglycans and endotoxins [42,43]. When these barriers are overcome by pathogens, plants initiate a two-layered immunity response. The first layer involves detection of the pathogen-associated molecular patterns (PAMP) by the surface-localized receptors; this phase is termed PAMP-triggered immunity or PTI. However, PTI usually only leads to a mild defense response [44,45], which can be overridden by some pathogen races. As a counter response, the second layer of inducible response, called effector-triggered immunity (ETI), is initiated. This response relies on the interaction of a plant resistance gene (*R* gene), encoding recognition receptors, with race-specific pathogen effectors, encoded by avirulence (*Avr*) genes. This interaction usually leads to a hypersensitive defense response, which is usually manifested in rapid cell death, thereby limiting further pathogen growth, and phenotypically observed as complete resistance [45–47].
Based on conserved motifs, domains and features, *R* genes may be grouped into different classes collectively known as resistance gene analogs (RGAs). Three broad classes of RGAs are known: nucleotide-binding site-leucine rich repeats (NLRs), receptor-like protein kinases (RLKs), and receptor-like proteins (RLPs) [44,48,49]. Among them, NLRs are the largest class of RGAs predominately involved in plant disease resistance [50–52], whilst surface-localised RLKs and membrane-associated RLPs are pattern recognition receptors and integral components of the first line of defense [49,53,54], and have also been known to be involved in growth and development processes in plants [55].

There are two mechanisms controlling blackleg resistance. Qualitative resistance is generally controlled by a single major gene and is race-specific seedling resistance, active from the cotyledon through to the adult plant [56–59], while quantitative resistance is governed by multiple minor genes and is a partial resistance that is expressed in the later stages at leaf petioles and stem tissues [32,60]. To date, at least 16 *R* genes against blackleg have been genetically mapped in *B. napus* and other *Brassica* species (Figures 1 and 2, Table 2). Of these, three have been cloned, and some of the 13 other genes are suspected to be identical or allelic forms due the different populations and markers used in their mapping (Figure 2). While *R* genes have been known to effect complete resistance, some *R* genes (*Rlm1, Rlm3, Rlm6, Rlm7, LepR1, and LepR3*) have been reported to break down and lose effectiveness in the field [38,61–66]. Currently, the deployment of *R* genes by crop rotation in canola cultivars is an integral approach to sustainably manage canola cultivation against blackleg infection and resistance breakdown [35,67,68].

![Figure 1](image-url)

**Figure 1.** The complex interaction between resistance (*R*) genes and counterpart avirulence (*Avr*) genes mediating blackleg resistance in canola. *R* genes located in the same block (green) are allelic or suspected to be allelic forms. *Avr* genes that mask other interactions are indicated by an “x” sign. Genes (*R* and *Avr*) with an asterisk represent cloned genes. *Avr* genes with a question mark (?) are hypothetical genes that have not been isolated/discovered to date.
Figure 2. Current physical location of the known blackleg R genes based on quantitative trail loci (QTL) and candidate gene positions. Mb = million base pairs; B. napus pangenome [69–71], B. oleracea pangenome [72,73], B. juncea genome v. 1.5 [74] and B. rapa genome v. 3.0 [75].

Table 2. List of candidate genes harbouring resistance to *Leptosphaeria maculans* with their reported resistance gene analog (RGA) function along with their closest gene ortholog having disease resistance/other function.

| Gene (Position) | Candidate Genes | RGA Type | Gene Ortholog (TAIR10) | Molecular Function | References |
|-----------------|-----------------|----------|------------------------|--------------------|------------|
| *Rlm1* (A07 in Bna) | BnaA07g28760D | RLP      | AT1G56140               | LRR TM prot_k      | [76]       |
|                 | BnaA07g29310D   | RLK      | AT1G71390               | RLP 11             | [76]       |
|                 | BnaA07g27720D   | NLR      | AT1G69160               | BIG GRAIN LIKE 1 supressor | [76]       |
|                 | BnaA07g28550D   | -        | AT1G33612               | Receptor for the Plant Natriuretic Peptide | [76]       |
|                 | BnaA07g28840D   | RLK      | AT1G70740               | Prot_k superfam_prot | [77]       |
|                 | BnaA07g27460D   | RLK      | AT1G68830               | STN7 prot_k        | [78]       |
Table 2. Cont.

| Gene (Position) | Candidate Genes | RGA Type | Gene Ortholog (TAIR10) | Molecular Function | References |
|-----------------|-----------------|----------|------------------------|--------------------|------------|
| **Rlm3, Rlm4 & Rlm7 (A07 in Bna)** | **BnaA07g20490D** | RLK | AT1G79909 | Protein PAT1 homolog | [76] |
|                 | **BnaA07g20910D** | NLR | AT1G77610 | UDP-galactose transporter 1 | [76] |
|                 | **BnaA07g17000D** | NLR | AT1G12220 | DRP RPS5/nucleotide binding | [79] |
|                 | **BnaA07g17760D** | RLK | AT1G56145 | LRR TM prot_k | [79] |
|                 | **BnaA07g18000D** | RLK | AT3G58690 | Prot_k superfam_prot | [79] |
|                 | **BnaA07g18480D** | RLK | AT3G59700 | L-type lectin-domain containing receptor kinase V.5 | [79] |
|                 | **BnaA07g20630D** | RLK | AT1G78290 | SRK2C/ST_k | [79] |
|                 | **BnaA07g18680D** | TM-CC | AT3G60470 | LRR TM prot_k | [79] |
|                 | **BnaA07g18770D** | TM-CC | AT3G60600 | VAP 1-1/protein binding | [79] |
|                 | **BnaA07g18880D** | TM-CC | AT3G61050 | NTMC2T4/lipid binding | [79] |
|                 | **BnaA07g19680D** | TM-CC | AT1G79830 | GC5 (golgin candidate 5)/protein binding | [79] |
|                 | **BnaA07g20240D** | RLK | AT1G79640 | Prot_k superfam_prot/ST_k tyrosine | [80] |
| **Rlm12 (A01 in Bna)** | **BnaA01g12900D** | RLP | AT4G23100 | Glutamate-cysteine ligase, chloroplastic | [81] |
|                 | **BnaA01g12800D** | RLP | AT4G22990 | Major Facilitator Superfamily with SPX | [81] |
|                 | **BnaA01g12940D** | RLP | AT4G23240 | Putative cysteine-rich RLP kinase 16 | [81] |
|                 | **BnaA02g15610D** | RLK | AT1G71870 | Protein DETOXIFICATION 54/MATE efflux fam_prot | [70,76] |
|                 | **BnaA02g15810D** | RLK | AT1G72140 | Protein NRT1/PTR FAMILY 5.12/proton-dependent oligopeptide transport (POT) fam_prot | [70,76] |
|                 | **BnaA02g15820D** | RLK | AT1G72150 | Patellin-1/transporter | [70,76] |
|                 | **BnaA02g15890D** | RLK | AT1G72290.1 (CDS) | Cysteine protease inhibitor WSCP | [70,76] |
|                 | **BnaA02g16700D** | RLK | AT2G18910 | Expressed protein/hydroxyproline-rich glycoprotein fam_prot | [70,76] |
|                 | **BnaA02g16770D** | RLK | AT1G74190 | RLP 15 | [70,76] |
|                 | **BnaA02g16960D** | NLR | AT1G30490.1 (CDS) | Homeobox-leucine zipper protein ATHB-9 | [70,76] |
|                 | **BnaA02g18160D** | TM-CC | AT1G76570 | Chlorophyll a-b binding protein 7, chloroplastic | [70,76] |
|                 | **BnaA02g20380D** | RLK | AT4G01440 | WAT1-related protein | [70,76] |
|                 | **BnaA02g20440D** | RLK | AT4G01590 | DNA-directed RNA polymerase III subunit | [70,76] |
|                 | **BnaA02g20610D** | RLK | AT4G02510 | Translocase of chloroplast 159, chloroplastic/TM receptor | [70,76] |
|                 | **BnaA02g21110D** | RLK | AT5G19010 | MAP kinase 16 | [70,76] |
Table 2. Cont.

| Gene (Position) | Candidate Genes | RGA Type | Gene Ortholog (TAIR10) | Molecular Function | References |
|-----------------|-----------------|----------|------------------------|--------------------|------------|
| BnaA02g21890D   | RLK             | AT4G11010| Nucleoside diphosphate kinase/ATP binding | [70,76]            |
| BnaA02g22210D   | RLK             | AT5G43370| Probable inorganic phosphate transporter 1-2 | [70,76]            |
| BnaA02g22280D   | RLK             | AT5G43710| Alpha-mannosidase/glycoside hydrolase family 47 protein | [70,76]            |
| BnaA02g22610D   | NLR             | AT5G40910| DRP (TNL class)         | [70,76]            |
| BnaA02g23050D   | TM-CC           | AT5G42570| Intracellular protein transport | [82,83]            |
| BnaA02g24000D   | NLR             | AT5G45490| Probable DRP            | [82,83]            |
| BnaA02g24440D   | RLP             | AT5G46330| LRR RLP kinase/TM ST_k   | [82,83]            |
| BnaA02g24500D   | NLR             | AT5G46510| DRP (TNL class)         | [82,83]            |
| BnaA02g24510D   | NLR             | AT5G46450| DRP (TNL class)         | [82,83]            |
| BnaA02g24530D   | NLR             | AT5G46450| DRP (TNL class)         | [82,83]            |
| BnaA02g24540D   | NLR             | AT5G46450| DRP (TNL class)         | [82,83]            |
| BnaA02g24560D   | NLR             | AT5G46451| DRP (TNL class)         | [82,83]            |
| BnaA02g25110D   | NLR             | AT5G47220| Ethylene responsive element binding factor 2 | [84]               |
| BnaA10g03460D   | RLK             | AT1G05300| Zinc transporter 5      | [70,76]            |
| BnaA10g06440D   | RLK             | AT5G30370| Ribosomal protein L9/RNase H1 | [70,76]            |
| BnaA10g07140D   | RLK             | AT3G15240| ST_k WNK (With No Lysine)-like protein | [70,76]            |
| BnaA10g09460D   | NLR             | AT5G55220| Trigger factor-like protein TIG, chloroplastic | [70,76]            |
| BnaA10g09870D   | RLK             | AT5G55670| RNA-binding (RRM/RBD/RNP motifs) fam_prot | [70,76]            |
| BnaA10g10000D   | NLR             | AT5G55910| ST_k D6PK               | [70,76]            |
| BnaA10g12510D   | RLK             | AT5G59200| Putative pentatricopeptide repeat-containing protein, chloroplastic | [70,76]            |
| BnaA10g13610D   | NLR             | AT5G60000| TM protein              | [70,76]            |
| BnaA10g14660D   | RLK             | AT5G20900| TIFY 3B/JAZ12 (JASMONATE-ZIM-DOMAIN PROTEIN 12) | [70,76]            |
| BnaA10g14840D   | RLK             | AT5G20670| Unknown protein         | [70,76]            |
| BnaA10g06390D   | RLK             | AT5G30300| PP2A regulatory subunit TAP46 | [70,76]            |
| BnaA10g07390D   | RLK             | AT5G52520| Proline-tRNA ligase, chloroplastic/mitochondrial | [70,76]            |
| BnaA10g07400D   | RLK             | AT5G52510| SCL8                    | [70,76]            |
| BnaA10g07410D   | RLK             | AT5G52510| SCL8                    | [70,76]            |
| BnaA10g07650D   | RLK             | AT5G51970| Sorbitol dehydrogenase  | [70,76]            |
| BnaA10g09120D   | RLK             | AT5G54850| Unknown protein         | [70,76]            |
| BnaA10g09500D   | RLK             | AT5G55280| Cell division protein FtsZ homolog 1, chloroplastic | [70,76]            |
Table 2. Cont.

| Gene (Position) | Candidate Genes | RGA Type | Gene Ortholog (TAIR10) | Molecular Function | References |
|----------------|-----------------|----------|------------------------|--------------------|------------|
| BnaA10g10380D | RLK             | AT5G56220| P-loop containing nucleoside triphosphate hydrolases superfam_prot/nucleotide binding | [70,76]           |
| BnaA10g10430D | RLK             | AT5G56210| WPP domain-interacting protein 2 | [70,76]           |
| BnaA10g11120D | RLK             | AT5G57110| Calcium-transporting ATPase | [70,76]           |
| BnaA10g11930D | RLK             | AT5G58410| E3 ubiquitin-protein ligase listerin/zinc ion binding | [70,76]           |
| BnaA10g12560D | RLK             | AT5G59610| Chaperone DnaJ-domain superfam_prot/DNAJ heat shock N-terminal domain-containing protein | [70,76]           |
| BnaA10g12830D | RLK             | AT4G34110| Polyadenylate-binding/RNA binding/translation initiation factor | [70,76]           |
| BnaA10g12860D | RLK             | AT5G59900| Putative pentatricopeptide repeat-containing protein | [70,76]           |
| BnaA10g12870D | RLK             | AT5G22880| Histone H2B/DNA binding | [70,76]           |
| BnaA10g12880D | RLK             | AT5G59950| RNA-binding fam_prot/RNA and export factor-binding protein | [70,76]           |
| BnaA10g12890D | RLK             | AT5G59990| CCT motif fam_prot | [70,76]           |
| BnaA10g12900D | RLK             | AT5G60020| Laccase-17 | [70,76]           |
| BnaA10g12950D | RLK             | AT5G60120| Target of early activation tagged (EAT) 2/TF | [70,76]           |
| BnaA10g14170D | RLK             | AT5G22170| TM protein | [70,76]           |
| BnaA10g14640D | RLK             | AT2G24080| F-box protein (DUF295) | [70,76]           |
| BnaA10g15480D | RLK             | AT5G19690| Dolichyl-diphosphooligosaccharide-protein glycosyltransferase subunit STT3A | [70,76]           |
| BnaA10g18330D | RLK             | AT5G16000| Protein NSP-INTERACTING KINASE 1 | [70,76]           |
| BnaA10g19700D | RLK             | AT5G13870| Xyloglucan endotransglucosylase/hydrolase | [70,76]           |
| BnaA10g20110D | RLK             | AT5G13180| NAC domain-containing protein 83/TF | [70,76]           |
| BnaA10g23030D | RLK             | AT5G08450| Zinc finger CCCH domain protein | [70,76]           |
| BnaA10g23040D | RLK             | AT5G08440| Unknown protein | [70,76]           |
| BnaA10g26650D | RLK             | AT5G03290| Isocitrate dehydrogenase (NAD) catalytic subunit 5, mitochondrial | [70,76]           |
| **BLMR1 (A10 in Bna)** | | | | | |
| BnaA10g21910D | -               | AT5G10360| 4OS ribosomal protein S6 (RPS6B) | [85]            |
| BnaA10g19660D | -               | AT3G17620| Putative F-box domain protein | [85]            |
| **BLMR2 (A10 in Bna)** | | | | | |
| BnaA10g11390D | -               | AT5G57340| Ras guanine nucleotide exchange factor Q-like protein | [85]            |
| BnaA10g11500D | TM              | AT5G57560| Xyloglucan endotransglucosylase/hydrolase | [85]            |
| Gene (Position) | Candidate Genes | RGA Type | Gene Ortholog (TAIR10) | Molecular Function | References |
|----------------|----------------|----------|------------------------|--------------------|-----------|
| **LepR4 (A06 in Bra)** | Bra018037 | NLR | AT5G17680 | DRP (TNL class) | [86] |
| | Bra018057 | NLR | AT5G66900 | DRP (CNL class) | [86] |
| | Bra018198 | NLR | AT3G46710 | DRP (CNL class) | [86] |
| | Bra019483 | NLR | AT2G15530 | RING/U-box superfamily_prot | [86] |
| **Rlm1 (C06 in Bol)** | Bo6g077080 | NLR | AT3G60490 | Ethylene-responsive TF ERF035 APETALA2 | [87] |
| | Bo6g088090 | RLK | AT1G73080 | RLP kinase LRR-RLK, STKc | [87] |
| | Bo6g080150 | RLK | AT1G80080 | Protein TOO MANY MOUTHS_TMM LRR | [87] |
| | Bo6g093010 | RLK | AT1G71830 | Somatic embryogenesis receptor kinase 1 LRR-RLK, STKc | [87] |
| | Bo6g089160 | NLR | AT1G72890 | DRP (TIR-NBS class) | [87] |
| | Bo6g089290 | NLR | AT1G72850 | DRP (TIR-NBS class) | [88] |
| **LepR1 (C02 in Bol)** | Bo2g093170 | NLR | AT1G57850 | TIR domain protein family | [88] |
| | Bo2g095430 | LRR | AT1G22000 | Putative F-box/LRR protein | [88] |
| | Bo2g095460 | RLK | AT1G79620 | LRR RLP kinase | [88] |
| | Bo2g103360 | NLR | AT5G36930 | DRP (TNL class) | [88] |
| | Bo2g103380 | LRR | AT4G03220 | Putative F-box/LRR protein | [88] |
| | Bo2g104830 | LRR | AT3G47580 | LRR RLP kinase | [88] |
| | Bo2g118150 | RLK | AT1G56120 | LRR TM prot_k | [88] |
| | Bo2g118200 | RLK | AT1G56130 | Probable LRR RLK ST_k | [88] |
| | Bo2g124490 | NLR | AT1G63730 | DRP (TNL class) | [88] |
| | Bo2g124590 | RLK | AT3G44700 | LRR RLK ST_k GSO2 | [88] |
| | Bo2g125680 | RLK | AT3G47570 | Probable LRR RLK ST_k | [88] |
| | Bo2g125700 | RLK | AT3G20480 | LRR RLK ST_k | [88] |
| | Bo2g126850 | NLR | AT5G45220 | DRP (TNL class) | [88] |
| | Bo2g126860 | NLR | AT2G17050 | DRP (TNL class) | [88] |
| | Bo2g126870 | NLR | AT3G45210 | DRP (TNL class) | [88] |
| | Bo2g126880 | NLR | AT5G17880 | Disease resistance-like protein CSA1 | [88] |
| | Bo2g126900 | NLR | AT5G45220 | DRP (TNL class) | [88] |
| | Bo2g126920 | NLR | AT5G45230 | DRP (TNL class) | [88] |
| | Bo2g126980 | NLR | AT5G45240 | DRP (TNL class) | [88] |
| | Bo2g127270 | NLR | AT5G45490 | Probable DRP | [88] |
| | Bo2g127290 | NLR | AT5G45490 | Probable DRP | [88] |
| | Bo2g127320 | NLR | AT5G45510 | Probable DRP | [88] |
| | Bo2g129990 | RLK | AT3G46330 | LRR RLP kinase | [88] |
| | Bo2g130040 | NLR | AT5G46470 | DRP RPS6 | [88] |
| | Bo2g130050 | LRR | AT3G40060 | DRP (NLR class) | [88] |
| | Bo2g130080 | NLR | AT5G46270 | DRP (TNL class) | [88] |
| | Bo2g130090 | NLR | AT5G46450 | DRP (TNL class) | [88] |
Table 2. Cont.

| Gene (Position) | Candidate Genes | RGA Type | Gene Ortholog (TAIR10) | Molecular Function | References |
|-----------------|-----------------|----------|------------------------|-------------------|------------|
| Bo2g130100      | NLR             | AT5G46450| DRP (TNL class)        | [88]              |
| Bo2g130110      | NLR             | AT4G08450| DRP (TNL class)        | [88]              |
| Bo2g130150      | NLR             | AT4G08450| DRP (TNL class)        | [88]              |
| Bo2g130180      | NLR             | AT5G46450| DRP (TNL class)        | [88]              |
| Bo2g131530      | NLR             | AT4G16920| DRP (TNL class)        | [88]              |
| Bo2g131540      | NLR             | AT5G46270| DRP (TNL class)        | [88]              |
| Bo2g131590      | NLR             | AT5G46450| DRP (TNL class)        | [88]              |
| Bo2g131610      | NLR             | AT5G46260| DRP (TNL class)        | [88]              |
| Bo2g131620      | NLR             | AT5G40060| DRP (NLR class)        | [88]              |
| LepR2 (C09 in Bol) | Bo9g111490      | LRR      | AT1G51370              | F-box domain/LRR protein | [89] |
|                 |                 |          | AT5G25850              | Putative F-box domain/LRR protein | [89] |
|                 |                 |          | AT3G53840              | F-box domain/LRR protein | [89] |
|                 |                 |          | AT5G53890              | LRR RLP kinase      | [89] |
|                 |                 |          | AT3G54380              | RLP kinase THESEUS 1 | [89] |
|                 |                 |          | AT5G55090              | MAP kinase 15       | [89] |
|                 |                 |          | AT5G66330              | LRR fam_prot       | [89] |
|                 |                 |          | AT5G65640              | LRR RLP kinase      | [89] |
|                 |                 |          | AT3G56780              | F-box domain/LRR protein | [89] |
|                 |                 |          | AT5G56560              | F-box domain/LRR protein | [89] |
|                 |                 |          | AT5G65650              | F-box domain/LRR protein | [89] |
|                 |                 | RLK      | AT3G47580              | MAP kinase 6        | [89] |
|                 |                 |          | AT2G42480              | MATH & CC domain-containing protein | [89] |
| LepR4 (C03 in Bol) | Bo3g099380      | RLK      | AT5G65240              | LRR prot_k         | [90] |
|                 |                 |          | AT4G36150              | DRP (TNL class)    | [90] |
|                 |                 |          | AT3G63710              | LRR prot_k         | [90] |
|                 |                 |          | AT3G62710              | LRR prot_k         | [90] |
|                 |                 |          | AT1G53510              | MAP Pkinase 18      | [90] |
|                 |                 |          | AT3G47090              | LRR prot_k         | [90] |
|                 |                 |          | AT3G47090              | MAP Pkinase_Tyr, ST_k | [90] |
|                 |                 |          | AT3G45640              | MAP Pkinase         | [90] |
|                 |                 |          | AT3G47580              | LRR protein Pkinase | [90] |
| LepR4 (C08 in Bol) | Bo8g077170      | RLK      | AT1G53510              | MAP Pkinase 18      | [90] |
|                 |                 |          | AT5G17680              | DRP (TNL class)    | [90] |
|                 |                 |          | AT3G48860              | CC domain containing protein SCD2 | [90] |
| Rlm6 (A07 in Bju) | BjuA027357      | RLK      | AT1G66830              | Probable inactive LRR RLP kinase | [91] |
|                 |                 |          | AT1G67510              | LRR prot_k fam_prot | [91] |
|                 |                 |          | AT1G10850              | LRR prot_k fam_prot/ST_k | [91] |
|                 |                 |          | AT1G11130              | LRR prot_k fam_prot/receptor signalling protein ST_k | [91] |
This review focuses on the gene for gene mechanism of blackleg resistance, *R* gene content in canola and its relatives, candidate blackleg *R* genes, genetic factors in *L. maculans* pathogenicity and resistance, and future work that can advance knowledge towards a more resistant canola crop.

2. The Current Resistance Genes Go Beyond Simple Allelism

The flax–rust interaction provided some of the first evidence of a gene for gene interaction between plants and pathogens, whereby resistance is conferred by the highly specific recognition between the plant *R* genes and the pathogen’s *Avr* genes [93]. This molecular interaction initiates a cascade of signalling pathways, resulting in a hypersensitive response in the plant, which restricts further pathogen growth [94] and in some cases leads to systemic acquired resistance (SAR) [95]. Whilst the flax–rust interaction laid the foundation for understanding the basic mechanisms of *R*-gene-mediated resistance in plants, recent advances indicate a rather complex interaction in several crop-pathosystems, which goes beyond the simple gene-for-gene recognition. Such a case has been documented in the *Brassica–L. maculans* interaction, where several *R* genes have been found to interact with the same *Avr* genes in the pathogen, and in some instances, some *R* gene–*Avr* pairs mask the resistance response in other interactions. On the side of the host, several genes are suspected to be allelic forms of other genes, adding another layer of complexity for understanding the *Brassica–L. maculans* interaction.

*Rlm2* is a natural allele for resistance in *B. napus*, while *LepR3* is an introgressed gene from *B. rapa* subsp. *sylvestris*; however, subsequent investigations proved they are variants of the same gene [96,97]. *Rlm2* and *LepR3* are located on chromosome A10 (14,404,296 to 14,408,251 bp of *B. napus* Darmor-bzh genome v4.1) [98] and encode an extracellular leucine-rich receptor (RLP), whose structure was found to be similar to the widely known *Cf*-a protein in tomato [99,100]. Further functional analysis of both of these genes found...
that their resistance expression is mediated by associating with the helper proteins SOBIR1 (Suppressor of BIR1) and BAK1 (BRI1-Associated Kinase-1) proteins [97,100,101].

Whilst Rlm2 and LepR3 are allelic, they each recognise different L. maculans Avr genes; Rlm2 interacts with AvrLm2 while LepR3 interacts with AvrLm1. The interaction of LepR3 and Rlm1 with the same Avr gene (AvrLm1) originating from different Brassica species [96,97] provides evidence of a two-for-one gene interaction for blackleg resistance (Rlm1 and LepR3-AvrLm1), deviating from the earliest classical gene-for-gene interaction [93]. Recently, LepR2 and Rlm5, reported as independent genes, were found to interact with the same Avr gene, AvrLm5-Lep2 [102]. However, since LepR2 and Rlm5 are from B. rapa subsp. sylvestris, they could be the same gene or allelic variants. Cloning of LepR2, Rlm5, and Rlm1 will help explain why two genes recognise the same Avr gene.

Rlm5 and Rlm9 also recognise the same Avr gene (AvrLm5-9) [103]. Rlm5 is a B. juncea R gene that resides in a region homologous to chromosome A10 of B. napus [104,105]. Rlm9 is on chromosome A07 (15.9 Mb in B. napus Darmor-bzh genome v4.1) and encodes a wall-associated kinase-like protein RLK [106]. However, as with the case of LepR3 and Rlm1, it is unclear if Rlm9 and Rlm5 are allelic variants or independent genes [103]. Only when Rlm5 is cloned can the relationship of these two genes be further dissected, which will explain why they share the same Avr gene.

In another interaction, genes Rlm4 and Rlm7 both recognise the same effector [107]. Rlm4 and Rlm7, along with Rlm3 and Rlm9, form a tightly linked cluster on chromosome A07 of B. napus, and may be alleles of the same R locus [108]. This hypothesis has a valid precedence as shown in the case of Rlm2 and LepR3, which were found to be allelic [109].

A further gene, a B. rapa subsp. sylvestris R gene, LepR4 is mapped on chromosome A06 (9,873,739 to 10,977,390 bp) in B. rapa v1.2 [110] but a recent finding in B. oleracea showed that LepR4 candidate genes were detected on two different chromosomes, C03 and C08 [90,111]. Earlier, this gene was reported to have two alleles, LepR4a and LepR4b, each having different levels of resistance [86]. In B. juncea, another gene Rlm6 has also been genetically mapped onto two different chromosomes, A07 and B04 [91]. Both LepR4 and Rlm6 are yet to be cloned. In B. nigra, the R gene Rlm10 mapped on chromosome B04 interacts with two Avr genes, AvrLm10a and AvrLm10b [112,113], indicating a gene-for-two-gene interaction.

Other interactions seemed to follow the gene-for-gene, R-gene-to-Avr-gene interaction, and are relatively more straightforward to analyse compared with the previous examples. These include the interaction of Rlm3 to AvrLm3, Rlm8 to AvrLm8, Rlm11 to AvrLm11, and LepR1 to AorLepR1 [104,108,114,115]. However, as with most R genes, the specific genes controlling such resistance have yet to be closed. Hence, the identification of their sequences will likely contribute to how they should be effectively deployed for blackleg management.

Due to differences in the mapping population and the pathogen race compositions used, some blackleg R genes identified are thought to be redundant with other previously known R genes. Furthermore, their corresponding effectors remain to be verified. For example, BLMR1 was thought to be redundant to LepR3 [97] but an RNA sequencing analysis revealed a difference in the N-terminal leucine-rich repeat motifs [116] (Figure 1). BLMR2, Rpg3Dun, RlmSkipton, and QRlm.awai-A10 are other genes that need confirmatory analysis [117–119] (Figure 1).

The simple gene-for-gene allelism provides a basic understanding in the Brassica-L. maculans interaction, however, complications exist for some of these genes, as some of them interact with the same Avr gene while several others are suspected to be allelic forms of the others. Furthermore, some of the interactions display an epistatic effect over the other interactions (Figure 1). These anomalies represent some of the challenges in studying the Brassica-L. maculans interaction, which need to be resolved to enhance current strategies for resistance deployment as a major component of blackleg management.

3. Exploring Resistance Genes in Brassica napus and Its Relatives

Despite natural resistance to L. maculans in the B. napus A-genome, there is a requirement to find novel sources of resistance for continuous improvement of the crop. One
method for this is to utilise exotic germplasm via intergeneric/interspecific hybridisation breeding [120]. Several Brassicaceae species have been successfully hybridised/crossed with *B. napus* to improve resistance to blackleg, but information on the derived progenies is limited (Table 3). Only a few of these lines, containing *B. rapa* and *B. juncea* genes, have been successfully converted into commercial cultivars [104,121]. Other species including *A. thaliana*, *Brassica insularis*, *Brassica atlantica*, *Brassica macrocarpa*, *C. sativa*, *Diplotaxis muralis*, *Eruca pinnatifida*, *Erucastrum gallicum*, *Raphanus raphanistrum*, *S. alba*, *Sisymbrium loeselii*, and *Thlaspi arvense* have been found with proteins/compounds that may benefit *B. napus* against *L. maculans* [122–134]. Only 13 of these species have published information on their *R* gene content (Table 4). There are between 87–641 NLRs, 300–1,556 RLKs, and 56–272 RLPs in the genome assemblies [135–143] (Table 3).

**Table 3.** Successful *Brassica napus* progenies hybridized/developed with selected Brassicaceae species having blackleg resistance in cotyledon stage.

| Species Types of Progenies References |
|--------------------------------------|
| *Brassica carinata* and *Brassica rapa* Double haploid (DH) lines [86,115,144–147] |
| *Brassica juncea* Recombinant and backcrossed (BC) lines [148–150] |
| *Brassica nigra* Hybrid and recombinant lines [149,151,152] |
| *Brassica elongata*, *Brassica fruticulosa*, *Brassica souliei* and *Diplotaxis tenuifolia* Hybrid [130] |
| *Cinque monensis* and *Hirschfeldia incana* Hybrid and BC lines [130,132] |
| *Sinapsis arvensis* Somatic hybrids and BC lines [130,132,153,154] |
| *Brassica tournefortii* Somatic hybrids [155] |

It can be noted that RLKs are more abundant than other *R* genes. In the *B. napus* pangenome, across the 52 lines, there were 35,181 more RLK genes than NLRs and 46,382 more RLK genes than RLPs, and in the 10 individuals in the *B. oleracea* pangenome, there were 316 more RLKs than NLRs and 709 more RLKs than RLPs [70,72]. The abundance of RLKs, over other *R*-genes type, could be due to their versatile roles in plants, as they are not only involved in defence but in other processes [156]. For example, RLKs are involved in growth and development such as cell proliferation and homeostasis, vascular differentiation, and steroid hormone perception [157–159]. RLKs interact with NLR/RLPs to initiate resistance [160–167] and their extracellular component suggests an ability to cope with the population of ligands from pathogens [168].

Most of the NLRs in the genome are involved in defence mechanisms [51] and some of the plant–pathogen interaction with effectors is indirect [169]. For example, a resistant tobacco with an NLR-N gene requires an *NRIP1* (NLR, specifically with TIR domain) before interacting with effector p50 of *Tobacco mosaic virus* [170]. A resistant *Arabidopsis* with *ZAR1* (NLR) requires *ZED1* pseudokinase (NLR) as a decoy, and thus *ZAR1*-mediated immunity is induced by interacting with type III *Aov HopZ1a* for resistance against *Pseudomonas syringae* [171]. NLRs perceive pathogen effector proteins in the cytoplasm, after which the plant initiates immunity through a hypersensitive response [172]. Of the 313 cloned *R* genes in plants, 191 are NLRs [169], with two NLRs in *Brassica*, *CrA* and *Crr1a*. *CrA* and *Crr1a* are resistant to isolates M85 and Ano-01 of *Plasmodiophora brassicae*, respectively, which causes clubroot disease in *B. rapa* [173,174].

RLPs are RLKs but without kinase domain, and usually an RLP gene would need other triggering genes to initiate resistance [54,175]. Aside from cloned RLP genes for resistance to *L. maculans*, other examples are *Cf-4* and *RLP23*. *Cf-4* perceives *Aov4* with the help of kinase-active *BAK1* to trigger an immunity response to *Cladosporium fulvum* in tomato [167]. *RLP23* requires NEP-like protein 20 and kinases (SOBIR1 and BAK1) with the effector to signal an immune response to potato late blight and rot caused by *Phytophthora infestans* and *Sclerotinia sclerotiorum* [161,162].
Table 4. List of Brassicaceae species containing resistance gene analogs like nucleotide-binding site leucine-rich repeat (NLR), receptor-like protein kinase (RLK), and receptor-like protein (RLP).

| Species (Common Name) | NLR | RLK | RLP | Software Used       | References |
|----------------------|-----|-----|-----|---------------------|------------|
| **Arabidopsis lyrata** (Lyre-leaved rock-cress) |     |     |     | RGAugury            | [140]      |
|                      | 243 | 514 | 73  | RGAugury            | [138]      |
|                      | 506 | 495 | 56  | RGAugury            | [143]      |
|                      | 198 | -   | -   | HMM/MEME            | [137]      |
|                      | 200 | -   | -   | HMM/LRRfinder       | [137]      |
| **Arabidopsis thaliana** (Mouse-ear cress) |     |     |     | RGAugury            | [140]      |
|                      | 205 | 516 | 73  | RGAugury            | [138]      |
|                      | 410 | 517 | 75  | RGAugury            | [141]      |
|                      | 152 | -   | -   | NLGenome Sweeper    |            |
|                      | 213 | -   | -   | HMMER               | [142]      |
|                      | 165 | -   | -   | HMM/MEME            | [143]      |
|                      | 167 | -   | -   | HMM/LRRfinder       | [137]      |
| **Brassica juncea** (Indian mustard) |     |     |     | RGAugury            | [140]      |
|                      | 315 | 1085| 191 | RGAugury            | [138]      |
|                      | -   | 493 | 228 | RGAugury            | [139]      |
| **Brassica napus** (Oilseed rape) |     |     |     | RGAugury            | [140]      |
|                      | 286 | 989 | 77  | RGAugury            | [140]      |
|                      | 208 | 680 | 122 | RGAugury            | [140]      |
|                      | 621 | 1497| 273 | RGAugury            | [140]      |
|                      | 566 | 1517| 260 | RGAugury            | [140]      |
|                      | 464 | -   | -   | HMMER               | [140]      |
| **B. napus pangenome** | 641 | -   | -   | MEME/MAST           | [145]      |
| **B. nigra** (Black mustard) |     |     |     | RGAugury            | [140]      |
|                      | 372 | 776 | 176 | RGAugury            | [138]      |
|                      | -   | 317 | 176 | RGAugury            | [139]      |
| **Brassica oleracea** (Cabbage) |     |     |     | RGAugury            | [72]        |
|                      | 493 | 822 | 159 | RGAugury            | [140]      |
|                      | 438 | 796 | 155 | RGAugury            | [140]      |
|                      | 146 | -   | -   | HMMER               | [140]      |
|                      | 443 | -   | -   | MEME/MAST           | [140]      |
|                      | 157 | -   | -   | HMMER               | [142]      |
|                      | 408 | -   | -   | HMMER               | [143]      |
| **B. oleracea pangenome** | 616 | 932 | 223 | RGAugury            | [72]        |
| **Brassica rapa** (Field mustard) |     |     |     | RGAugury            | [140]      |
|                      | 263 | 670 | 106 | RGAugury            | [138]      |
|                      | 488 | 747 | 118 | RGAugury            | [138]      |
|                      | -   | 300 | 65  | RGAugury            | [139]      |
|                      | 202 | -   | -   | HMMER               | [140]      |
|                      | 249 | -   | -   | MEME/MAST           | [140]      |
|                      | 206 | -   | -   | HMMER               | [141]      |
|                      | 204 | -   | -   | HMM/MEME            | [143]      |
|                      | 201 | -   | -   | HMM/LRRfinder       | [137]      |
| **Brassica macrocarpa**('Egadi' cabbage) | 447 | 862 | 186 | RGAugury            | [72]        |
| **Camelina sativa** (False flax) |     |     |     | RGAugury            | [140]      |
|                      | 504 | 1469| 280 | RGAugury            | [140]      |
| **Capsella rubella** (pink shepherd’s-purse) |     |     |     | RGAugury            | [140]      |
|                      | 180 | 539 | 87  | RGAugury            | [138]      |
|                      | 200 | 536 | 97  | RGAugury            | [138]      |
|                      | 127 | -   | -   | HMM/MEME            | [143]      |
| **Eutrema salsugineum** (Saltwater cress) |     |     |     | RGAugury            | [140]      |
|                      | 165 | 509 | 77  | RGAugury            | [138]      |
|                      | 348 | 483 | 83  | RGAugury            | [143]      |
|                      | 88  | -   | -   | HMM/MEME            | [143]      |
|                      | 87  | -   | -   | HMM/LRRfinder       | [137]      |
| **Raphanus raphanistrum** (Wild radish) |     |     |     | RGAugury            | [140]      |
|                      | 206 | 585 | 142 | RGAugury            | [140]      |
| **Thlaspi arvense** (Field penny-cress) |     |     |     | RGAugury            | [140]      |
|                      | 183 | 474 | 120 | RGAugury            | [140]      |

1 Brassica napus cv. Darmor v.8, 2 Brassica napus cv. Tapidor, 3 Brassica napus cv. Darmor v.4, 4 Brassica napus cv. ZS11.
Among the relatives of canola, B-genome-containing species (B. nigra, B. carinata, and B. juncea) are excellent sources of resistance to L. maculans [148,176,177]. Five R genes (Rlm6, Rlm10, LMJR1, LMJR2, and rjlm2) have been identified in the B-genome but only Rlm6 is utilised in canola cultivars. Of the B genome species, B. nigra [178] and B. juncea [74] reference genomes have been published, while B. carinata genome assembly has yet to become available. Microsatellite markers indicated that resistance in B. carinata resides on chromosomes B01, B03, B06, and B07 in B. napus-B. carinata doubled haploid populations [145–147]. Nonetheless, studies can now rely on a pseudo-reference for B. carinata using its diploid ancestors: B. nigra and B. oleracea [179].

In other species, A. thaliana has been found to confer resistance to L. maculans; RESISTANCE TO LEPTOSPHAERIA MACULANS (RLM) 1 or AtRLM1A, a 4.93 Kb gene on chromosome 1 (23,779,223 to 23,784,155 bp of A. thaliana Araport11), AtRLM2 or AtRLM1B, a 5.59 Kb gene on chromosome 1 (23,711,420 to 23,717,006 bp of A. thaliana Araport11), and AtRLM1A [180–182]. AtRLM1 and AtRLM2 require camalexin production for resistance that causes lignification and the formation of vascular plugs as physical barriers [183,184]. AtRLM3, a 9.71 Kb gene on chromosome 4 9,557,175 to 9,566,887 bp of A. thaliana Araport11 [180], confers resistance not only to L. maculans but also to other diseases including Botrytis cinerea, Alternaria brassicicola and Alternaria brassicae [185]. AtRLM3 has three BREVIS RADIX domains instead of leucine-rich repeats (LRR) that possibly regulate downstream defence signalling responses [186]. AtRLM gene homologs have been found in Arabidopsis lyrata, B. rapa, C. sativa, Capsella rubella, and Eutrema salsugineum based on annotation studies [181,186]. An AtRLM1A-like gene was identified in C. rubella, AtRLM1B and other AtRLM1-like genes in A. lyrata, B. rapa and E. salsugineum; and the AtRLM3 gene is conserved in A. lyrata and C. sativa [181,186]. These species are potential sources to search for new resistance against L. maculans.

Other Brassicaceae relatives such as C. monensis, S. arvensis, S. alba, D. muralis and Diplotaxis tenuifolia have been found to have a resistance response against L. maculans in cotyledons and adult stages [122,123,132,133,154]. These species may contain vast numbers of disease resistance genes based on transcriptomic analysis [187–189]. The Brassicaceae, especially the wild relatives of B. napus, are indeed a potential source of novel R genes and alleles in improving resistance to L. maculans and for other diseases in the family. Their genome sequences provide an opportunity to search for orthologous allelic variants to the existing R genes for L. maculans, and a vast genetic resource that could considerably enrich B. napus in many years to come.

4. Genome Sequencing in Brassica Species Hastened the Identification of Resistance Genes

The availability of genome sequences marked a milestone in the identification of R genes and their cloning. B. rapa was the first Brassica species to have a genome sequence available [110]. Subsequently, the genome sequences of B. napus, B. oleracea, B. juncea, and B. nigra have become available [69,74,75,98,180,190,191], some of which have multiple genome assemblies. Recent genomic analysis has highlighted a significant gene presence/absence variation in plant species, with disease resistance genes tending to demonstrate significant presence/absence variation [70,73,192–194]. This has led to the construction of pangenomes along with corresponding structural variation data including copy number variation and presence/absence variations for a wide range of crop species [195,196] including Brassica species [70–73,197].

The first two cloned genes for L. maculans resistance, LepR3 and Rlm2, correspond to BnaA10g20720D and Rlm9 to BnaA07g20220D in B. napus cv. Darmor bzh genome v4.1 [97,100,106], and the physical location has been updated in the B. napus pangenome (Figure 2). Most of the candidate genes for blackleg resistance encode RLKs followed by NLRs and RLPs, and a few encode TM-CCs, secreted peptides (SP) and enzymatic R genes (Table 2). These candidate genes can be useful a reference for researchers moving towards gene cloning and functional analyses. It is expected that the number of cloned R genes for blackleg resistance will increase in the near future.
5. Genetic Factors Involving the Pathogenicity and Resistance in *Leptosphaeria maculans*

Unlocking the genome of pathogens gives a better understanding of their pathogenicity, life-cycle, and evolution [198]. To date, 10 *L. maculans* *Avr* genes have been cloned (Figure 1). *AvrLm2*, *AvrLm3*, *AvrLm4-7*, *AvrLm5-9*, *AvrLm10a* and *AvrLm10b*, *AvrLm11*, and *AvrLmS-Lep2* encode cysteine-rich proteins [102,103,107,113,199–203], while *AvrLm1* contains only one cysteine residue [204].

All cloned and current candidate *Avr* genes reside in AT-rich sequences with degenerated transposable elements, where repeat-induced point mutation (RIP) often occurs [102,103,113,114,200–203,205]. As such, it was initially thought that RIP accounts for most of the virulence in *L. maculans* [109]. However, amino acid substitutions are the major cause of virulence, as occurs in *AvrLm2*, *AvrLm3*, *AvrLm4*, *AvrLm5-9* and gene deletions to *AvrLm1*, *AvrLm6*, *AvrLm10a* and *AvrLm10b*, and *AvrLm11* [103,109,113,114,200,201,206–208]. In *AvrLm7*, it is either RIP mutation or gene deletion causes virulence [109].

*AvrLm4-7* promotes *L. maculans* pathogenicity to susceptible *B. napus* and suppresses SA and ET signalling pathways, including abscisic acid (ABA) and hydrogen peroxide (H₂O₂) [209]. Similarly, *AvrLm1* suppresses SA and JA signalling pathways in transient gene expression of *A. thaliana* (Columbia-0 line) and targets phosphorylation of *B. napus* mitogen-activated protein kinase (MAP_k) 9 (*BnMAP_k9*) gene, which leads to an increase in cell death in *A. thaliana* [210]. As *AvrLm2* suppressed JA signalling, an MAP_k signal was induced; the mechanism could be similar to *AvrLm1* to *BnMAP_k9* gene but needs to further verification [211]. In a different study in *A. thaliana*–pathogen interaction, as the AP2C1 gene (protein phosphatase gene) influenced MAP_k4 and MAP_k6 genes, the levels of JA and ET signalling genes were lowered, which subsequently compromised the plant immunity [212]. When MAP_k signalling genes were suppressed by *Xanthomonas* type III *Avr* genes (*XopE1, XopM, XopQ, AvrBs1* and *AvrXv4*), cell death occurs in *Nicotiana benthamiana* [213]. Another adenosine kinase has been found to be significant for proper fungal growth, hyphae development and virulence of *L. maculans* in *B. napus* [214]. *LmSNF1* (sucrose non-fermenting protein kinase 1 gene), *LmStuA* (TF gene), NEP1-like proteins, immunophilin gene family, isocitrate lyase, candidate secreted effector proteins, CAZymes, glycosyl hydrolase, cytokinin profiles, and carbohydrate with esterase domain containing genes play roles in *L. maculans* pathogenicity [215–222].

Generally, when *L. maculans* enters the plant, SA and JA-related genes are affected and act as initial defence compounds [84,209,216–218,223–225]. There are also genes that may contribute or act as basal defence, such as pattern recognition receptor CERK1 (e.g., chitin elicitor receptor kinase 1), WRKY transcription factors (TF) (e.g., WRKYs 33, 40 and 51), glucosinolate-related genes (e.g., *cytochrome P450, SUPERROOT1*, and *nitrile-specifier protein 5*), and calcium-related biological functions (e.g., homologs of *CAM1, CAM5* and *CAM7*, *CYCLIC NUCLEOTIDE-GATED CALCIUM CHANNEL 3, 12* and *19; CALMODULIN-DOMAIN PROTEIN KINASE 5, 9; CALCIUM-DEPENDENT PROTEIN KINASE 6 and 28; and CALCINEURIN B-LIKE GENE 1*) [211,216].

When there is resistance, ABA is induced in plants harbouring *Rlm4*, *LepR3*, and *Rlm2* [116,209]. On the other hand, high expression of calcium-related signalling genes and TFs (basic leucine zipper (bZIP) and basic helix–loop–helix (bHLH)) aside from JA and ABA were found in plants containing *Rlm2* [211]. Calcium-dependent protein kinases have been reported to trigger signalling pathways for an immediate plant defence [226,227], while for TFs, bZIP acts as a precursor in plant immunity [228] and bHLH interacts with signalling plant defence receptors [229,230]. bHLH might have an important role in *Rlm2*-mediated defence, as it activates SOBIR1 gene in *Gossypium barbadense* against Verticillium wilt [211,230]. Lastly, *LepR1*-mediated resistance was correlated with indole-derived phytoalexins [84], which may be *Brassica*’s counterpart to camalexin that has been found to be effective against *L. maculans* [183,231].
6. Conclusions

*L. maculans* can adapt to the host over time in the field. Thus, canola breeders and scientists should use genomics and bioinformatics tools and platforms in *Brassica* research [232] to hasten the search for novel *R* genes for identification, cloning and deployment. The extensive applications of genomics, pangenomics, and superpangenomics to canola and its relatives [233] will result in genomic-driven breeding strategies. Additionally, applying these methodologies to the host will result in an *L. maculans*-informed canola breeding. We see transcriptomics uncover the *Brassica-L. maculans* interaction and reveal role players in the pathogenicity and resistance, which opens an opportunity for gene editing such as CRISPR technology by gene activation or inactivation [234–237]. Transcriptomics is also used to study the relatives of canola, which present a novel variation that may have natural and better resistance to the pathogen. Furthermore, physiological and other molecular mechanisms acting not only in the genes of canola but to other Brassicaceae species could also be explored for information which can be translated and useful in improving the crop [238]. The comprehensive information in this review allow breeders to integrate *Brassica* and *L. maculans*-sequencing-based information for developing a better and resistant *B. napus*.

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