Review

Not peer-reviewed version

Interspecific and Intergeneric Crosses for Clubroot Resistance: Review Article

Piotr Kamiński * and Marta Zofia Konopacka

Posted Date: 28 October 2025

doi: 10.20944/preprints202510.2076.v1

Keywords: clubroot; brassiaceae; intercrosses; resistance; hybridization; breeding

Preprints.org (www.preprints.org) | NOT PEER-REVIEWED | Posted: 28 October 2025 doi:10.20944/preprints202510.2076.v1

Review

Interspecific and Intergeneric Crosses for Clubroot Resistance: Review Article

Piotr Kamiński [1,*] and Marta Konopacka [2]

[1] Department of Horticultural Crop Breeding, the National Institute of Horticulture Research, Konstytucji 3 Maja 1/3 Str., 96-100 Skierniewice, Poland
[2] Library, the National Institute of Horticulture Research, Konstytucji 3 Maja 1/3 Str., 96-100 Skierniewice, Poland
* Correspondence: piotr.kaminski@inhort.pl

Abstract

Clubroot disease, caused by *Plasmodiophora brassicae*, is a major global threat, causing severe yield losses of up to 100% in heavily infested fields. Interspecific hybridization is essential for the transfer of clubroot resistance genes among the Brassica species. This review aimed to describe the sources of clubroot resistance, categorize their types in Brassica crops, and identify the most effective techniques and underutilized sources for both intergeneric and interspecific hybridization. A systematic literature review served as the foundation for expert analysis, encompassing a comprehensive list of known sources of resistance and a detailed description of their characteristics, including monogenic, polygenic, dominant, and recessive traits. In addition, this review specifies techniques suitable for gene transfer, such as markers, embryo rescue, somatic hybridization, and CRISPR/Cas. Based on literature, underutilized directions for genetic crosses have been proposed. These conclusions suggest that combining biotechnological methods, including markers, CRISPR/Cas, and embryo rescue, with intergeneric crosses offers the potential to transfer resistance genes from previously untapped sources.

Keywords: clubroot; brassiaceae; intercrosses; resistance; hybridization; breeding

---

1. Introduction

1.1. Background

Clubroot disease, caused by the obligate biotrophic protist *Plasmodiophora brassicae (P. brassicae),* is a major threat to Brassica crops worldwide, including oilseed rape (*Brassica napus*), cabbage (*Brassica oleracea*), and Chinese cabbage (*Brassica rapa*). The disease is characterized by the formation of galls on the roots, which leads to reduced nutrient and water uptake and, ultimately, severe yield losses [1–3] Symptoms of clubroot primarily affect the roots, leading to the development of galls (clubs) in the infected root tissues, which are characterized by abnormal proliferation. These galls severely deplete nutrient levels, disrupt the organization of vascular bundles in the roots, and obstruct water and mineral uptake. Consequently, the aboveground portions of afflicted plants exhibit yellowing, wilting, and eventual demise [4]

1.2. Significance

The socioeconomic impact of clubroots is significant as it affects major agricultural commodities. For instance, in regions such as Latin America and Australia, where Brassica crops are extensively cultivated, the disease poses substantial challenges, leading to economic losses and necessitating extensive management efforts [1,5]. In China, Brassicaceae crops suffer yield losses of 20–30% due to this disease [6]. Clubroot can cause up to 100% yield loss in heavily infested fields planted with susceptible canola cultivars [7].

1.3. Challenges in Clubroot Management

Environmental conditions, such as temperature and soil moisture, play crucial roles in the incidence and severity of clubroot, and climate change may exacerbate its spread by creating more favorable conditions for *P. brassicae* [8].

One of the challenges in managing clubroot disease is the longevity of the resting spores *of P. brassicae*, which can persist in soil for up to 20 years. This persistence combined with the ability of the pathogen to rapidly evolve and overcome host resistance makes clubroot a particularly challenging disease to control [8–10]

To date, there is a lack of effective methods to control clubroot in Brassicaceae. Thus, cultivation of resistant varieties has become the primary approach to prevent the occurrence of clubroot disease.

1.4. Genetic Resistance and Sustainable Solution

Control strategies focus on integrated disease management, including crop rotation, liming to maintain soil pH, and the use of resistant cultivars. However, the identification and development of robust resistance remain critical, as the disease can persist through long-lived resting spores in the soil and adapt rapidly to overcome existing plant defenses [11,12]). The genetic diversity of *P. brassicae* populations further complicates disease management. Multiple pathotypes have been identified with varying degrees of virulence and host specificity, which necessitatating the development of broad-spectrum and durable resistance strategies in Brassica crops. *P. brassicae* isolated from different regional sources may have different genetic backgrounds, resulting in different phenotypic characteristics of specific host plants. *P. brassicae* can be classified into different pathotypes (physiological races), based on their virulence patterns in different host plants. The genetic diversity of *P. brassicae* contributes to the mutation of its field populations into multiple pathotypes, and the large variation in the pathogenicity of different pathotypes increases the difficulty in controlling these pathogens [4,10,13–17].

Although current strategies for clubroot resistance exist, the rapid evolution of *P. brassicae* pathotypes poses significant challenges to existing disease management approaches, necessitating the investigation of novel sources of resistance. Given these limitations, the development of resistant cultivars through breeding programs, including interspecific and intergeneric crosses, has emerged as a promising and sustainable approach for clubroot management. This shift towards genetic resistance underscores the importance of exploring diverse genetic resources within the *Brassicaceae* family to enhance clubroot resistance in cultivated Brassica crops [4,10,12,17–22]. Genetic resistance offers a more durable and cost-effective solution than chemical or cultural resistance control. Once incorporated into cultivars, resistance can offer protection to farmers without incurring additional input costs [7,23,24]. Unlike chemical control methods, genetic resistance does not pose the risk of soil or water contamination, aligning with the growing demand for environmentally friendly agricultural practices. By combining multiple resistance genes, breeders can develop cultivars resistant to various *P. brassicae* pathotypes thereby addressing the challenge of pathogen diversity. Genetic resistance can be effectively integrated with other control methods as part of a comprehensive disease management strategy that enhances the overall efficacy. The ability to incorporate new resistance genes through breeding allows for the development of cultivars that can keep pace with evolving pathogen populations [4,10,17,25,26].

1.5. Role of Wide Hybridization

Interspecific crosses refer to the hybridization between different species within the same genus, whereas intergeneric crosses refer to the hybridization between species from different genera. These approaches allow breeders to access a broader pool of genetic resources, incorporating traits from wild relatives or related species such as disease resistance. In some cases, interspecific and intergeneric crosses have led to the development of entirely new crop types, broadening agricultural diversity [4,22,27,28]. Moreover, interspecific hybridization can result in genomic rearrangements and variability. Breeding efforts have led to the successful introgression of numerous resistant cultivars, enhancing the resilience of Brassica crops against various pathogens and pests and highlighting the utility of hybridization to access resistance genes not present in cultivated species [29–31]. The success of these techniques has not only improved crop yields but also reduced reliance on chemical pesticides, contributing to more sustainable agricultural practices.

Interspecific crosses play a crucial role in transferring clubroot resistance genes among Brassica species [19,32–38]. The success of these techniques has not only improves crop yields but also reduces reliance on chemical pesticides, contributing to more sustainable agricultural practices. Ongoing research continues to explore new sources of resistance genes from wild Brassica relatives and related species, promising further advancements in crop protection and productivity [39,40].

Interspecific hybridization has significant implications for the genetic diversity of Brassica species. This induces genomic variations, including chromosomal rearrangements and retrotransposon activation, resulting in the formation of new genomic patterns. Such genetic recombination can introduce novel traits and enhance the genetic diversity of Brassica crops, thereby expanding their adaptability to various environmental challenges and improving their characteristics such as yield and disease resistance [41]. Interspecific hybridization broadens the genetic diversity by facilitating the crossing of different species. It introduces traits related to stress tolerance and agronomy, thereby broadening the genetic foundation of brassica crops [42]. Interspecific hybridization alleviates these limitations by introducing genetic diversity from related Brassica species, thereby overcoming bottlenecks and supporting the development of crops with improved traits [43]. This process generates phenotypic variation, which is crucial for the selection of traits for improved yield, quality, and stress resistance. Such diversity emerges from genetic variation through hybridization and selection pressures that stabilize desired traits.

1.6. Objectives of the Review

This review aims to evaluate the success of interspecific and intergeneric hybridization in developing clubroot-resistant Brassica crops and to identify promising yet underutilized genetic resources and techniques for future breeding efforts.

2. Methods of Literature Review

The initial collection of literature was compiled from Scopus and Web of Science databases using three primary criteria: (1) mentions of Brassicacea in general, or Brassica species and cultivars, or agriculturally and industrially significant Brassicacea species, or Brassicacea species considered underutilized in agricultural and industrial context; (2) along with mentions of *Plasmodiophora brassicae*; (3) in the context of interspecific or intergeneric hybridization as a tool for introducing resistance. Subsequently, selected publications were critically analyzed, focusing on sources of resistance and practical constraints of their utilization. Finally, a narrative review was constructed based on this analysis.

3. Genetic Diversity in Brassica and Related Genera

The *Brassica* genus, part of the *Brassicaceae* family, encompasses a diverse group of economically important crops. Brassica species have undergone an additional whole genome triplication event compared with *Arabidopsis thaliana*. This triplication is instrumental in speciation and diversification within Brassica, leading to a broad range of morphotypes, and enabling genetic adaptation over time. Restructuring of the genome following this polyploidy event has facilitated species richness and morphotype expansion in Brassica species [44]. Interactions between genotypic and phenotypic variability in Brassica are evident, demonstrating the ability of these species to adapt morphologically and biochemically to environmental pressure [45]. The genetic relationships within this genus are often represented by the "Triangle of U," which illustrates the genomic connections between six principal Brassica species: *B. rapa* (A genome), *B. nigra* (B genome), and *B. oleracea* (C genome), and three allotetraploid species: *B. juncea* (AB genome), *B. napus* (AC genome), and *B. carinata* (BC genome). Reconstruction of *Brassica* genomes, such as that of *B. napus*, by incorporating subgenomic diversity from related species (e.g., *B. rapa* and *B. carinata*) has led to novel genetic pools with high allelic diversity. Reconstructed genomes offer new opportunities for sustainable breeding practices and improved crop varieties [46]. This genetic framework provides a foundation for understanding the potential for interspecific crosses within the *Brassica* genus [4,46–50]. Beyond the primary *Brassica* species, this genus is closely related to other genera within the *Brassicaceae* family, such as *Raphanus* (radish) and *Sinapis* (white mustard), which offer opportunities for intergeneric crosses and broaden the genetic base for traits, such as clubroot resistance [4,22,49,51,52].

4. Methods for the Interspecific and Intergeneric Hybridization for Clubroot Resistance

Utilizing new sources of resistance genes from wild Brassica relatives and related species often requires overcoming hybridization barriers and addressing challenges, such as linkage drag. Advanced breeding techniques are crucial for facilitating the introgression of resistance genes from wild relatives into cultivated Brassica crops [10,19,20,49,53,54].

4.1. Embryo Rescue

Embryo rescue is used to produce interspecific and intergeneric hybrids, overcome reproductive barriers, and incorporate beneficial alleles into cultivated species [20]. The advent of embryo rescue techniques in the late 20th century greatly facilitated the success of wide crosses by overcoming the post-zygotic barriers that cause embryo abortion, which were previously challenging [42,55–59]. This method not only aids in obtaining interspecific and intergeneric hybrids, but also supports the production of haploid and doubled haploid plants, which are crucial for plant breeding programs [57,60]. Embryo rescue techniques in Brassicaceae have been used to breed biotic and abiotic stress-resistant lines, including synthetic amphidiploid and alien gene introgression lines for genetic studies [20]. The transfer of clubroot resistance genes from resistant Chinese cabbage to *B. napus* via distant hybridization and embryo rescue has been described by Liu et al. (2018). This approach has successfully identified true hybrids with clubroot resistance [61].

4.2. Polyploid Breeding

Polyploid breeding plays a significant role in enabling intergeneric and interspecific crosses for clubroot resistance in Brassica species [32,61–64]. Interspecific and intergeneric hybridization within Brassicaceae enables the production of synthetic amphidiploids and other engineered chromosomal lines. These lines, developed through polyploid breeding strategies, serve as valuable genetic resources for studying the effects of chromosomes on plant traits and for improving crop resistance to biotic stresses such as clubroot [20]. In polyploid Brassica species, the formation of double haploid (DH) lines allows for fixation and stability of clubroot resistance traits. DH lines are genetically uniform, facilitating the mapping and stable expression of resistance genes across generations [65]. Several studies have mapped clubroot resistance loci across various chromosomes of *B. napus*, thereby revealing the polygenic resistance mechanisms. Polyploidy can help stabilize these diverse resistance loci by providing multiple copies of homologous chromosomes, allowing for more complex gene interactions that contribute to resistance [22]. Diederichsen and Sacristan crossed resistant *B. rapa* with *B. oleracea* and created synthetic *B. napus* lines that were resistant to *P. brassicae*. The broad resistance of these synthetic lines suggests durable protection against *P. brassicae* pathotypes [66]. Polyploid breeding facilitates intergeneric crosses between radish (*Raphanus sativus*) and *B. oleracea* and the development of allotetraploid *Brassicoraphanus* (RRCC). This artificial polyploid is resistant to various clubroot pathotypes. The significant homeologous recombination observed suggests the potential for transferring resistance traits from radish to *Brassica napus*, thereby improving clubroot resistance [49].

4.3. Protoplast Fusion

Somatic hybridization is a prominent method that utilizes protoplast electrofusion, resulting in hybrid plants that exhibit a high resistance to clubroot. This technique has been employed in interspecific or intergeneric crosses to overcome sexual incompatibility and introduce desired traits such as clubroot resistance. This allows the merging of genetic material from different species, such as *B. rapa* and *B. oleracea*, to enhance resistance traits against diseases [67]. The integration of clubroot resistance traits from various Brassica species through protoplast fusion allows the combination of different resistance loci. This technique effectively creates hybrids with enhanced disease resistance by providing genetic diversity that stabilizes resistance traits against multiple pathotypes of *Plasmodiophora brassicae* [68]. Asymmetric protoplast fusion between *B. nigra* and *B. napus*, performed by Sacristán et al. (1989), resulted in asymmetric somatic hybrids with the aim of co-transfer of disease-resistance traits, such as resistance to *Phoma lingam* and *Plasmodiophora brassicae* [69]. Protoplast fusion has been used to create intergeneric hybrids of red cabbage (*B. oleracea*) and radish (*R. sativus*). The resulting hybrids inherited chloroplasts from radish and exhibited male sterility and other traits, demonstrating cytoplasmic inheritance patterns. Notably, some hybrids from Japanese radish and cauliflower (B. oleracea) have demonstrated the ability to produce seeds when backcrossed with the parent species, indicating their potential for transferring clubroot resistance genes to Brassica crops [70,71]. Using protoplast fusion, resynthesized *B. napus* lines were developed to incorporate clubroot resistance from *B. rapa* and *B. oleracea*. These lines exhibited broad resistance against *P. brassicae*, with effectiveness depending on the combination of resistance genes from both parental species. [72].

4.4. Molecular Markers

Molecular markers play a crucial role in the breeding of interspecies clubroot resistance by allowing precise mapping, identification, verification, and selection of desirable traits from wide crosses, thereby supporting intergeneric and interspecific breeding to enhance clubroot resistance [73–77].

4.4.1. SNP Markers

Single nucleotide polymorphisms (SNP) and gene expression markers (GEM) offer crucial data for marker-assisted breeding to develop clubroot-resistant cultivars by pyramiding multiple resistance genes. These markers are abundant across genomes and can be used to analyze hereditary traits, genome-wide association studies, and population genetics. Using an associative transcriptomic approach in *B. napus*, the two major loci on chromosomes A2 and A3 that control resistance to clubroot have been identified [18].

4.4.2. RAPD Markers

Random Amplified Polymorphic DNA (RAPD) markers are a type of molecular marker used in genetic analysis that rely on the amplification of random DNA segments using short primers of arbitrary nucleotide sequences. This method does not require prior knowledge of the DNA sequence, making it advantageous for work with anonymous genomes and diverse species. Random amplified polymorphic DNA (RAPD) markers linked to clubroot resistance have been identified in *Brassica rapa*, with three specific markers (RA12-75A, WE22B, and WE49B) associated with resistance loci. These markers have been used in DH lines derived from interspecific crosses, assisting in marker-assisted selection and breeding of resistant varieties [36].

4.4.3. SCAR Markers

Sequence-Characterized Amplified Region (SCAR) markers are DNA markers developed from Random Amplified Polymorphic DNA (RAPD) fragments. SCAR markers are widely used in various applications including species and cultivar identification, germplasm characterization, and marker-assisted selection in plant breeding. Sequence-characterized amplified region (SCAR) markers such as tau_cBrCR404 have been used to tightly link clubroot resistance loci in Chinese cabbage, enabling effective marker-assisted selection. This facilitates the breeding of new resistant cultivars by ensuring that selected plants possess the desired resistance traits [37].

4.4.4. RFLP Markers

Restriction Fragment Length Polymorphism (RFLP) markers involve the use of restriction enzymes to cut DNA at specific sequences, resulting in fragments of varying lengths due to genetic variation among individuals. Restriction fragment length polymorphism (RFLP) markers have been used to map clubroot resistance genes, such as CRa in Chinese cabbage. These markers enable breeders to select for resistance by identifying plants carrying beneficial gene arrangements [63]. RFLP markers have also been used to construct a genetic linkage map in a study involving a cross between resistant broccoli (*B. oleracea* var. *italica*) and susceptible cauliflower (*B. oleracea* var. *botrytis*). This map identifies the major factors contributing to clubroot resistance and enables the selection of individuals with combined resistance from both parent sources, thereby enhancing breeding efficiency [78].

4.4.5. SNP Markers

Single Nucleotide Polymorphisms (SNPs) are among the most abundant and widely used genetic markers for genomic studies. They represent variations at a single nucleotide position in the DNA sequence among the individuals of a species. SNPs are frequently used in genetic studies to identify associations with heritable traits, understand evolutionary processes, and investigate genetic predispositions to diseases [79,80]. SNP markers are used in associative transcriptomic approaches to map resistance loci, providing a detailed understanding of the genetic architecture of resistance and allowing for more targeted breeding strategies [18].

4.4.6. MAS

Marker-Assisted Selection *(MAS)* involves the use of molecular markers to indirectly select desirable traits in plant- and animal-breeding programs. These markers are linked to genes or quantitative trait loci (QTL) associated with traits of interest, providing a more efficient and precise selection process than traditional breeding methods. While Marker-Assisted Selection (MAS) offers a precise way to select desirable traits using molecular markers, it also presents challenges, such as linkage drag, where undesirable genes may be inadvertently selected because of their proximity to the target genes. MAS is particularly beneficial for traits that are difficult to measure or have a low heritability. This has significantly accelerated the breeding process by allowing the selection of individuals carrying beneficial alleles early in the developmental stages, reducing the time required to develop new varieties [10,73]. For instance, in *B. napus*, two simple sequence repeat (SSR) markers and two intron-polymorphic (IP) markers have been identified and linked to clubroot resistance genes, aiding the transfer and validation of resistance traits [61]. The identification and mapping of quantitative trait loci (QTLs) associated with clubroot resistance in various species, such as radish (*R. sativus*) and turnips (*B. rapa*), has allowed researchers to identify specific genomic regions that can be transferred to other species within the Brassicaceae family. These studies have facilitated the use of marker-assisted selection in breeding programs to efficiently transfer clubroot resistance traits [19,81].

4.4.7. QTL

Quantitative Trait Loci (QTL) markers are identified through QTL mapping, which involves the use of genetic markers such as Simple Sequence Repeats (SSRs), Single Nucleotide Polymorphisms (SNPs), and Amplified Fragment Length Polymorphisms (AFLPs) to detect the genomic locations of QTLs [82]. The identification and mapping of QTLs associated with clubroot resistance can facilitate breeding of resistant varieties. Genomic regions such as the novel CRs locus on chromosome A08 have been identified in *B. napus* and *B. rapa*, providing new avenues for breeding resistant cultivars [83,84]. Molecular markers were developed for three independent dominant resistance loci identified in the turnip accessions of *B. rapa.* These markers are essential for the introgression of resistance genes into different germplasms, aiding the selection and breeding of clubroot-resistant Brassica species [19].

5. Sources of Clubroot Resistance

Genetic resistance to clubroot has been identified in most Brassicaceae species, suggesting potential sources for the development of durable resistance [85]. This genetic diversity reduces the risk of pathogen resistance breakdown and ensures sustainability of crop production, particularly in regions heavily affected by this disease [18,61]). Efforts to use wide crosses for breeding Brassica have been ongoing for several decades. The transfer of clubroot resistance (CR) across different species and genera has been explored using various breeding techniques, including distant hybridization, genetic mapping, and the use of molecular markers. Through these efforts, the genetic diversity of clubroot resistance can be expanded beyond the usual barriers of species and genera, thereby providing a broader basis for developing resistant cultivars. This cross-species and cross-genera transfer remains a key strategy for managing clubroot disease across various cruciferous crops globally.

5.1. Transfer of Clubroot Resistance Inside Triangle of U

5.1.1. Brassica Rapa

Brassica rapa (European Turnip) is known for its high level of resistance to clubroot, and serves as a robust source of resistance genes that are utilized across other Brassica crops, including *B. napus* and *Brassica* vegetables. The European clubroot differential set includes turnip accessions with high resistance levels and serves as a key genetic resource for breeding resistant cultivars [19]. Resistance in *B. rapa* is frequently characterized by race-specific, single-dominant R genes, in contrast to the more continuous resistance profile observed in *B. oleracea* species. Thus, *B. rapa* is a promising source of resistance genes for future breeding programs in the future [4,12,22,28,37,38,86–92]. Several major clubroot resistance genes have been mapped, predominantly on chromosome A3, including CRa, CRb, CRb, Kato, CRk and Crr3. The Crr1 locus on chromosome A8 comprises two genes: Crr1a and Crr1b. Additional resistance loci include Crr2 on chromosome A1 and Crr4 on chromosome A6. Rcr1, also referred to as Rpb1, has been mapped to chromosome A3, in proximity to CRa and CRb, and is predicted to be a TIR-NBS-LRR-type resistance gene. Two CR genes were cloned from *B. rapa*, Crr1a and CRa, both of which encode TIR-NB-LRR proteins. Recent studies have identified additional resistance loci including Rcr2, Rcr4, Rcr8, and Rcr9. Wild *B. rapa* accessions, particularly turnip types, have been identified as a significant source of clubroot resistance genes [19,33,36,93].

Through interspecific hybridization and marker-assisted selection, the clubroot resistance locus CRd from Chinese cabbage (*B. rapa*) was successfully transferred to canola (*B. napus*). The European turnip cultivar ECD04, which is recognized for its robust clubroot resistance, has been used as a source of resistance [18,49,61,66]. A clubroot R gene was also transferred from *B. rapa* Chinese cabbage "Qulihuang" into *B. napus* "Topas" using marker-assisted selection [94]. Dominant resistance loci such as Crr1 and Crr2 have been identified in *B. rapa* and mapped to distinct chromosomes. These loci are complementary, ensuring stronger resistance when both loci are present [91]. Crr1 and Crr2 from *B. rapa* have been transferred to *B. oleracea* using interspecific hybridization and embryo rescue techniques [95]. The transfer of CR genes from *B. rapa* to cabbage provides strong evidence that homoeologous exchange facilitates this transfer, and validates the effectiveness of the resulting resistant cabbage lines, offering valuable materials and insights for future clubroot breeding programs [90]. Three clubroot resistance genes (CRa, CRb, and Pb8.1) have been successfully transferred from *B. rapa* to *B. oleracea*, providing a crucial germplasm for breeding clubroot-resistant vegetable crops [38,96]. This approach is partly required because resistant F_1 hybrids are generated only when one of the inbred parents carries dominant resistance. Furthermore, *B. rapa* has been extensively studied for its clubroot resistance and numerous QTLs have been identified. The CRa gene in *B. rapa*, which is characterized by clubroot resistance, is an example of the targeting and utilization of specific resistance genes in breeding programs [12]. A significant milestone was the creation of resynthesized *B. napus* by crossing *B. rapa* and *B. oleracea*, which has been used to introduce diverse traits including clubroot resistance [52,97]. A clubroot resistance gene, which is believed to be present in the A genome of *B. rapa*, has also been transferred from *B. napus* to *B. oleracea* [98].

5.1.2. Brassica Oleracea

The C genome of *B. oleracea* with varying levels of clubroot resistance can exploit these genetic variations and integrate genomic insights into intercrosses and traditional breeding techniques, to achieve successful disease management. [53,96,99]. Evaluation of the *B. oleracea* germplasm has identified new sources of resistance, particularly in European kale and cabbage varieties. In contrast to the single dominant genes found in the A genome, clubroot resistance in the C genome is usually controlled by several quantitative trait loci (QTLs) and exhibits continuous resistance profiles [14,22,100–102]. Numerous clubroot resistance (CR) genes and QTLs are present in *B. oleracea*, with QTLs mapped to chromosomes C2, C3, C5, C7, and C9, conferring resistance to various pathotypes [28,96,103]. For instance, significant QTLs such as qCRc7-2, qCRc7-3, and qCRc7-4 have been identified on chromosome C07 of *B. oleracea*. These QTLs contribute significantly to resistance against specific pathotypes of clubroot, and candidate genes associated with these loci show differential expression upon pathogen challenge, suggesting their vital role in conferring resistance [100]. Karim and Yu (2023) identified major and minor QTLs across multiple chromosomes, including prominent loci such as Rcr_C03-1 and Rcr_C08-1, which together explain the substantial phenotypic variance in resistance to multiple pathotypes of the pathogen [101]. Functional analysis of specific QTLs, such as BolC.Pb9.1, identified in a wild *B. oleracea* relative, revealed key genes, such as BoUGT76C2, involved in clubroot resistance. This highlights the importance of integrating wild genotypes to improve the resistance of cultivated *B. oleracea* to clubroot [92]. Crs1, a resistance gene derived from *R. sativus*, was also associated with the C genome. Wild relatives of *B. oleracea*, such as *B. macrocarpa*, have shown promise for identifying novel resistance genes. Several studies have identified and utilized quantitative trait loci (QTLs) for clubroot resistance in *B. oleracea*, which serves as a basis for breeding programs aimed at introducing these resistances into other Brassica species.[14,26,90,92,101,104,105].

Efforts to utilize the resistance found in *B. oleracea* have occasionally resulted in resistance being overcome by more virulent races [4,15,106,107]. Despite this, seed companies do not breed recessive forms of resistance because this requires resistance alleles to be present in both inbred parents used for F_1 hybrid production. The C genome of *B. oleracea* with varying levels of clubroot resistance can exploit these genetic variations and integrate genomic insights into intercrosses and traditional breeding techniques to achieve successful disease management [53,96,99].

5.1.3. Brassica Nigra and Related Genera

The B genome of *B. nigra* has significantly fewer clubroot resistance genes than the A and C genomes [108]. The presence of pathotype-specific resistance in *B. nigra* provides a strategic advantage for broadening the genetic base of resistance in commercial cultivars, potentially enhancing resilience against diverse pathotypes encountered in agricultural settings [73–77].

The first dominant clubroot resistance gene in the B genome, Rcr6, was identified and mapped to a region homologous to chromosome A08 in the A genome of *B. rapa*. Rcr6 can potentially be integrated into *B. napus* using marker-assisted selection technology, with SNP markers tightly linked to Rcr6 developed during the screening process [89,108,109]. However, the potential susceptibility of its hybrids indicates challenges in directly transferring CR resistance. According to Hasan et al. (2021), amphidiploids such as *B. juncea* (AABB) and *B. carinata* (BBCC), with the B genome incorporated from *B. nigra*, were found to be completely susceptible to clubroot [110]. Therefore, although *B. nigra* shows promise as a source of resistance, its utilization in CR breeding requires further exploration and innovative breeding strategies to overcome the limitations observed in the hybrids [4,109].

5.1.4. Brassica Juncea

The development of clubroot-resistant *Brassica juncea* through interspecific crosses primarily involves the utilization of distant hybridization and embryo rescue techniques in various *Brassica* species. Although *B. juncea* traditionally lacks inherent resistance to clubroot, efforts have been made to introduce resistance genes from other Brassica species into *B. juncea*. Resistance in *B. juncea* is achieved by crossing it with other species such as *B. rapa*, which carries dominant resistance genes. Mapping studies have identified resistance loci across *Brassica* genomes that confer resistance to *P. brassicae* pathotypes [19,83].

5.1.5. Resynthesis of Brassica Species for Clubroot Resistance

The resynthesis of *Brassica* species significantly contributes to the development of durable clubroot resistance by expanding the genetic diversity, combining multiple sources of resistance, and facilitating the creation of novel genetic combinations. A significant milestone was the creation of resynthesized *B. napus* by crossing *B. rapa* and *B. oleracea*, which has been used to introduce diverse traits including clubroot resistance [52,97]. This approach provides breeders with valuable tools for developing cultivars with more robust and potentially longer-lasting resistance to clubroot diseases [61,66,111–114]. The primary aim was to incorporate resistance traits from different Brassica germplasms and related species into widely grown cultivars such as canola (*B. napus*). This involves identification and mapping of quantitative trait loci (QTLs) responsible for clubroot resistance across various species. For instance, a study of *B. napus* identified two major QTLs and several minor QTLs using associative transcriptomics. These loci are potential targets for breeding programs aimed at combining multiple resistance genes into new cultivars [18]. Both clubroot resistance (CR) sources were less efficient in the *B. napus* background than in the original parent. In particular, CR from *B. oleracea* appears to be strongly diluted, indicating the presence of epistatic factors in the *B. rapa* genome [19,22,32,97,115].

5.2. Transfer of Clubroot Resistance Outside Triangle of U

5.2.1. Raphanus Sativus

The radish (*Raphanus sativus*) has the potential to confer clubroot resistance when hybridized with *Brassica* spp. The introduction of resistance genes from *R. sativus* into Brassica species is considered a viable strategy for improving disease resistance [70,116–119]. Several radish accessions exhibit high resistance to clubroot disease, cover a wide range of horticultural traits, and have the potential to serve as novel sources of resistance genes for breeding programs [103]. Systematic evaluations have identified accessions showing strong resistance to clubroot, enriching the genetic diversity of resistance genes available in the radish gene pool, and indicating their utility in breeding programs aimed at enhancing resistance in Brassica crops [27]. Another significant approach involves the development of a synthetic allotetraploid, *Brassicoraphanus* (RRCC, 2n = 36), derived from a cross between *R. sativus* and *B. oleracea*. The creation of *Raphanobrassica*, an intergeneric hybrid of *Raphanus* and *Brassica*, has opened new avenues for trait introgression in these crops [4,20,22,49,118,120]. This allotetraploid demonstrated resistance to multiple strains of clubroot pathogens. Interspecific hybridization efforts have also highlighted the potential of radish to transfer its resistance traits to *B. napus* (canola), illustrating its high potential for genetic exchange and improvement via distant hybridization approaches, by ensuring successful chromosome pairing and recombination [49]. Research on F_1 hybrids derived from crosses between *Brassicoraphanus* and *B. napus* has revealed a substantial degree of chromosomal recombination between the genomes of these plant species, suggesting promising potential for incorporating resistance traits into *B. napus*. Development of *B.*

napus-R. sativus monosomic alien addition lines (MAALs) have facilitated the investigation and potential transfer of clubroot resistance genes. Additionally, backcrossed progenies have demonstrated clubroot resistance, offering a genetic resource for breeding resistant cultivars of *B. napus* [22,49,81]. Overall, the identified resistant radish accessions and associated QTLs enriched the genetic resources available for clubroot resistance breeding, making radish a valuable contributor to the development of resistant cultivars in cruciferous crops. These loci are important for understanding resistance mechanisms, and serve as targets for marker-assisted selection in breeding programs. For example, a CR locus, distinguished as Crs1, has been identified in the radish genome with genetic markers showing sequence homology to similar regions in *Arabidopsis thaliana* and *B. rapa* [103]. Notably, a high-density genetic linkage map has helped identify several QTLs responsible for resistance, which can be leveraged for breeding clubroot-resistant varieties of radish as well as other cruciferous crops [81].

5.2.2. Other Cruciferous Species

To date, no substantial study has specifically targeted non-*Brassica* and non-*Raphanus* cruciferous species for clubroot resistance. Further research on cruciferous plants may reveal unexplored resources. Ongoing research and screening of wild relatives and less common species within the *Cruciferae* family are crucial for expanding the genetic basis of resistance breeding. A collection of species within the *Cruciferae* family, including *B.juncea*, Chinese cabbage, radishes, and kales, has been evaluated and used in hybridization efforts to confer clubroot resistance to *B. napus* (Liu et al., 2018). This endeavor could uncover novel resistance genes that could be utilized in breeding programs to develop robust disease-resistant cultivars. The model organism study of *Arabidopsis thaliana* shares several commonalities with clubroot resistance, particularly concerning research and genetic insights, despite not being commercially significant for breeding programs [121]. For example, specific genes in *A. thaliana* have been shown to play a role in clubroot resistance. Resistance to the *P. brassicae* (RPB1) gene, which is essential for clubroot resistance in *Arabidopsis*, has been reported by Ochoa et al., 2023 [122]. The absence of a functional RPB1 gene in certain *A. thaliana* accessions results in susceptibility to *P. brassicae*, highlighting its critical role in defence mechanisms. This study also identified a broad-spectrum clubroot resistance gene isolated from *Arabidopsis* [122,123]. Recent studies have explored the genetic and physiological responses of *A. thaliana* to clubroot infection. For example, the role of SnRK1.1-mediated resistance and the effect of trehalose metabolism on partial resistance have been evaluated, providing insights into how *A. thaliana* responds to *P. brassicae* infection at the molecular level [124,125]

6. Perspectives and Future Directions

6.1. Integrating Multiple Clubroot Resistance

Integrating multiple clubroot resistance (CR) genes from various sources into intercrosses is an effective strategy to enhance resistance against diverse races of *P. brassicae*. Research using associative transcriptomics in *B. napus* has identified several major and minor loci associated with clubroot resistance that are suitable for the integration of clubroot genes and broadening of the genetic base. These findings facilitate pyramiding of resistance genes by combining multiple loci to create new varieties with enhanced resistance [18]. Detailed mapping of CR loci, such as CRb in *B. rapa*, has revealed their position alongside other closely linked CR genes CRa and CR [93]. This highlights the possibility of stacking of these genes in breeding programs to develop robust resistance [92,126]. Additionally, comparative studies characterizing QTLs for clubroot resistance across *B. rapa* and *B. oleracea* may facilitate the transfer and integration of resistance genes across Brassica species. This approach enables breeders to exploit existing resistance from a wider genetic pool [96]. The exploration of a broader genetic base for intercrosses is becoming increasingly feasible with the advent of advanced genomic tools such as quantitative trait loci sequencing (QTL-Seq) and bulked segregant analysis. These methodologies are instrumental in identifying and integrating additional

CR resistance genes, thereby enhancing the efficacy of intercrosses and facilitating the development of cultivars with comprehensive resistance profiles [88].

6.2. Employing Advanced Technologies

Employing advanced technologies, such as CRISPR/Cas9, for precise gene editing may accelerate breeding by rapidly introducing clubroot resistance through interspecific and intergeneric hybridization and reducing the development time for new resistant cultivars [127]. CRISPR/Cas9-based vector systems are powerful tools for breeding crops with enhanced clubroot resistance, through interspecific and intergeneric crosses. CRISPR/Cas9 enables precise modifications at specific genomic sites to introduce resistance traits against clubroot disease, which is crucial for integrating resistance genes into the desired species [128–131]. This system can be used to develop selection-marker-free plants, avoid traditional transgenesis issues, and facilitate regulatory approval of genetically edited plants [132]. CRISPR/Cas9's high specificity minimizes off-target effects, while enabling the stacking of resistance traits across species, making it feasible to integrate resistance mechanisms into crop genomes [133].

6.3. Exploration of Genetic Resources

Exploration of genetic resources in cruciferous species beyond *Brassica* and *Raphanus* presents an opportunity to integrate multiple CR resistance genes to improve the durability and spectrum of resistance against clubroot in *Brassica* crops through strategic intercrossing. Genetic resistance studies have generally focused on *Brassica species*; however, examining other cruciferous species offers the potential to discover novel resistance genes and mechanisms. Advanced genomic tools, such as quantitative trait loci sequencing (QTL-Seq) and bulked segregant analysis (BSA), enable researchers to identify and integrate valuable traits such as clubroot resistance (CR) genes from a wider range of cruciferous species. By expanding the genetic pool and leveraging advanced genomic tools, researchers can potentially develop cultivars with enhanced resistance profiles and other desirable traits that can contribute to the overall improvement of cruciferous crops [88].

6.4. High-Density Genetic Linkage Maps

A critical approach involves creating high-density genetic linkage maps and conducting QTL analyses similar to those applied to map resistance in radish [81]. Synteny analysis using model organisms such as *A. thaliana* could also provide insights into conserved genetic mechanisms across diverse cruciferous species [12]. Utilizing associative transcriptomics, such as that of *Brassica napus*, could aid in identifying candidate genes linked to resistance traits in other cruciferous plants [18].

6.5. Advanced Genomic Technologies

Moreover, employing advanced genomic technologies, such as next-generation sequencing and genome-wide association studies (GWAS), will facilitate the discovery of novel resistance genes and inform marker-assisted breeding programs aimed at developing clubroot-resistant cultivars [35,127,134]. These efforts will mark a significant step toward improving the agricultural sustainability and productivity of cruciferous crop species globally.

7. Implications for Breeding Programs:

1. Interspecific and intergeneric hybridization allows for the broadening of the genetic base, which is essential for developing resistance to clubroot. The addition of genetic material from related species or genera can introduce novel alleles for resilience against diseases and enhance breeding programs [49]. The most promising types of clubroot resistance in Brassica species for intercrosses are those that employ a combination of genetic and molecular approaches to address the challenges posed by various pathotypes of *P. brassicae*. The key strategies that show promise are as follows.

2. Combining resistance traits: By integrating resistance traits from multiple species, hybridization can lead to the development of cultivars with enhanced and durable resistance to various pathotypes of *P. brassicae* [20].
3. Combination of dominant resistance loci: The use of multiple resistance loci such as those on different chromosomes can lead to durable resistance. For example, integration of several resistance loci (such as Crr and CR) through marker-assisted breeding offers a robust approach for Chinese cabbage [37].
4. Production of synthetic hybrids: Synthetic amphidiploids and other types of hybrids provide valuable platforms for breeding programs. For example, synthetic hybrids enable the transfer of resistance genes across species barriers, which is vital for developing resistant varieties [61].
5. Quantitative trait locus (QTL) mapping: Identification and mapping of QTLs associated with resistance can facilitate the breeding of resistant varieties. Genomic regions, such as the novel CRs locus on chromosome A08, have been identified in *B. napus* and *B. rapa*, providing new avenues for breeding resistant cultivars [83,84].
6. Utilization of European Fodder Turnips: Resistance genes from European fodder turnips that exhibit broad-spectrum resistance have been introduced into susceptible Brassica lines. For example, CRa gene confers specific resistance to *B. rapa* and has been characterized using molecular techniques [12].
7. Diverse genetic backgrounds: Screening of diverse *Brassica* germplasms revealed pathotype-specific resistance, which is crucial for identifying different strains of *P. brassicae*. For instance, *B. oleracea* has shown promising QTLs associated with resistance to pathotypes sourced from both its acephala and capitata varieties [14,83].
8. Associative transcriptomics: This approach involves a combination of genome-wide association studies (GWAS) and gene expression data to identify resistance genes. In *B. napus*, Two major loci that control resistance have been identified in *B. napus*, providing essential information for marker-assisted breeding [18].
9. CRISPR/Cas9: The proposed use of CRISPR/Cas9 gene editing technology is a forward-thinking technique. This tool offers unparalleled precision in genome modification, allowing for the rapid introduction of resistance traits with minimal off-target effects and potentially avoiding complex regulatory hurdles associated with traditional GMOs. This technique overcomes sexual incompatibility and creates hybrids for transferring desired traits such as clubroot resistance.

By integrating these resistance strategies with interspecific or intergeneric hybridization, breeders can develop *Brassica* cultivars with enhanced durability and adaptability to various *P. brassicae* pathotypes, thereby ensuring a sustained crop yield and economic viability.

Author Contributions: P.K.: Conceptualization, methodology, project administration, visualization, writing—original draft, review, and editing; M.K.: methodology, review, and editing. All authors have read and agreed to the published version of the manuscript.

Funding: This study was supported by statutory funds from The National Institute of Horticultural Research, Skierniewice, Poland and in the frame of subsidy of the Ministry of Agriculture and Rural Development special-purpose—Task 3.3: “The development of breeding materials for white head cabbage with higher resistance to drought stress under field conditions, cytoplasmic male sterility and increased tolerance to bacterial rot”.

Ethical Compliance: All procedures performed in this study involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and the 1964 Helsinki Declaration and its later amendments or comparable ethical standards.

Data Availability Statement: No new data were created or analyzed in this study.

Declaration of Generative AI and AI-Assisted Technologies in the Writing Process: During the preparation of this manuscript, we used Paperpal to check grammar and spelling. After using this tool/service, the authors reviewed and edited the content as required and took full responsibility for the publication.

Conflicts of Interest: The authors declare that they have no affiliations with or involvement in any organization or entity with any financial interest in the subject matter or materials discussed in this manuscript.

References

1. Botero, A.; García, C.; Gossen, B.D.; Strelkov, S.E.; Todd, C.D.; Bonham-Smith, P.C.; Pérez-López, E. Clubroot Disease in Latin America: Distribution and Management Strategies. *Plant Pathol.* **2019**, *68*, 827–833, doi:10.1111/ppa.13013.
2. Salih, R.; Brochu, A.-S.; Labbé, C.; Strelkov, S.E.; Franke, C.; Bélanger, R.; Pérez-López, E. A Hydroponic-Based Bioassay to Facilitate Plasmodiophora Brassicae Phenotyping. *Plant Dis.* **2024**, *108*, 131–138, doi:10.1094/PDIS-05-23-0959-RE.
3. Xu, X.; Wu, C.; Zhang, F.; Yao, J.; Fan, L.; Liu, Z.; Yao, Y. Comprehensive Review of Plasmodiophora Brassicae: Pathogenesis, Pathotype Diversity, and Integrated Control Methods. *Front. Microbiol.* **2025**, *16*, 1531393, doi:10.3389/fmicb.2025.1531393.
4. Diederichsen, E.; Frauen, M.; Linders, E.G.A.; Hatakeyama, K.; Hirai, M. Status and Perspectives of Clubroot Resistance Breeding in Crucifer Crops. *J. Plant Growth Regul.* **2009**, *28*, 265–281, doi:10.1007/s00344-009-9100-0.
5. Donald, E.C.; Porter, I.J. Clubroot in Australia: The History and Impact of *Plasmodiophora Brassicae* in *Brassica* Crops and Research Efforts Directed towards Its Control. *Can. J. Plant Pathol.* **2014**, *36*, 66–84, doi:10.1080/07060661.2013.873482.
6. Chai, A.L.; Xie, X.W.; Shi, Y.X.; Li, B.J. Research Status of Clubroot (*Plasmodiophora Brassicae*) on Cruciferous Crops in China. *Can. J. Plant Pathol.* **2014**, *36*, 142–153, doi:10.1080/07060661.2013.868829.
7. Bruce, T.J.A. GM as a Route for Delivery of Sustainable Crop Protection. *J. Exp. Bot.* **2012**, *63*, 537–541, doi:10.1093/jxb/err281.
8. Struck, C.; Rüsch, S.; Strehlow, B. Control Strategies of Clubroot Disease Caused by Plasmodiophora Brassicae. *Microorganisms* **2022**, *10*, 620, doi:10.3390/microorganisms10030620.
9. Dixon, G.R. Clubroot (*Plasmodiophora Brassicae* Woronin) – an Agricultural and Biological Challenge Worldwide. *Can. J. Plant Pathol.* **2014**, *36*, 5–18, doi:10.1080/07060661.2013.875487.
10. Hasan, J.; Megha, S.; Rahman, H. Clubroot in Brassica: Recent Advances in Genomics, Breeding, and Disease Management. *Genome* **2021**, *64*, 735–760, doi:10.1139/gen-2020-0089.
11. Ahmed, H.U.; Hwang, S.F.; Strelkov, S.E.; Gossen, B.D.; Peng, G.; Howard, R.J.; Turnbull, G.D. Assessment of Bait Crops to Reduce Inoculum of Clubroot (*Plasmodiophora Brassicae*) of Canola. *Can. J. Plant Sci.* **2011**, *91*, 545–551, doi:10.4141/cjps10200.
12. Ueno, H.; Matsumoto, E.; Aruga, D.; Kitagawa, S.; Matsumura, H.; Hayashida, N. Molecular Characterization of the CRa Gene Conferring Clubroot Resistance in Brassica Rapa. *Plant Mol. Biol.* **2012**, *80*, 621–629, doi:10.1007/s11103-012-9971-5.
13. Dakouri, A.; Lamara, M.; Karim, M.M.; Wang, J.; Chen, Q.; Gossen, B.D.; Strelkov, S.E.; Hwang, S.-F.; Peng, G.; Yu, F. Identification of Resistance Loci against New Pathotypes of Plasmodiophora Brassicae in Brassica Napus Based on Genome-Wide Association Mapping. *Sci. Rep.* **2021**, *11*, doi:10.1038/s41598-021-85836-9.
14. Farid, M.; Yang, R.-C.; Kebede, B.; Rahman, H. Evaluation of Brassica Oleracea Accessions for Resistance to Plasmodiophora Brassicae and Identification of Genomic Regions Associated with Resistance. *Genome* **2020**, *63*, 91–101, doi:10.1139/gen-2019-0098.
15. Hollman, K.B.; Hwang, S.F.; Manolii, V.P.; Strelkov, S.E. Pathotypes of Plasmodiophora Brassicae Collected from Clubroot Resistant Canola (Brassica Napus L.) Cultivars in Western Canada in 2017-2018. *Can. J. Plant Pathol.* **2021**, *43*, 622–630, doi:10.1080/07060661.2020.1851893.
16. Holtz, M.D.; Hwang, S.-F.; Strelkov, S.E. Genotyping of Plasmodiophora Brassicae Reveals the Presence of Distinct Populations. *BMC Genomics* **2018**, *19*, 254, doi:10.1186/s12864-018-4658-1.
17. Zeng, L.; Zhang, Y.; Wu, Y.; Zhang, X.; Zhao, C.; Ren, L.; Huang, J.; Cheng, X.; Liu, S.; Liu, L. Pathotype Characterization of Plasmodiophora Brassicae by European Clubroot Differential and Williams Sets in China. *Plant Dis.* **2024**, *108*, 847–851, doi:10.1094/PDIS-08-23-1571-SC.

18. Hejna, O.; Havlickova, L.; He, Z.; Bancroft, I.; Curn, V. Analysing the Genetic Architecture of Clubroot Resistance Variation in Brassica Napus by Associative Transcriptomics. *Mol. Breed.* **2019**, *39*, doi:10.1007/s11032-019-1021-4.
19. Hirani, A.H.; Gao, F.; Liu, J.; Fu, G.; Wu, C.; McVetty, P.B.E.; Duncan, R.W.; Li, G. Combinations of Independent Dominant Loci Conferring Clubroot Resistance in All Four Turnip Accessions (Brassica Rapa) From the European Clubroot Differential Set. *Front. Plant Sci.* **2018**, *9*, 1628, doi:10.3389/fpls.2018.01628.
20. Kaneko, Y.; Bang, S.W. Interspecific and Intergeneric Hybridization and Chromosomal Engineering of Brassicaceae Crops. *Breed. Sci.* **2014**, *64*, 14–22, doi:10.1270/jsbbs.64.14.
21. Mehraj, H.; Akter, A.; Miyaji, N.; Miyazaki, J.; Shea, D.J.; Fujimoto, R.; Doullah, M.A.-U. Genetics of Clubroot and Fusarium Wilt Disease Resistance in Brassica Vegetables: The Application of Marker Assisted Breeding for Disease Resistance. *Plants* **2020**, *9*, 1–15, doi:10.3390/plants9060726.
22. Piao, Z.; Ramchiary, N.; Lim, Y.P. Genetics of Clubroot Resistance in Brassica Species. *J. Plant Growth Regul.* **2009**, *28*, 252–264, doi:10.1007/s00344-009-9093-8.
23. Pilet-Nayel, M.-L.; Moury, B.; Caffier, V.; Montarry, J.; Kerlan, M.-C.; Fournet, S.; Durel, C.-E.; Delourme, R. Quantitative Resistance to Plant Pathogens in Pyramiding Strategies for Durable Crop Protection. *Front. Plant Sci.* **2017**, *8*, 1838, doi:10.3389/fpls.2017.01838.
24. Reglinski, T.; Havis, N.; Rees, H.J.; De Jong, H. The Practical Role of Induced Resistance for Crop Protection. *Phytopathology®* **2023**, *113*, 719–731, doi:10.1094/PHYTO-10-22-0400-IA.
25. Botero-Ramirez, A.; Kirk, B.; Strelkov, S.E. Optimizing Clubroot Management and the Role of Canola Cultivar Mixtures. *Pathogens* **2024**, *13*, 640, doi:10.3390/pathogens13080640.
26. Peng, G.; Lahlali, R.; Hwang, S.-F.; Pageau, D.; Hynes, R.K.; McDonald, M.R.; Gossen, B.D.; Strelkov, S.E. Crop Rotation, Cultivar Resistance, and Fungicides/Biofungicides for Managing Clubroot (*Plasmodiophora Brassicae*) on Canola. *Can. J. Plant Pathol.* **2014**, *36*, 99–112, doi:10.1080/07060661.2013.860398.
27. Ma, Y.; Wang, H.; Song, J.; Yang, W.; Jia, H.; Agerbirk, N.; Chen, Y.; Li, C.; Piao, Y.; Li, S.; et al. Identification of Clubroot-Resistant Germplasm in a Radish (Raphanus Sativus L.) Core Collection. *Agronomy* **2024**, *14*, 157, doi:10.3390/agronomy14010157.
28. Neik, T.X.; Barbetti, M.J.; Batley, J. Current Status and Challenges in Identifying Disease Resistance Genes in Brassica Napus. *Front. Plant Sci.* **2017**, *8*, doi:10.3389/fpls.2017.01788.
29. Ahuja, I.; Rohloff, J.; Bones, A.M. Defence Mechanisms of Brassicaceae: Implications for Plant-Insect Interactions and Potential for Integrated Pest Management. A Review. *Agron. Sustain. Dev.* **2010**, *30*, 311–348, doi:10.1051/agro/2009025.
30. Lamichhane, J.R.; Arseniuk, E.; Boonekamp, P.; Czembor, J.; Decroocq, V.; Enjalbert, J.; Finckh, M.R.; Korbin, M.; Koppel, M.; Kudsk, P.; et al. Advocating a Need for Suitable Breeding Approaches to Boost Integrated Pest Management: A European Perspective. *Pest Manag. Sci.* **2018**, *74*, 1219–1227, doi:10.1002/ps.4818.
31. Rato, C.; Carvalho, M.F.; Azevedo, C.; Oblessuc, P.R. Genome Editing for Resistance against Plant Pests and Pathogens. *Transgenic Res.* **2021**, *30*, 427–459, doi:10.1007/s11248-021-00262-x.
32. Fredua-Agyeman, R.; Rahman, H. Mapping of the Clubroot Disease Resistance in Spring Brassica Napus Canola Introgressed from European Winter Canola Cv. 'Mendel.' *Euphytica* **2016**, *211*, 201–213, doi:10.1007/s10681-016-1730-2.
33. Hirai, M.; Harada, T.; Kubo, N.; Tsukada, M.; Suwabe, K.; Matsumoto, S. A Novel Locus for Clubroot Resistance in Brassica Rapa and Its Linkage Markers. *Theor. Appl. Genet.* **2004**, *108*, 639–643, doi:10.1007/s00122-003-1475-x.
34. Hu, H.; Zhang, Y.; Yu, F. A CRISPR/Cas9-Based Vector System Enables the Fast Breeding of Selection-Marker-Free Canola with Rcr1-Rendered Clubroot Resistance. *J. Exp. Bot.* **2024**, *75*, 1347–1363, doi:10.1093/jxb/erad471.
35. Kopec, P.M.; Mikolajczyk, K.; Jajor, E.; Perek, A.; Nowakowska, J.; Obermeier, C.; Chawla, H.S.; Korbas, M.; Bartkowiak-Broda, I.; Karlowski, W.M. Local Duplication of TIR-NBS-LRR Gene Marks Clubroot Resistance in Brassica Napus Cv. Tosca. *Front. Plant Sci.* **2021**, *12*, doi:10.3389/fpls.2021.639631.
36. Kuginuki, Y.; Ajisaka, H.; Yui, M.; Yoshikawa, H.; Hida, K.-I.; Hirai, M. Rapd Markers Linked to a Clubroot-Resistance Locus in Brassica Rapa L. *Euphytica* **1997**, *98*, 149–154, doi:10.1023/A:1003147815692.

37. Nguyen, M.L.; Monakhos, G.F.; Komakhin, R.A.; Monakhos, S.G. The New Clubroot Resistance Locus Is Located on Chromosome A05 in Chinese Cabbage (Brassica Rapa L.). *Russ. J. Genet.* **2018**, *54*, 296–304, doi:10.1134/S1022795418030080.
38. Zhang, T.; Zhao, Z.; Zhang, C.; Pang, W.; Choi, S.R.; Lim, Y.P.; Piao, Z. Fine Genetic and Physical Mapping of the CRb Gene Conferring Resistance to Clubroot Disease in Brassica Rapa. *Mol. Breed.* **2014**, *34*, 1173–1183, doi:10.1007/s11032-014-0108-1.
39. Hajjar, R.; Hodgkin, T. The Use of Wild Relatives in Crop Improvement: A Survey of Developments over the Last 20 Years. *Euphytica* **2007**, *156*, 1–13, doi:10.1007/s10681-007-9363-0.
40. Quezada-Martinez, D.; Addo Nyarko, C.P.; Schiessl, S.V.; Mason, A.S. Using Wild Relatives and Related Species to Build Climate Resilience in Brassica Crops. *Theor. Appl. Genet.* **2021**, *134*, 1711–1728, doi:10.1007/s00122-021-03793-3.
41. Zou, J.; Gao, S.; Zhang, B.; Ge, W.; Zhang, J.; Ji, R. Chinese Cabbage BrCAP Has Potential Resistance against Plasmodiophora Brassicae. *Horticulturae* **2023**, *9*, doi:10.3390/horticulturae9040517.
42. Hu, D.; Jing, J.; Snowdon, R.J.; Mason, A.S.; Shen, J.; Meng, J.; Zou, J. Exploring the Gene Pool of *Brassica Napus* by Genomics-based Approaches. *Plant Biotechnol. J.* **2021**, *19*, 1693–1712, doi:10.1111/pbi.13636.
43. Snowdon, R.J. Cytogenetics and Genome Analysis in Brassica Crops. *Chromosome Res.* **2007**, *15*, 85–95, doi:10.1007/s10577-006-1105-y.
44. Cheng, F.; Wu, J.; Wang, X. Genome Triplication Drove the Diversification of Brassica Plants. *Hortic. Res.* **2014**, *1*, 14024, doi:10.1038/hortres.2014.24.
45. Nikolov, L.A. Brassicaceae Flowers: Diversity amid Uniformity. *J. Exp. Bot.* **2019**, *70*, 2623–2635, doi:10.1093/jxb/erz079.
46. Hu, D.; Zhang, W.; Zhang, Y.; Chang, S.; Chen, L.; Chen, Y.; Shi, Y.; Shen, J.; Meng, J.; Zou, J. Reconstituting the Genome of a Young Allopolyploid Crop, *Brassica Napus*, with Its Related Species. *Plant Biotechnol. J.* **2019**, *17*, 1106–1118, doi:10.1111/pbi.13041.
47. Chen, S.; Nelson, M.N.; Chèvre, A.-M.; Jenczewski, E.; Li, Z.; Mason, A.S.; Meng, J.; Plummer, J.A.; Pradhan, A.; Siddique, K.H.M.; et al. Trigenomic Bridges for *Brassica* Improvement. *Crit. Rev. Plant Sci.* **2011**, *30*, 524–547, doi:10.1080/07352689.2011.615700.
48. Wei, Z.; Wang, M.; Chang, S.; Wu, C.; Liu, P.; Meng, J.; Zou, J. Introgressing Subgenome Components from Brassica Rapa and B. Carinata to B. Juncea for Broadening Its Genetic Base and Exploring Intersubgenomic Heterosis. *Front. Plant Sci.* **2016**, *7*, doi:10.3389/fpls.2016.01677.
49. Zhan, Z.; Nwafor, C.C.; Hou, Z.; Gong, J.; Zhu, B.; Jiang, Y.; Zhou, Y.; Wu, J.; Piao, Z.; Tong, Y.; et al. Cytological and Morphological Analysis of Hybrids between Brassicoraphanus, and Brassica Napus for Introgression of Clubroot Resistant Trait into Brassica Napus L. *PLoS ONE* **2017**, *12*, doi:10.1371/journal.pone.0177470.
50. Zou, J.; Hu, D.; Mason, A.S.; Shen, X.; Wang, X.; Wang, N.; Grandke, F.; Wang, M.; Chang, S.; Snowdon, R.J.; et al. Genetic Changes in a Novel Breeding Population of *Brassica Napus* Synthesized from Hundreds of Crosses between *B. Rapa* and *B. Carinata*. *Plant Biotechnol. J.* **2018**, *16*, 507–519, doi:10.1111/pbi.12791.
51. Kamiński, P.; Marasek-Ciołakowska, A.; Podwyszyńska, M.; Nowakowska, M.; Nowak, K.; Szczechura, W.; Kowalska, U. Development and Characteristics of Intergeneric Brassica Rapa L. Subsp. Pekinensis × Sinapis Alba Hybrids as a New Germplasm for the Breeding. *Sci. Hortic.* **2025**, *344*, 114102, doi:10.1016/j.scienta.2025.114102.
52. Pelletier, G.; Primard, C.; Vedel, F. Intergeneric Cytoplasm Hybridization in Cruciferae by Protoplast Fusion. In *Protoplasts 1983*; Potrykus, I., Harms, C.T., Hinnen, A., Hütter, R., King, P.J., Shillito, R.D., Eds.; Birkhäuser Basel: Basel, 1983; pp. 286–287 ISBN 978-3-0348-6557-9.
53. Crisp, P.; Crute, I.R.; Sutherland, R.A.; Angell, S.M.; Bloor, K.; Burgess, H.; Gordon, P.L. The Exploitation of Genetic Resources of Brassica Oleracea in Breeding for Resistance to Clubroot (Plasmodiophora Brassicae). *Euphytica* **1989**, *42*, 215–226, doi:10.1007/BF00034457.
54. Matsumoto, E.; Ueno, H.; Aruga, D.; Sakamoto, K.; Hayashida, N. Accumulation of Three Clubroot Resistance Genes through Marker-Assisted Selection in Chinese Cabbage (Brassica Rapa Ssp. Pekinensis). *J. Jpn. Soc. Hortic. Sci.* **2012**, *81*, 184–190, doi:10.2503/jjshs1.81.184.

55. Cardoza, V.; Stewart, C.N. Brassica Biotechnology: Progress in Cellular and Molecular Biology. *Vitro Cell. Dev. Biol. - Plant* **2004**, *40*, 542–551, doi:10.1079/IVP2004568.
56. Momotaz, A.; Kato, M.; Kakihara, F. Production of Intergeneric Hybrids between Brassica and Sinapis Species by Means of Embryo Rescue Techniques. *Euphytica* **1998**, *103*, 123–130, doi:10.1023/A:1018331528368.
57. Sharma, D.R.; Kaur, R.; Kumar, K. Embryo Rescue in Plants—a Review. *Euphytica* **1996**, *89*, 325–337, doi:10.1007/BF00022289.
58. Snowdon, R.J.; Friedt, W. Molecular Markers in *Brassica* Oilseed Breeding: Current Status and Future Possibilities. *Plant Breed.* **2004**, *123*, 1–8, doi:10.1111/j.1439-0523.2003.00968.x.
59. Tonguç, M.; Griffiths, P.D. Development of Black Rot Resistant Interspecific Hybrids between Brassica Oleracea L. Cultivars and Brassica Accession A 19182, Using Embryo Rescue. *Euphytica* **2004**, *136*, 313–318, doi:10.1023/B:EUPH.0000032733.47031.5f.
60. Rogo, U.; Fambrini, M.; Pugliesi, C. Embryo Rescue in Plant Breeding. *Plants* **2023**, *12*, 3106, doi:10.3390/plants12173106.
61. Liu, Y.; Xu, A.; Liang, F.; Yao, X.; Wang, Y.; Liu, X.; Zhang, Y.; Dalelhan, J.; Zhang, B.; Qin, M.; et al. Screening of Clubroot-Resistant Varieties and Transfer of Clubroot Resistance Genes to Brassica Napus Using Distant Hybridization. *Breed. Sci.* **2018**, *68*, 258–267, doi:10.1270/jsbbs.17125.
62. Chiang, M.S.; Chiang, B.Y.; Grant, W.F. Transfer of Resistance to Race 2 of Plasmodiophora Brassicae from Brassica Napus to Cabbage (B. Oleracea Var. Capitata). I. Interspecific Hybridization between B. Napus and B. Oleracea Var. Capitata. *Euphytica* **1977**, *26*, 319–336, doi:10.1007/BF00026993.
63. Matsumoto, E.; Yasui, C.; Ohi, M.; Tsukada, M. Linkage Analysis of RFLP Markers for Clubroot Resistance and Pigmentation in Chinese Cabbage (Brassica Rapa Ssp. Pekinensis). *Euphytica* **1998**, *104*, 79–86, doi:10.1023/A:1018370418201.
64. Rahman, H.; Shakir, A.; Jakir Hasan, M. Breeding for Clubroot Resistant Spring Canola (Brassica Napus L.) for the Canadian Prairies: Can the European Winter Canola Cv. Mendel Be Used as a Source of Resistance? *Can. J. Plant Sci.* **2011**, *91*, 447–458, doi:10.4141/cjps10073.
65. Fredua-Agyeman, R.; Hwang, S. -F.; Strelkov, S.E.; Zhou, Q.; Feindel, D. Potential Loss of Clubroot Resistance Genes from Donor Parent *Brassica Rapa* Subsp. *Rapifera* (ECD 04) during Doubled Haploid Production. *Plant Pathol.* **2018**, *67*, 892–901, doi:10.1111/ppa.12816.
66. Diederichsen, E.; Sacristan, M.D. Disease Response of Resynthesized Brassica Napus L. Lines Carrying Different Combinations of Resistance to Plasmodiophora Brassicae Wor. *Plant Breed.* **1996**, *115*, 5–10, doi:10.1111/j.1439-0523.1996.tb00862.x.
67. Ren, J.P.; Dickson, M.H.; Earle, E.D. Improved Resistance to Bacterial Soft Rot by Protoplast Fusion between Brassica Rapa and B. Oleracea. *Theor. Appl. Genet.* **2000**, *100*, 810–819, doi:10.1007/s001220051356.
68. Yu, F.; Zhang, Y.; Wang, J.; Chen, Q.; Karim, M.M.; Gossen, B.D.; Peng, G. Identification of Two Major QTLs in Brassica Napus Lines With Introgressed Clubroot Resistance From Turnip Cultivar ECD01. *Front. Plant Sci.* **2022**, *12*, doi:10.3389/fpls.2021.785989.
69. Sacristán, M.D.; Gerdemann-Knörck, M.; Schieder, O. Incorporation of Hygromycin Resistance in Brassica Nigra and Its Transfer to B. Napus through Asymmetric Protoplast Fusion. *Theor. Appl. Genet.* **1989**, *78*, 194–200, doi:10.1007/BF00288799.
70. Hagimori, M.; Nagaoka, M.; Kato, N.; Yoshikawa, H. Production and Characterization of Somatic Hybrids between the Japanese Radish and Cauliflower. *Theor. Appl. Genet.* **1992**, *84*, 819–824, doi:10.1007/BF00227390.
71. Kameya, T.; Kanzaki, H.; Toki, S.; Abe, T. Transfer of Radish (Raphanus Sativus L.) Chloroplasts into Cabbage (Brassica Oleracea L.) by Protoplast Fusion. *Jpn. J. Genet.* **1989**, *64*, 27–34, doi:10.1266/jjg.64.27.
72. Diederichsen, E.; Wagenblatt, B.; Schallehn, V.; Deppe, U.; Sacristan, M.D. Transfer of Clubroot Resistance from Resynthesised Brassica Napus into Oilseed Rape - Identification of Race- Specific Interactions with Plasmodiophora Brassicae. In Proceedings of the Acta Hortic.; International Society for Horticultural Science, 1996; Vol. 407, pp. 423–429.
73. Francia, E.; Tacconi, G.; Crosatti, C.; Barabaschi, D.; Bulgarelli, D.; Dall'Aglio, E.; Valè, G. Marker Assisted Selection in Crop Plants. *Plant Cell Tissue Organ Cult.* **2005**, *82*, 317–342, doi:10.1007/s11240-005-2387-z.

74. Hu, H.; Zhang, Y.; Yu, F. A CRISPR/Cas9-Based Vector System Enables the Fast Breeding of Selection-Marker-Free Canola with *Rcr1* -Rendered Clubroot Resistance. *J. Exp. Bot.* **2024**, *75*, 1347–1363, doi:10.1093/jxb/erad471.
75. Jonas, E.; Koning, D.-J.D. Genomic Selection Needs to Be Carefully Assessed to Meet Specific Requirements in Livestock Breeding Programs. *Front. Genet.* **2015**, *6*, doi:10.3389/fgene.2015.00049.
76. Neyhart, J.L.; Lorenz, A.J.; Smith, K.P. Multi-Trait Improvement by Predicting Genetic Correlations in Breeding Crosses. *G3 GenesGenomesGenetics* **2019**, *9*, 3153–3165, doi:10.1534/g3.119.400406.
77. Wang, Q.; Wang, Y.; Qian, H.; Zhang, Z.; Zhang, L. Evaluation of Germplasm and Development of Markers for Resistance to Plasmodiophora Brassicae in Radish (Raphanus Sativus L.). *Agronomy* **2022**, *12*, doi:10.3390/agronomy12030554.
78. Figdore, S.S.; Ferreira, M.E.; Slocum, M.K.; Williams, P.H. Association of RFLP Markers with Trait Loci Affecting Clubroot Resistance and Morphological Characters in Brassica Oleracea L. *Euphytica* **1993**, *69*, 33–44, doi:10.1007/BF00021723.
79. Duran, C.; Appleby, N.; Edwards, D.; Batley, J. Molecular Genetic Markers: Discovery, Applications, Data Storage and Visualisation. *Curr. Bioinforma.* **2009**, *4*, 16–27, doi:10.2174/157489309787158198.
80. Mammadov, J.; Aggarwal, R.; Buyyarapu, R.; Kumpatla, S. SNP Markers and Their Impact on Plant Breeding. *Int. J. Plant Genomics* **2012**, *2012*, 1–11, doi:10.1155/2012/728398.
81. Gan, C.; Deng, X.; Cui, L.; Yu, X.; Yuan, W.; Dai, Z.; Yao, M.; Pang, W.; Ma, Y.; Yu, X.; et al. Construction of a High-Density Genetic Linkage Map and Identification of Quantitative Trait Loci Associated with Clubroot Resistance in Radish (Raphanus Sativus L.). *Mol. Breed.* **2019**, *39*, doi:10.1007/s11032-019-1020-5.
82. You, F.M.; Cloutier, S. Mapping Quantitative Trait Loci onto Chromosome-Scale Pseudomolecules in Flax. *Methods Protoc.* **2020**, *3*, 28, doi:10.3390/mps3020028.
83. Jakir Hasan, M.; Strelkov, S.E.; Howard, R.J.; Rahman, H. Screening of *Brassica* Germplasm for Resistance to *Plasmodiophora Brassicae* Pathotypes Prevalent in Canada for Broadening Diversity in Clubroot Resistance. *Can. J. Plant Sci.* **2012**, *92*, 501–515, doi:10.4141/cjps2010-006.
84. Laila, R.; Park, J.-I.; Robin, A.H.K.; Natarajan, S.; Vijayakumar, H.; Shirasawa, K.; Isobe, S.; Kim, H.-T.; Nou, I.-S. Mapping of a Novel Clubroot Resistance QTL Using ddRAD-Seq in Chinese Cabbage (Brassica Rapa L.). *BMC Plant Biol.* **2019**, *19*, 13, doi:10.1186/s12870-018-1615-8.
85. Zhang, H.; Feng, J.; Manolii, V.P.; Strelkov, S.E.; Hwang, S.-F. Characterization of a Gene Identified in Pathotype 5 of the Clubroot Pathogen Plasmodiophora Brassicae. *Phytopathology* **2015**, *105*, 764–770, doi:10.1094/PHYTO-10-14-0270-R.
86. Chen, J.; Jing, J.; Zhan, Z.; Zhang, T.; Zhang, C.; Piao, Z. Identification of Novel QTLs for Isolate-Specific Partial Resistance to Plasmodiophora Brassicae in Brassica Rapa. *PLoS ONE* **2013**, *8*, doi:10.1371/journal.pone.0085307.
87. Fredua-Agyeman, R.; Jiang, J.; Hwang, S.-F.; Strelkov, S.E. QTL Mapping and Inheritance of Clubroot Resistance Genes Derived From Brassica Rapa Subsp. Rapifera (ECD 02) Reveals Resistance Loci and Distorted Segregation Ratios in Two F2 Populations of Different Crosses. *Front. Plant Sci.* **2020**, *11*, 899, doi:10.3389/fpls.2020.00899.
88. Hatakeyama, K.; Suwabe, K.; Tomita, R.N.; Kato, T.; Nunome, T.; Fukuoka, H.; Matsumoto, S. Identification and Characterization of Crr1a, a Gene for Resistance to Clubroot Disease (Plasmodiophora Brassicae Woronin) in Brassica Rapa L. *PLoS ONE* **2013**, *8*, doi:10.1371/journal.pone.0054745.
89. Karim, Md.M.; Dakouri, A.; Zhang, Y.; Chen, Q.; Peng, G.; Strelkov, S.E.; Gossen, B.D.; Yu, F. Two Clubroot-Resistance Genes, Rcr3 and Rcr9wa, Mapped in Brassica Rapa Using Bulk Segregant RNA Sequencing. *Int. J. Mol. Sci.* **2020**, *21*, 5033, doi:10.3390/ijms21145033.
90. Lee, J.; Izzah, N.K.; Choi, B.-S.; Joh, H.J.; Lee, S.-C.; Perumal, S.; Seo, J.; Ahn, K.; Jo, E.J.; Choi, G.J.; et al. Genotyping-by-Sequencing Map Permits Identification of Clubroot Resistance QTLs and Revision of the Reference Genome Assembly in Cabbage (*Brassica Oleracea* L.). *DNA Res.* **2015**, dsv034, doi:10.1093/dnares/dsv034.
91. Suwabe, K.; Tsukazaki, H.; Iketani, H.; Hatakeyama, K.; Fujimura, M.; Nunome, T.; Fukuoka, H.; Matsumoto, S.; Hirai, M. Identification of Two Loci for Resistance to Clubroot (Plasmodiophora Brassicae Woronin) in Brassica Rapa L. *Theor. Appl. Genet.* **2003**, *107*, 997–1002, doi:10.1007/s00122-003-1309-x.

92. Zhang, H.; Liu, X.; Zhou, J.; Strelkov, S.E.; Fredua-Agyeman, R.; Zhang, S.; Li, F.; Li, G.; Wu, J.; Sun, R.; et al. Identification of Clubroot (Plasmodiophora Brassicae) Resistance Loci in Chinese Cabbage (Brassica Rapa Ssp. Pekinensis) with Recessive Character. *Genes* **2024**, *15*, doi:10.3390/genes15030274.
93. Kato, T.; Hatakeyama, K.; Fukino, N.; Matsumoto, S. Fine Mapping of the Clubroot Resistance Gene CRb and Development of a Useful Selectable Marker in Brassica Rapa. *Breed. Sci.* **2013**, *63*, 116–124, doi:10.1270/jsbbs.63.116.
94. Hirani, A.H.; Gao, F.; Liu, J.; Fu, G.; Wu, C.; Yuan, Y.; Li, W.; Hou, J.; Duncan, R.; Li, G. Transferring Clubroot Resistance from Chinese Cabbage (Brassica Rapa) to Canola (B. Napus). *Can. J. Plant Pathol.* **2016**, *38*, 82–90, doi:10.1080/07060661.2016.1141799.
95. Cheng, F.; Wu, J.; Cai, C.; Fu, L.; Liang, J.; Borm, T.; Zhuang, M.; Zhang, Y.; Zhang, F.; Bonnema, G.; et al. Genome Resequencing and Comparative Variome Analysis in a Brassica Rapa and Brassica Oleracea Collection. *Sci. Data* **2016**, *3*, 160119, doi:10.1038/sdata.2016.119.
96. Nagaoka, T.; Doullah, M.A.U.; Matsumoto, S.; Kawasaki, S.; Ishikawa, T.; Hori, H.; Okazaki, K. Identification of QTLs That Control Clubroot Resistance in Brassica Oleracea and Comparative Analysis of Clubroot Resistance Genes between B. Rapa and B. Oleracea. *Theor. Appl. Genet.* **2010**, *120*, 1335–1346, doi:10.1007/s00122-010-1259-z.
97. Rahman, H.; Peng, G.; Yu, F.; Falk, K.C.; Kulkarni, M.; Selvaraj, G. Special Issue: Genetics and Breeding for Clubroot Resistance in Canadian Spring Canola (Brassica Napus L.). *Can. J. Plant Pathol.* **2014**, *36*, 122–134, doi:10.1080/07060661.2013.862571.
98. Chiang, B.Y.; Chiang, M.S.; Grant, W.F.; Crete, R. Transfer of Resistance to Race 2 of Plasmodiophora Brassicae from Brassica Napus to Cabbage (B. Oleracea Spp. Capitata). IV. A Resistant 18-Chromosome B1 Plant and Its B2 Progenies. *Euphytica* **1980**, *29*, 47–55, doi:10.1007/BF00037248.
99. Peng, L.; Zhou, L.; Li, Q.; Wei, D.; Ren, X.; Song, H.; Mei, J.; Si, J.; Qian, W. Identification of Quantitative Trait Loci for Clubroot Resistance in Brassica Oleracea with the Use of Brassica SNP Microarray. *Front. Plant Sci.* **2018**, *9*, doi:10.3389/fpls.2018.00822.
100. Ce, F.; Mei, J.; He, H.; Zhao, Y.; Hu, W.; Yu, F.; Li, Q.; Ren, X.; Si, J.; Song, H.; et al. Identification of Candidate Genes for Clubroot-Resistance in Brassica Oleracea Using Quantitative Trait Loci-Sequencing. *Front. Plant Sci.* **2021**, *12*, doi:10.3389/fpls.2021.703520.
101. Karim, Md.M.; Yu, F. Identification of QTLs for Resistance to 10 Pathotypes of Plasmodiophora Brassicae in Brassica Oleracea Cultivar ECD11 through Genotyping-by-Sequencing. *Theor. Appl. Genet.* **2023**, *136*, 249, doi:10.1007/s00122-023-04483-y.
102. Lindhout, P. The Perspectives of Polygenic Resistance in Breeding for Durable Disease Resistance. *Euphytica* **2002**, *124*, 217–226, doi:10.1023/A:1015686601404.
103. Kamei, A.; Tsuro, M.; Kubo, N.; Hayashi, T.; Wang, N.; Fujimura, T.; Hirai, M. QTL Mapping of Clubroot Resistance in Radish (Raphanus Sativus L.). *Theor. Appl. Genet.* **2010**, *120*, 1021–1027, doi:10.1007/s00122-009-1230-z.
104. A. Camargo, L.E. Mapping of Quantitative Trait Loci Controlling Resistance of *Brassica Oleracea* to *Xanthomonas Campestris* Pv. *Campestris* in the Field and Greenhouse. *Phytopathology* **1995**, *85*, 1296, doi:10.1094/Phyto-85-1296.
105. Okazaki, K.; Sakamoto, K.; Kikuchi, R.; Saito, A.; Togashi, E.; Kuginuki, Y.; Matsumoto, S.; Hirai, M. Mapping and Characterization of FLC Homologs and QTL Analysis of Flowering Time in Brassica Oleracea. *Theor. Appl. Genet.* **2007**, *114*, 595–608, doi:10.1007/s00122-006-0460-6.
106. Hirai, M. Genetic Analysis of Clubroot Resistance in Brassica Crops. *Breed. Sci.* **2006**, *56*, 223–229, doi:10.1270/jsbbs.56.223.
107. Kato, T.; Hatakeyama, K.; Fukino, N.; Matsumoto, S. Identificaiton of a Clubroot Resistance Locus Conferring Resistance to a Plasmodiophora Brassicae Classified into Pathotype Group 3 in Chinese Cabbage (Brassica Rapa L.). *Breed. Sci.* **2012**, *62*, 282–287, doi:10.1270/jsbbs.62.282.
108. Chang, A.; Lamara, M.; Wei, Y.; Hu, H.; Parkin, I.A.P.; Gossen, B.D.; Peng, G.; Yu, F. Clubroot Resistance Gene Rcr6 in Brassica Nigra Resides in a Genomic Region Homologous to Chromosome A08 in B. Rapa. *BMC Plant Biol.* **2019**, *19*, 224, doi:10.1186/s12870-019-1844-5.

109. Peng, G.; Falk, K.C.; Gugel, R.K.; Franke, C.; Yu, F.; James, B.; Strelkov, S.E.; Hwang, S.-F.; McGregor, L. Sources of Resistance to *Plasmodiophora Brassicae* (Clubroot) Pathotypes Virulent on Canola. *Can. J. Plant Pathol.* **2014**, *36*, 89–99, doi:10.1080/07060661.2013.863805.
110. Hasan, M.J.; Strelkov, S.E.; Howard, R.J.; Rahman, H. Screening of Brassica Germplasm for Resistance to Plasmodiophora Brassicae Pathotypes Prevalent in Canada for Broadening Diversity in Clubroot Resistance. *Can. J. Plant Sci.* **2012**, *92*, 501–515, doi:10.4141/CJPS2010-006.
111. Girke, A.; Schierholt, A.; Becker, H.C. Extending the Rapeseed Genepool with Resynthesized Brassica Napus L. I: Genetic Diversity. *Genet. Resour. Crop Evol.* **2012**, *59*, 1441–1447, doi:10.1007/s10722-011-9772-8.
112. Jesske, T.; Olberg, B.; Schierholt, A.; Becker, H.C. Resynthesized Lines from Domesticated and Wild Brassica Taxa and Their Hybrids with B. Napus L.: Genetic Diversity and Hybrid Yield. *Theor. Appl. Genet.* **2013**, *126*, 1053–1065, doi:10.1007/s00122-012-2036-y.
113. Rygulla, W.; Snowdon, R.J.; Eynck, C.; Koopmann, B.; Von Tiedemann, A.; Lühs, W.; Friedt, W. Broadening the Genetic Basis of *Verticillium Longisporum* Resistance in *Brassica Napus* by Interspecific Hybridization. *Phytopathology®* **2007**, *97*, 1391–1396, doi:10.1094/PHYTO-97-11-1391.
114. Werner, S.; Diederichsen, E.; Frauen, M.; Schondelmaier, J.; Jung, C. Genetic Mapping of Clubroot Resistance Genes in Oilseed Rape. *Theor. Appl. Genet.* **2008**, *116*, 363–372, doi:10.1007/s00122-007-0674-2.
115. Rusholme, R.L.; Higgins, E.E.; Walsh, J.A.; Lydiate, D.J. Genetic Control of Broad-Spectrum Resistance to Turnip Mosaic Virus in Brassica Rapa (Chinese Cabbage). *J. Gen. Virol.* **2007**, *88*, 3177–3186, doi:10.1099/vir.0.83194-0.
116. Brown, J.; Brown, A.P.; Davis, J.B.; Erickson, D. Intergeneric Hybridization between Sinapis Alba and Brassica Napus. *Euphytica* **1997**, *93*, 163–168, doi:10.1023/A:1002905816887.
117. Declercq, B.; Van Buyten, E.; Claeys, S.; Cap, N.; De Nies, J.; Pollet, S.; Höfte, M. Molecular Characterization of Phytophthora Porri and Closely Related Species and Their Pathogenicity on Leek (Allium Porrum). *Eur. J. Plant Pathol.* 2010, *127*, 341–350.
118. Katche, E. Interspecific Hybridization for Brassica Crop Improvement. *Crop Breed. Genet. Genomics* **2019**, doi:10.20900/cbgg20190007.
119. Peterka, H.; Budahn, H.; Schrader, O.; Ahne, R.; Schütze, W. Transfer of Resistance against the Beet Cyst Nematode from Radish (Raphanus Sativus) to Rape (Brassica Napus) by Monosomic Chromosome Addition. *Theor. Appl. Genet.* **2004**, *109*, 30–41, doi:10.1007/s00122-004-1611-2.
120. Sohn, S.-I.; Thamilarasan, S.K.; Pandian, S.; Oh, Y.-J.; Ryu, T.-H.; Lee, G.-S.; Shin, E.-K. Interspecific Hybridization of Transgenic Brassica Napus and Brassica Rapa—An Overview. *Genes* **2022**, *13*, 1442, doi:10.3390/genes13081442.
121. Alix, K.; Lariagon, C.; Delourme, R.; Manzanares-Dauleux, M.J. Exploiting Natural Genetic Diversity and Mutant Resources of *Arabidopsis Thaliana* to Study the *A. Thaliana – Plasmodiophora Brassicae* Interaction. *Plant Breed.* **2007**, *126*, 218–221, doi:10.1111/j.1439-0523.2007.01314.x.
122. Ochoa, J.C.; Mukhopadhyay, S.; Bieluszewski, T.; Jędryczka, M.; Malinowski, R.; Truman, W. Natural Variation in Arabidopsis Responses to *Plasmodiophora Brassicae* Reveals an Essential Role for *Resistance to Plasmodiophora Brasssicae 1* (*RPB1*). *Plant J.* **2023**, *116*, 1421–1440, doi:10.1111/tpj.16438.
123. Zhao, Y.; Bi, K.; Gao, Z.; Chen, T.; Liu, H.; Xie, J.; Cheng, J.; Fu, Y.; Jiang, D. Transcriptome Analysis of Arabidopsis Thaliana in Response to Plasmodiophora Brassicae during Early Infection. *Front. Microbiol.* **2017**, *8*, 673, doi:10.3389/fmicb.2017.00673.
124. Chen, W.; Li, Y.; Yan, R.; Ren, L.; Liu, F.; Zeng, L.; Sun, S.; Yang, H.; Chen, K.; Xu, L.; et al. SnRK1.1-mediated Resistance of *Arabidopsis Thaliana* to Clubroot Disease Is Inhibited by the Novel *Plasmodiophora Brassicae* Effector PBZF1. *Mol. Plant Pathol.* **2021**, *22*, 1057–1069, doi:10.1111/mpp.13095.
125. Gravot, A.; Grillet, L.; Wagner, G.; Jubault, M.; Lariagon, C.; Baron, C.; Deleu, C.; Delourme, R.; Bouchereau, A.; Manzanares-Dauleux, M.J. Genetic and Physiological Analysis of the Relationship between Partial Resistance to Clubroot and Tolerance to Trehalose in *Arabidopsis Thaliana*. *New Phytol.* **2011**, *191*, 1083–1094, doi:10.1111/j.1469-8137.2011.03751.x.
126. Hatakeyama, K.; Niwa, T.; Kato, T.; Ohara, T.; Kakizaki, T.; Matsumoto, S. The Tandem Repeated Organization of NB-LRR Genes in the Clubroot-Resistant CRb Locus in Brassica Rapa L. *Mol. Genet. Genomics* **2017**, *292*, 397–405, doi:10.1007/s00438-016-1281-1.

127. Wang, Y.; Zafar, N.; Ali, Q.; Manghwar, H.; Wang, G.; Yu, L.; Ding, X.; Ding, F.; Hong, N.; Wang, G.; et al. CRISPR/Cas Genome Editing Technologies for Plant Improvement against Biotic and Abiotic Stresses: Advances, Limitations, and Future Perspectives. *Cells* **2022**, *11*, 3928, doi:10.3390/cells11233928.
128. Ahmad, S.; Wei, X.; Sheng, Z.; Hu, P.; Tang, S. CRISPR/Cas9 for Development of Disease Resistance in Plants: Recent Progress, Limitations and Future Prospects. *Brief. Funct. Genomics* **2020**, *19*, 26–39, doi:10.1093/bfgp/elz041.
129. Erdoğan, İ.; Cevher-Keskin, B.; Bilir, Ö.; Hong, Y.; Tör, M. Recent Developments in CRISPR/Cas9 Genome-Editing Technology Related to Plant Disease Resistance and Abiotic Stress Tolerance. *Biology* **2023**, *12*, 1037, doi:10.3390/biology12071037.
130. Langner, T.; Kamoun, S.; Belhaj, K. CRISPR Crops: Plant Genome Editing Toward Disease Resistance. *Annu. Rev. Phytopathol.* **2018**, *56*, 479–512, doi:10.1146/annurev-phyto-080417-050158.
131. Tiwari, J.K.; Singh, A.K.; Behera, T.K. CRISPR/Cas Genome Editing in Tomato Improvement: Advances and Applications. *Front. Plant Sci.* **2023**, *14*, 1121209, doi:10.3389/fpls.2023.1121209.
132. Dong, G.; Fan, Z. CRISPR/Cas-Mediated Germplasm Improvement and New Strategies for Crop Protection. *Crop Health* **2024**, *2*, 2, doi:10.1007/s44297-023-00020-x.
133. Chen, K.; Wang, Y.; Zhang, R.; Zhang, H.; Gao, C. CRISPR/Cas Genome Editing and Precision Plant Breeding in Agriculture. *Annu. Rev. Plant Biol.* **2019**, *70*, 667–697, doi:10.1146/annurev-arplant-050718-100049.
134. Zhang, H.; Ma, X.; Liu, X.; Zhang, S.; Li, F.; Li, G.; Sun, R.; Zhang, S. Identification and Fine-Mapping of Clubroot (Plasmodiophora Brassicae) Resistant QTL in Brassica Rapa. *Horticulturae* **2022**, *8*, doi:10.3390/horticulturae8010066.