agronomy

MDPI

Review

Interspecific and Intergeneric Crosses for Clubroot Resistance in Brassica Crops

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; marta.konopacka@inhort.pl
* 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 the 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

Academic Editor: Jianbo Wang

Received: 23 October 2025
Revised: 5 December 2025
Accepted: 6 December 2025
Published: 9 December 2025

Citation: Kamiński, P.; Konopacka, M. Interspecific and Intergeneric Crosses for Clubroot Resistance in Brassica Crops. *Agronomy* **2025**, *15*, 2827. https://doi.org/10.3390/agronomy15122827

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. Developing galls act as strong metabolic sinks, actively drawing carbohydrates, amino acids, and minerals from the shoots and surrounding healthy roots; this redirected nutrient flow, combined with disruption of vascular tissue, markedly impairs the plant's ability to transport water and minerals. Consequently, the aboveground portions of afflicted plants exhibit yellowing, wilting, and eventual demise [4].

1.2. Significance

The socioeconomic impact of clubroot 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].

So far, there are no chemical control strategies for clubroot in Brassicaceae that can be considered both effective and sustainable. 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 for clubroot include integrated disease management such as crop rotation, the application of lime to raise soil pH to levels unfavorable for pathogen development, and the use of resistant cultivars. However, managing the disease remains challenging due to the persistence of long-lived resting spores and the substantial genetic diversity of *Plasmodiophora brassicae*, which results in multiple pathotypes with varying virulence and host specificity [4,10–17].

This variability further complicates control efforts, necessitating the development of broad-spectrum and durable resistance strategies. Genetic differences among regional isolates lead to variation in pathogenicity, underscoring the need for detailed pathotype classification. To better characterize this diversity and improve resistance breeding, several differential systems—including the Williams system, the European Clubroot Differential (ECD) set, the Canadian Clubroot Differential (CCD) set, the Somé et al. set, and the Sinitic Clubroot Differential (SCD) set—enable more precise classification of clubroot populations [18–20].

Classical differential-host studies documented distinct pathogenicity patterns among races [21], whereas recent advances, including a telomere-to-telomere genome assembly of strain Pb3A, provide a foundation for dissecting infection mechanisms [22]. Transcriptomic analyses reveal hormone-signaling and defense pathways underlying resistance in *Brassica rapa* [6,23]. Current research emphasizes developing rapid molecular pathotyping tools to complement phenotypic assays, supporting more precise detection and sustainable management of *P. brassicae* [24].

Genetic studies of Benoit Landry provided the first evidence that clubroot resistance could be mapped to discrete loci, forming the conceptual foundation for later QTL and marker-based analyses. Current resistance strategies face challenges from rapidly evolving pathotypes, highlighting the need for novel resistance sources. Breeding resistant cultivars, including interspecific and intergeneric crosses, offers a sustainable approach by tapping diverse Brassicaceae genetic resources [4,10,12,17–22]. Genetic resistance is more durable and cost-effective than chemical or cultural controls, providing protection without added input costs and avoiding environmental contamination [7,23,24]. Pyramiding multiple

resistance genes can better address pathogen diversity, and integrating genetic resistance with other methods enhances overall disease management. Breeding allows incorporation of new resistance genes to keep pace with evolving *P. brassicae* populations [4,10,17,25,26].

1.5. Role of Wide Hybridization

Wide hybridization—including both interspecific crosses and intergeneric crosses expands the accessible genetic variation by enabling the transfer of agronomically valuable traits from wild relatives or related species [4,27–35]. These approaches allow breeders to introgress resistance genes and other beneficial traits into cultivated Brassica crops, strengthening their resilience to pathogens and pests and providing access to resistance sources absent in domesticated germplasm [36–38].

In Brassicaceae, interspecific hybridization plays a central role in transferring clubroot resistance genes among Brassica species [26,39–45]. Successful introgression has improved crop performance while reducing dependence on chemical control measures. Continued exploration of wild relatives and related genera offers the potential to uncover additional resistance sources, supporting further progress in disease management and crop productivity [46,47].

Wide hybridization also enhances the genetic diversity of Brassica species. Genomic consequences such as chromosomal rearrangements, retrotransposon activation, and homeologous recombination contribute to novel genomic configurations that broaden phenotypic variability [48]. This increased diversity facilitates the introduction of stress-tolerance and agronomic traits, overcoming genetic bottlenecks in cultivated forms and supporting long-term crop improvement [49,50].

Despite its value, wide hybridization is constrained by biological barriers that limit fertilization success, embryo development, and hybrid fertility. Post-zygotic incompatibilities—particularly endosperm failure—often cause embryo abortion, making embryo-rescue techniques essential for recovering viable hybrids [17,51]. Early studies demonstrated that intergeneric *Brassica* × *Sinapis* hybrids could be obtained only when immature ovules were excised and cultured, greatly improving hybrid survival [52]. Similar approaches enabled introgression of powdery mildew resistance from *B. carinata* into *B. oleracea*, confirming that embryos from wide crosses rarely mature without intervention [51]. Beyond embryo recovery, chromosome doubling is critical for stabilizing recombinant genomes. Colchicine treatment of isolated microspores in *B. napus* can yield doubling efficiencies up to 70%, facilitating the production of doubled haploids that fix introgressed chromosomal segments [53]. Nevertheless, wide hybrids frequently exhibit sterility, aneuploidy, and irregular homeologous pairing, limiting fertility and the efficiency of introgression [54–56]. Crossability barriers are often asymmetric, as shown in *Brassica* × *Sinapis* crosses, where viable hybrids were obtained mainly when *Brassica* served as the female parent [52].

Collectively, these studies highlight that embryo and ovule culture, chromosome engineering, amphidiploid formation, and fertility restoration are essential components of successful interspecific and intergeneric hybridization pipelines in Brassicaceae [27,57–59].

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. 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 [60]. Interactions between genotypic and phenotypic variability in *Brassica* are evident, demonstrating the ability of these species to adapt morphologically and biochemically to environmental pressure [61].Reconstruction of *Brassica* genomes, such as that of *B. napus*, by incorporating sub-genomic 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 [62]. This genetic framework provides a foundation for understanding the potential for interspecific crosses within the *Brassica* genus [4,62–66]. 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 [4,29,65,67,68].

3. 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 [10,26,27,64,68,69].

3.1. Embryo Rescue

Embryo rescue is used to produce interspecific and intergeneric hybrids, overcome reproductive barriers, and incorporate beneficial alleles into cultivated species [27]. 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 [49,51,52,70–72]. 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 [57,71]. 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 [27]. 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) [73]. This approach has successfully identified true hybrids with clubroot resistance.

3.2. Polyploid Breeding

Polyploid breeding plays a significant role in enabling intergeneric and interspecific crosses for clubroot resistance in *Brassica* species [40,73–77]. 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 [27]. 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 [39]. 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 [29]. 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 [78]. Masud Karim and Yu (2024) resynthesized *B. napus* lines using a *B. rapa* donor carrying race-specific resistance genes and *B. oleracea* donors harboring race-non-specific QTLs. All resynthesized and semi-resynthesized lines showed high resistance to multiple *P. brassicae* races, confirming the effective transfer and stacking of resistance loci [79]. 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 [56].

3.3. 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 [80]. 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* [81]. 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* [82]. 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 [83,84]. 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 [85].

3.4. Molecular Markers

Molecular markers are essential tools for transferring and validating clubroot resistance across *Brassica* species and intergeneric hybrids. They enable precise mapping of resistance loci, assist in tracking desirable alleles during wide crosses, and accelerate breeding through marker-assisted selection. Various marker systems—including SNPs, RAPDs, SCARs, RFLPs, SSRs, IPs, and QTL-associated markers—have been applied to identify, map, and introgress clubroot resistance genes from diverse Brassicaceae germplasm, greatly improving the efficiency and accuracy of resistance breeding [42,86–89] (Table 1).

Table 1. Overview of molecular markers used in clubroot resistance breeding in *Brassica* crops.

Marker Type	Key Features	Use in Clubroot Resistance Research	Examples/Notes
SNP (Single-Nucleotide Po-lymorphism)	Highly abundant, high-resolution, genome-wide; suitable for GWAS and population studies	Precise mapping of CR loci; supports pyramiding; used in associative transcriptomics	Major CR loci mapped on A2 and A3 in *B. napus* [25]
RAPD (Random Amplified Polymorphic DNA)	Fast, low-cost, no prior sequence required; low reproducibility	Early identification of markers linked to CR; useful for diverse germplasm	RA12-75A, WE22B, WE49B linked to CR in *B. rapa* [44]
SCAR (Sequence-Characte-rized Amplified Region)	Derived from RAPD; more specific and reproducible	Marker-assisted selection of CR alleles	SCAR marker tau_cBrCR404 linked to CR in Chinese cabbage [45]
RFLP (Restriction Fragment Length Polymorphism)	Reliable but labor-intensive; requires high-quality DNA	Mapping CR genes (e.g., CRa); linkage map construction for interspecific crosses	Used in broccoli × cauliflower CR mapping [75,90]
SSR (Simple Sequence Repeat)	Co-dominant, reproducible, widely used in MAS	Accelerates selection of CR traits and reduces breeding time	CR QTL mapping in *B. oleracea* and *B. rapa* [91] mapping *CRd* in *B. rapa* [92] used in MAS for CR introgression into *B. napus* [73] used for high-density mapping of *CRb* [93] QTL analyses of CR in *B. napus* [94] SSRs/SCARs used for pyramiding *CRa*, *CRk*, *CRc* [69] analysis of *P. brassicae* isolate variation and resistance responses [95]
AFLP (Amplified Fragment Length Polymorphism)	Highly polymorphic, no prior sequence required; good genome coverage	Useful in detecting polymorphisms in wild relatives and supporting introgression of CR from related species	AFLP markers included in maps identifying CR QTL in *B. oleracea* (e.g., *pb-Bo(Anju)1*) [91]. Used in classical BSA workflows relevant to CR gene mapping [92]. Method validated for resistance-gene mapping in other crops [96].
QTL-based markers	Identify genomic regions controlling quantitative resistance	Mapping major and minor CR loci for introgression	*CRs* on A08 (*B. napus*/*B. rapa*); *qCRc7-2*(3,4) on C07; *Crr1-3*; *Cr4Ba1.1* on A01; *Cr4Ba8.1* on A08; *Pb-Bo1* [19,83,84]

4. Sources of Clubroot Resistance

Genetic resistance to clubroot occurs across numerous *Brassica* species [97] and remains a cornerstone of sustainable disease management [25,73]. Interspecific hybridization and genetic mapping have greatly expanded the accessible diversity of resistance, enabling gene transfer both within and beyond the Triangle of U.

The following section summarizes the principal resistance sources and their relevance for resistance breeding (Table 2).

Table 2. Sources of clubroot resistance.

Source/Species	Genome	Key CR Genes/Loci	Type of Resistance	Notes/Identified CR Sources
Brassica rapa	A	*CRa*, *CRb*, *CRk*, *Crr1a/b*, *Crr2*, *Crr3*, *Crr4*, *Rcr1* (*Rpb1*), *Rcr2*, *Rcr4*, *Rcr8*, *Rcr9*, *CRd*	Mostly dominant, race-specific	Turnips (ECD set), wild accessions, major donor species
Brassica oleracea	C	Multiple QTLs: *C2*, *C3*, *C5*, *C7*, *C9*; *qCRc7-2/3/4*; *Rcr_C03-1*, *Rcr_C08-1*; *BolC.Pb9.1*	Quantitative resistance	Kale, cabbage; wild relatives (e.g., *B. macrocarpa*)
Brassica nigra	B	*Rcr6*, *Rcr1*	Pathotype-specific	Limited CR; donor for B genome introgression
Brassica juncea	AB	Introgressed loci from *B. rapa*	Depends on donor	Acquires CR via distant hybridization
Resynthesized *Brassica* spp.	A+C; A+B; B+C	QTLs in A and C genomes (various)	Broad, combined	Resynthesized *B. napus* with CR from *B. rapa*, *B. oleracea*
Raphanus sativus	R	*Crs1*; *CRd-like* loci on A03 & A08 (in *Brassicoraphanus*)	Strong, broad-spectrum	Valuable CR donors; resistant accessions and MAALs
Other crucifers	–	*RPB1*, other loci (*Arabidopsis*)	Broad-spectrum	Wild relatives; potential but underexplored sources

4.1. Marker-Assisted Selection (MAS)

Marker-assisted selection (MAS) enhances the efficiency of breeding for clubroot resistance by enabling the selection of alleles linked to CR genes or QTLs. MAS is particularly valuable for traits with complex inheritance or difficult phenotyping and supports early-generation selection, thereby accelerating breeding progress [10,86].

In *B. napus*, SSR and intron-polymorphic (IP) markers linked to clubroot resistance loci have been developed and successfully used for trait introgression and validation [73]. Mapping efforts in *B. rapa*, *R. sativus*, and other *Brassica* species have identified multiple CR QTLs, providing marker sets that facilitate the targeted transfer of resistance across species and breeding pools [26,98].

Although MAS increases precision, its effectiveness may be constrained by linkage drag and marker–trait recombination, emphasizing the need for fine mapping and high-resolution markers in clubroot resistance breeding.

4.2. Cloned Clubroot Resistance (CR) Genes and Their Relevance for Resistance Breeding

Several clubroot resistance (CR) genes have been cloned from *Brassica* species, most of them belonging to the *TIR–NB–LRR* (Toll/interleukin-1 receptor–nucleotide-binding–leucine-rich repeat) family and serving as core resources for marker-assisted breeding. In *B. rapa*, the *CRa/CRb* locus on chromosome A03 comprises a cluster of NLR genes; *CRa* has been shown to be identical to *CRb* and confers resistance to pathotype group 3. This locus has been finely mapped and is routinely deployed in Chinese cabbage improvement [45,99,100]. The *Crr1a* gene encodes a TIR–NB–LRR protein active in hypocotyls and roots, and gain-of-function analyses confirmed its role in race-specific resistance, while a truncated allele underlies susceptibility [101].

The *Rcr1* gene, also located on A03, mediates a distinct, calcium-independent defense pathway supported by proteomic and transcriptomic studies and is widely used in breeding resistant canola cultivars [102,103]. The dominant *CRd* gene, mapped upstream of *Crr3*, provides resistance to local race 4 isolates and enables efficient marker-assisted

selection [104]. In *B. oleracea*, QTL-seq and RNA-seq approaches identified three major QTLs on C07, with two inducible candidate genes allowing the development of functional markers for cabbage [105].

4.3. Transfer of Clubroot Resistance Inside the Triangle of U

4.3.1. *Brassica rapa*

Numerous accessions included in the European clubroot differential (ECD) set show high levels of resistance [26], and the species has been the major contributor of dominant, race-specific resistance genes used across *Brassica* breeding programs [4,12,29,35,44,45,101,106–111]. Resistance loci are distributed across several chromosomes, with the A3 and A8 regions representing major hotspots. Continued screening has identified additional loci in diverse wild *B. rapa* accessions [26,41,44,112].

Interspecific hybridization and MAS have enabled efficient transfer of *B. rapa* resistance into *B. napus* and *B. oleracea*. The locus *CRd* has been introgressed into canola backgrounds, including transfers from highly resistant turnip cultivar ECD04 and Chinese cabbage sources [25,56,73,78,113]. Complementary loci originating from *B. rapa*, including *Crr1* and *Crr2*, have also been successfully introduced into cabbage via embryo rescue approaches [110,114]. Resistance alleles derived from *B. rapa* have been incorporated into synthetic and natural amphiploids such as resynthesized *B. napus* [68,115], although some alleles may be diluted depending on genome context [116].

4.3.2. *Brassica oleracea*

Although resistance in *B. oleracea* is generally more quantitative than that of the A genome, extensive germplasm evaluations—especially of kale and cabbage types—have revealed multiple valuable QTLs across the C2, C3, C5, C7, and C9 regions [14,29,105,117–120]. Several major-effect QTLs on C07 and C08 (e.g., *qCRc7-2*, *qCRc7-3*, *qCRc7-4*) have been functionally characterized, with candidate genes showing resistance-associated expression following infection [105,111,118]. Wild relatives such as *B. macrocarpa* further expand the available diversity, providing loci that can be integrated into cultivated backgrounds [111].

Despite occasional breakdown of resistance by virulent pathotypes [4,15,100,121], *B. oleracea* remains essential for pyramiding strategies, particularly for combining quantitative resistance with major genes transferred from *B. rapa* [68,117,122].

4.3.3. *Brassica nigra* and Related Genera

The B genome carries fewer documented resistance loci than the A or C genomes [123], yet *B. nigra* possesses pathotype-specific resistance that enhances the diversity of available sources [42,86–89]. The dominant gene *Rcr6*, identified in a region syntenic to A08 [108,123,124], represents the first major CR gene described for the B genome. Its introgression into *B. napus* is feasible with MAS, although amphidiploids containing the B genome (e.g., *B. juncea*, *B. carinata*) often show susceptibility [125], indicating that additional strategies are required for stable transfer. A recently identified CR locus in the B genome, together with the work of Hu et al. (2024), who demonstrated the efficient, marker-free CRISPR/Cas9-mediated incorporation of *Rcr1* from *B. rapa* into *B. napus*, highlights the growing potential of genome editing in CR breeding [41].

4.3.4. *Brassica juncea*

B. juncea generally lacks inherent resistance but can acquire it through crosses with *B. rapa* and other *Brassica* species. Distant hybridization and embryo rescue enabled stable integration of resistance loci into the AABB background, with mapping studies identifying several genomic regions associated with resistance to *Plasmodiophora brassicae* [26,125].

4.3.5. Resynthesis of *Brassica* Species for Clubroot Resistance

Resynthesized *Brassica* species enable the combination of multiple resistance alleles, improving resilience through allele stacking and diversification. Resynthesized *B. napus* derived from *B. rapa* × *B. oleracea* crosses is particularly valuable for overcoming species barriers in resistance introgression [67,115]. Numerous QTLs detected via associative transcriptomics and classical mapping—including major loci on A02 and A03—serve as targets for pyramiding in modern canola breeding [18]. However, the expression of A- and C-genome resistance can vary depending on epistatic interactions [26,29,39,115,126].

4.4. Transfer of Clubroot Resistance Outside the Triangle of U

4.4.1. *Raphanus sativus*

Radish provides the most significant non-*Brassica* source of clubroot resistance, with broad-spectrum resistance documented across many accessions [59,83,127–129]. Several QTLs and loci—such as *Crs1*—have been mapped in radish germplasm [34,98,120]. Intergeneric hybrids such as *Brassicoraphanus* (RRCC) have facilitated stable introgression of radish-derived resistance into *B. napus* and *B. oleracea* [4,27,29,59,65,130]. Cytogenetic studies have demonstrated recombination between radish and *Brassica* chromosomes, confirming the feasibility of transferring radish-derived loci [65,97,131,132]. MAALs and backcrossed progenies have enabled targeted introgression of radish resistance regions, expanding the genomic toolkit for resistance breeding [29,65,98] (Table 3).

Table 3. Examples of successful interspecific introgression of clubroot resistance.

Recipient Species	Donor Species	Transferred CR Gene(s)/Locus	Method	Outcome/Notes
B. napus	*B. rapa* (Chinese cabbage)	*CRd*	Interspecific hybridization, MAS	Stable CR introgression; used in canola breeding
B. napus	*B. rapa* (“*Qulihuang*”)	CR gene linked to *CRb*/*CRa* region	MAS	Resistance transferred into ‘Topas’
B. oleracea	*B. rapa*	*Crr1*, *Crr2*	Distant hybridization, embryo rescue	Complementary resistance; stable lines obtained
B. oleracea	*B. rapa*	*CRa*, *CRb*, *Pb8.1*	Wide crossing	Major CR donor for cabbage and broccoli
B. napus (resynth.)	*B. rapa* × *B. oleracea*	Multiple QTLs from A and C genomes	Resynthesis	Broader CR base, though diluted in B. napus background
B. napus	*R. sativus*	*Crs1* (and additional radish QTLs)	Interspecific hybridization, MAALs, backcrossing	Broad-spectrum CR; chromosome recombination confirmed
B. napus	*Brassicoraphanus* (R–C allotetraploid)	*CRd* (A03) + A08 locus	Hybridization	Strong resistance; successful gene transfer potential
B. juncea	*B. rapa*	Dominant CR loci	Distant hybridization, embryo rescue	Enables CR in otherwise susceptible species

4.4.2. *Arabidopsis* and Other Cruciferous Species

No major resistance sources have yet been identified outside *Brassica* and radish, but ongoing exploration of wild crucifers continues to expand the genetic basis for resistance breeding. A range of species—including *B. juncea*, has been screened as potential donors in hybridization programs with *B. napus* [73]. Mechanistic studies of *Arabidopsis thaliana*

identified genes such as *RPB1* and regulators such as *SnRK1.1* as contributors to partial or broad-spectrum resistance [126–137], offering insights into conserved pathways relevant to *Brassica* breeding.

5. Perspectives and Future Directions

Future progress in developing durable clubroot resistance will depend on effectively integrating diverse genetic resources with advanced genomic and gene-editing technologies. A central priority will be the continued expansion of the genetic base through interspecific and intergeneric introgression, which offers access to additional CR genes from cruciferous species beyond *Brassica* and *Raphanus* [101]. The use of synthetic hybrids and distant crosses complements this effort by enabling the transfer of resistance alleles that are otherwise inaccessible through conventional breeding, thereby enhancing resilience to diverse *P. brassicae* pathotypes.

At the same time, advances in genomic mapping will play a pivotal role in guiding more targeted resistance introgression. Approaches such as QTL-Seq and BSA provide rapid means of identifying CR loci suitable for strategic intercrossing [101], while high-density linkage maps, QTL analyses, and synteny comparisons with *A. thaliana* deepen understanding of conserved resistance mechanisms and support the efficient deployment of beneficial alleles [12,101]. These tools are complemented by transcriptomic strategies, including associative transcriptomics, which continues to be instrumental in identifying candidate genes underlying resistance variation [25]. As genomic platforms evolve, next-generation sequencing and GWAS will further accelerate the discovery of novel loci and enhance the predictive capacity of modern breeding pipelines [42,138–140].

A key issue in interpreting newly reported clubroot resistance genes is the strong possibility that several of them are not truly novel but correspond to previously described loci. Because many studies use different mapping populations, marker systems, and race differentials, resistance loci appearing under new names—especially those repeatedly detected on chromosomes A02, A03, and A08—may represent the same underlying gene [26,81,113,130]. This ambiguity is further amplified by high synteny and the presence of homeologous genome regions across *Brassica* species, which frequently place resistance factors in conserved chromosomal blocks [12,25,42,106,140].

To avoid redundant naming and overestimating the diversity of available resistance sources, future work should emphasize high-resolution mapping, comparative genomics, and sequence-level validation. Functional confirmation through allele sequencing, haplotype comparison, or CRISPR-mediated gene disruption will be essential to determine whether a locus is genuinely novel [69,99,100,108]. Clarifying these relationships is critical for breeding programs, as misidentification of CR genes can compromise pyramiding strategies and lead to ineffective combinations of resistance sources.

CRISPR/Cas9 should be viewed as a potential alternative to interspecific crosses for the development of clubroot resistance (CR). In contrast to conventional introgression, which requires wide crosses and is constrained by linkage drag, genome editing enables direct modification of resistance loci within adapted genetic backgrounds. Effective application of this approach in polyploid *Brassica* species depends on precise characterization of the targeted CR locus and its homeologous copies at the sequence level, as similar challenges have been widely documented for other polyploid crops [141–146]. Because multiple homeologous gene copies must often be edited simultaneously, guide RNA design must be informed by sequence comparison among all alleles, and target sites require validation for on-target activity [136,137]. Additional methodological considerations include appropriate delivery of CRISPR/Cas reagents and strategies to ensure efficient editing across complex polyploid genomes [138]. When these requirements are met, CRISPR/Cas9 provides a

means to reconstruct or modify known CR alleles and to combine multiple resistance factors without the genetic constraints associated with interspecific hybridization.

Taken together, these developments point toward a future in which *Brassica* breeding programs can more effectively assemble broad and durable resistance to clubroot. The convergence of expanded germplasm exploration, high-resolution genomic tools, and precision gene editing will be essential not only for enhancing cultivar resilience but also for ensuring long-term agricultural sustainability in clubroot-affected production systems.

Author Contributions: P.K.: Conceptualization, methodology, project administration, visualization, writing—original draft, review, and editing; M.K.: methodology. 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".

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

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. Zotero, 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. [CrossRef]
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. [CrossRef] [PubMed]
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. [CrossRef] [PubMed]
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. [CrossRef]
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. [CrossRef]
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. [CrossRef]
7. Bruce, T.J.A. GM as a route for delivery of sustainable crop protection. *J. Exp. Bot.* **2012**, *63*, 537–541. [CrossRef]
8. Struck, C.; Rüsch, S.; Streklov, B. Control strategies of clubroot disease caused by *Plasmodiophora brassicae*. *Microorganisms* **2022**, *10*, 620. [CrossRef]
9. Dixon, G.R. Clubroot (*Plasmodiophora brassicae* Woronin)—An agricultural and biological challenge worldwide. *Can. J. Plant Pathol.* **2014**, *36*, 5–18. [CrossRef]
10. Hasan, J.; Megha, S.; Rahman, H. Clubroot in *Brassica*: Recent advances in genomics, breeding, and disease management. *Genome* **2021**, *64*, 735–760. [CrossRef]
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. [CrossRef]
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. [CrossRef]
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*, 85836. [CrossRef] [PubMed]
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. [CrossRef] [PubMed]
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. [CrossRef]

16. Holtz, M.D.; Hwang, S.-F.; Strelkov, S.E. Genotyping of *Plasmodiophora brassicae* reveals the presence of distinct populations. *BMC Genom.* **2018**, *19*, 254. [CrossRef]
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. [CrossRef]
18. Askarian, H.; Hwang, S.-F.; Akhavan, A.; Manolii, V.P.; Strelkov, S.E.; Cao, T. Virulence spectrum of single-spore and field isolates of *Plasmodiophora brassicae* able to overcome resistance in canola (*Brassica napus*). *Plant Dis.* **2021**, *105*, 43–52. [CrossRef]
19. Jones, D.R.; Ingram, D.S.; Dixon, G.R. Factors affecting tests for differential pathogenicity in populations of *Plasmodiophora brassicae*. *Plant Pathol.* **1982**, *31*, 229–238. [CrossRef]
20. Pang, W.; Liang, Y.; Zhan, Z.; Li, X.; Piao, Z. Development of a Sinitic clubroot differential set for the pathotype classification of *Plasmodiophora brassicae*. *Front. Plant Sci.* **2020**, *11*, 568771. [CrossRef]
21. Ayers, G.W. Races of *Plasmodiophora brassicae*. *Can. J. Bot.* **1957**, *35*, 923–932. [CrossRef]
22. Javed, M.A.; Pérez-López, E.; Mukhopadhyay, S.; Normandeau, E.; Brochu, A.-S. Telomere-to-telomere genome assembly of the clubroot pathogen *Plasmodiophora brassicae*. *Genome Biol. Evol.* **2024**, *16*, evae122. [CrossRef] [PubMed]
23. Jia, H.; Zhang, X.; Wang, Z.; Wei, X.; Yuan, Y.; Yang, Y.; Wei, F.; Tian, B.; Zhao, Y.; Yang, S.; et al. Root RNA-seq analysis reveals a distinct transcriptome landscape between clubroot-susceptible and clubroot-resistant Chinese cabbage lines after *Plasmodiophora brassicae* infection. *Plant Soil* **2017**, *421*, 93–105. [CrossRef]
24. Tso, H.H.; Strelkov, S.E.; Galindo-González, L. Current and future pathotyping platforms for *Plasmodiophora brassicae* in Canada. *Plants* **2021**, *10*, 1446. [CrossRef]
25. 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*, 1021–1034. [CrossRef]
26. 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 four turnip accessions (*Brassica rapa*) from the European Clubroot Differential set. *Front. Plant Sci.* **2018**, *9*, 1628. [CrossRef]
27. Kaneko, Y.; Bang, S.W. Interspecific and intergeneric hybridization and chromosomal engineering of *Brassicaceae* crops. *Breed. Sci.* **2014**, *64*, 14–22. [CrossRef]
28. 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*, 726. [CrossRef]
29. Piao, Z.; Ramchiary, N.; Lim, Y.P. Genetics of clubroot resistance in *Brassica* species. *J. Plant Growth Regul.* **2009**, *28*, 252–264. [CrossRef]
30. 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. [CrossRef]
31. Reglinski, T.; Havis, N.; Rees, H.J.; de Jong, H. The practical role of induced resistance for crop protection. *Phytopathology* **2023**, *113*, 719–731. [CrossRef] [PubMed]
32. Botero-Ramirez, A.; Kirk, B.; Strelkov, S.E. Optimizing clubroot management and the role of canola cultivar mixtures. *Pathogens* **2024**, *13*, 640. [CrossRef] [PubMed]
33. 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. [CrossRef]
34. 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. [CrossRef]
35. 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*, 1788. [CrossRef]
36. 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. [CrossRef]
37. 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. [CrossRef]
38. 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. [CrossRef]
39. 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. [CrossRef]
40. 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. [CrossRef]

41. Hu, H.; Zhang, Y.; Yu, F. A CRISPR/Cas9-based vector system enables fast breeding of selection marker-free canola with Rcr1-rendered clubroot resistance. *J. Exp. Bot.* **2024**, *75*, 1347–1363. [CrossRef] [PubMed]
42. 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*, 639631. [CrossRef] [PubMed]
43. 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. [CrossRef]
44. 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. [CrossRef]
45. 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. [CrossRef]
46. 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. [CrossRef]
47. 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. [CrossRef]
48. Zou, J.; Gao, S.; Zhang, B.; Ge, W.; Zhang, J.; Ji, R. Chinese cabbage BrCAP has potential resistance against *Plasmodiophora brassicae*. *Horticulturae* **2023**, *9*, 517. [CrossRef]
49. 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. [CrossRef]
50. Snowdon, R.J. Cytogenetics and genome analysis in *Brassica* crops. *Chromosome Res.* **2007**, *15*, 85–95. [CrossRef]
51. 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. [CrossRef]
52. 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. [CrossRef]
53. Chen, Z.Z.; Snyder, S.; Loh, W.H.; Fan, Z.G. Efficient Production of Doubled Haploid Plants through Chromosome Doubling of Isolated Microspores in *Brassica napus*. *Plant Breed.* **1994**, *113*, 217–221. [CrossRef]
54. Leflon, M.; Coriton, O.; Jenczewski, E.; Huteau, V.; Eber, F.; Chèvre, A.M.; Letanneur, J.C.; Chelysheva, L.; Barker, G.; Ryder, C.D. Pairing and recombination at meiosis of *Brassica rapa* (AA) × *Brassica napus* (AACC) hybrids. *Theor. Appl. Genet.* **2006**, *113*, 1467–1480. [CrossRef]
55. Zou, J.; Yang, T.; Xia, W.; Li, R.; Qian, W.; Pires, J.C.; Mason, A.S.; Park, B.S.; Fu, D.; Lim, Y.P.; et al. De novo genetic variation associated with retrotransposon activation, genomic rearrangements and trait variation in a recombinant inbred line population of *Brassica napus* derived from interspecific hybridization with *Brassica rapa*. *Plant J.* **2011**, *68*, 212–224. [CrossRef]
56. 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*, e0177470. [CrossRef]
57. Rogo, U.; Fambrini, M.; Pugliesi, C. Embryo Rescue in Plant Breeding. *Plants* **2023**, *12*, 3106. [CrossRef]
58. Chalhoub, B.; Denoeud, F.; Liu, S.; Parkin, I.A.; Golicz, A.A.; Tang, H.; Wang, X.; Chiquet, J.; Belcram, H.; Tong, H.; et al. Plant genetics. Early allopolyploid evolution in the post-Neolithic *Brassica napus* oilseed genome. *Science* **2014**, *345*, 950–953. [CrossRef]
59. Katche, E. Interspecific Hybridization for *Brassica* Crop Improvement. *Crop Breed. Genet. Genom.* **2019**, *1*, e190007. [CrossRef]
60. Cheng, F.; Wu, J.; Wang, X. Genome Triplication Drove the Diversification of *Brassica* Plants. *Hortic. Res.* **2014**, *1*, 14024. [CrossRef]
61. Nikolov, L.A. *Brassicaceae* Flowers: Diversity amid Uniformity. *J. Exp. Bot.* **2019**, *70*, 2623–2635. [CrossRef] [PubMed]
62. 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. [CrossRef] [PubMed]
63. 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. [CrossRef]
64. 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*, 1677. [CrossRef]
65. 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. [CrossRef]
66. 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. [CrossRef]

67. 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, Switzerland, 1983; pp. 286–287, ISBN 978-3-0348-6557-9.
68. 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. [CrossRef]
69. 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. [CrossRef]
70. Cardoza, V.; Stewart, C.N. *Brassica* Biotechnology: Progress in Cellular and Molecular Biology. *Vitr. Cell. Dev. Biol.-Plant* **2004**, *40*, 542–551. [CrossRef]
71. Sharma, D.R.; Kaur, R.; Kumar, K. Embryo Rescue in Plants—A Review. *Euphytica* **1996**, *89*, 325–337. [CrossRef]
72. Snowdon, R.J.; Friedt, W. Molecular Markers in *Brassica* Oilseed Breeding: Current Status and Future Possibilities. *Plant Breed.* **2004**, *123*, 1–8. [CrossRef]
73. 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. [CrossRef] [PubMed]
74. 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. [CrossRef]
75. 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. [CrossRef]
76. 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. [CrossRef]
77. 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. [CrossRef]
78. 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. [CrossRef]
79. Karim, M.; Yu, F. Resynthesizing *Brassica napus* with race specific resistance genes and race non-specific QTLs to multiple races of *Plasmodiophora brassicae*. *Sci. Rep.* **2024**, *14*, 14627. [CrossRef]
80. 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. [CrossRef]
81. 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*, 785989. [CrossRef]
82. 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. [CrossRef]
83. 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. [CrossRef]
84. 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. [CrossRef]
85. 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: Leuven, Belgium, 1996; Volume 407, pp. 423–429.
86. 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. [CrossRef]
87. 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*, 49. [CrossRef]
88. Neyhart, J.L.; Lorenz, A.J.; Smith, K.P. Multi-Trait Improvement by Predicting Genetic Correlations in Breeding Crosses. *G3* **2019**, *9*, 3153–3165. [CrossRef] [PubMed]
89. 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*, 554. [CrossRef]
90. 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. [CrossRef]
91. 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. [CrossRef]

92. Pang, W.; Fu, P.; Li, X.; Zhan, Z.; Yu, S.; Piao, Z. Identification and Mapping of the Clubroot Resistance Gene *CRd* in Chinese Cabbage (*Brassica rapa* ssp. *pekinensis*). *Front. Plant Sci.* **2018**, *9*, 653. [CrossRef]
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. [CrossRef]
94. 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. [CrossRef]
95. Shah, N.; Sun, J.; Yu, S.; Yang, Z.; Wang, Z.; Huang, F.; Dun, B.; Gong, J.; Liu, Y.; Li, Y.; et al. Genetic Variation Analysis of Field Isolates of Clubroot and Their Responses to *Brassica napus* Lines Containing Resistant Genes *CRb* and *PbBa8.1* and Their Combination. *Mol. Breed.* **2019**, *39*, 153. [CrossRef]
96. Xu, M.L.; Korban, S.S. Saturation Mapping of the Apple Scab Resistance Gene *Vf* Using AFLP Markers. *Theor. Appl. Genet.* **2000**, *101*, 844–851. [CrossRef]
97. 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. [CrossRef] [PubMed]
98. 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 QTLs Associated with Clubroot Resistance in Radish (*Raphanus sativus* L.). *Mol. Breed.* **2019**, *39*, 1020–1025. [CrossRef]
99. Hatakeyama, K.; Niwa, T.; Kato, T.; Ohara, T.; Kakizaki, T.; Matsumoto, S. Tandem Repeated Organization of NB-LRR Genes in the Clubroot-Resistant *CRb* Locus in *Brassica rapa* L. *Mol. Genet. Genom.* **2017**, *292*, 397–405. [CrossRef] [PubMed]
100. Kato, T.; Hatakeyama, K.; Fukino, N.; Matsumoto, S. Identification of a Clubroot Resistance Locus Conferring Resistance to *Plasmodiophora brassicae* Pathotype Group 3 in Chinese Cabbage (*Brassica rapa* L.). *Breed. Sci.* **2012**, *62*, 282–287. [CrossRef]
101. 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 in *Brassica rapa* L. *PLoS ONE* **2013**, *8*, e54745. [CrossRef]
102. Chu, M.; Falk, K.C.; Peng, G.; Zhang, X.; Song, T.; Chang, A.; Lahlali, R.; Gossen, B.D.; Yu, F.; Liu, X.; et al. Fine Mapping of *Rcr1* and Analyses of Its Effect on Transcriptome Patterns during Infection by *Plasmodiophora brassicae*. *BMC Genom.* **2014**, *15*, 1166. [CrossRef]
103. Song, T.; Peng, G.; Yu, F.; Chu, M.; Lahlali, R. Shotgun Label-Free Proteomic Analysis of Clubroot Resistance Conferred by *Rcr1* in *Brassica rapa*. *Front. Plant Sci.* **2016**, *7*, 1013. [CrossRef] [PubMed]
104. 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 QTL-Seq. *Front. Plant Sci.* **2021**, *12*, 703520. [CrossRef]
105. 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*, e85307. [CrossRef] [PubMed]
106. 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. [CrossRef] [PubMed]
107. Karim, M.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. [CrossRef]
108. 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**, *23*, dsv034. [CrossRef]
109. 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. [CrossRef]
110. 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*, 274. [CrossRef]
111. 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. [CrossRef]
112. 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. [CrossRef]
113. 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. [CrossRef]
114. 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. [CrossRef]

115. Karim, M.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. [CrossRef]
116. Lindhout, P. The Perspectives of Polygenic Resistance in Breeding for Durable Disease Resistance. *Euphytica* **2002**, *124*, 217–226. [CrossRef]
117. 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. [CrossRef] [PubMed]
118. Hirai, M. Genetic Analysis of Clubroot Resistance in *Brassica* Crops. *Breed. Sci.* **2006**, *56*, 223–229. [CrossRef]
119. 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*, 822. [CrossRef]
120. 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. [CrossRef]
121. 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. [CrossRef]
122. 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. [CrossRef]
123. 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. [CrossRef] [PubMed]
124. Brown, J.; Brown, A.P.; Davis, J.B.; Erickson, D. Intergeneric Hybridization between *Sinapis alba* and *Brassica napus*. *Euphytica* **1997**, *93*, 163–168. [CrossRef]
125. 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. [CrossRef] [PubMed]
126. 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. [CrossRef]
127. 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. [CrossRef] [PubMed]
128. Kim, H.; Jo, E.J.; Choi, Y.H.; Jang, K.S.; Choi, G.J. Pathotype classification of *Plasmodiophora brassicae* isolates using clubroot-resistant cultivars of Chinese cabbage. *Plant Pathol. J.* **2016**, *32*, 423–430. [CrossRef]
129. Laila, R.; Nou, I.-S.; Park, J.-I.; Vijayakumar, H.; Robin, A.H.K.; Shirasawa, K.; Isobe, S.; Natarajan, S.; Kim, H.-T. Mapping of a novel clubroot resistance QTL using ddRAD-seq in Chinese cabbage (*Brassica rapa* L.). *BMC Plant Biol.* **2019**, *19*, 93. [CrossRef]
130. 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. [CrossRef]
131. 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. [CrossRef]
132. 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. [CrossRef]
133. 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. [CrossRef] [PubMed]
134. 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. [CrossRef] [PubMed]
135. 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. [CrossRef] [PubMed]
136. 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*, 66. [CrossRef]
137. Suwabe, K.; Tsukazaki, H.; Iketani, H.; Hatakeyama, K.; Kondo, M.; Fujimura, M.; Nunome, T.; Fukuoka, H.; Hirai, M.; Matsumoto, S. Simple sequence repeat-based comparative genomics between *Brassica rapa* and *Arabidopsis thaliana*: The genetic origin of clubroot resistance. *Genetics* **2006**, *173*, 309–319. [CrossRef]
138. Schaart, J.G.; Smulders, M.J.M.; Van de Wiel, C.C.M. Genome editing of polyploid crops: Prospects, achievements and bottlenecks. *Transgenic Res.* **2021**, *30*, 337–351. [CrossRef]

139. Hussin, S.H.; Iqbal, M.A.; Liu, X.; Diaby, M.; Jatoi, G.H.; Li, C.; Imran, M.; Ahmed, R. An updated overview on insights into sugarcane genome editing via CRISPR/Cas9 for sustainable production. *Sustainability* **2022**, *14*, 12285. [CrossRef]
140. Gao, W.; Long, L.; Tian, X.; Xu, F.; Liu, J.; Singh, P.K.; Botella, J.R.; Song, C. Genome editing in cotton with the CRISPR/Cas9 system. *Front. Plant Sci.* **2017**, *8*, 1364. [CrossRef]
141. Ryder, P.; Spillane, C.; McHale, M.; Fort, A. Generation of stable nulliplex autopolyploid lines of *Arabidopsis thaliana* using CRISPR/Cas9 genome editing. *Plant Cell Rep.* **2017**, *36*, 1005–1008. [CrossRef]
142. Laforest, L.C.; Nadakuduti, S.S. Advances in delivery mechanisms of CRISPR gene-editing reagents in plants. *Front. Genome Ed.* **2022**, *4*, 830178. [CrossRef]
143. 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. Genom.* **2020**, *19*, 26–39. [CrossRef] [PubMed]
144. 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. [CrossRef]
145. Dong, G.; Fan, Z. CRISPR/Cas-Mediated Germplasm Improvement and New Strategies for Crop Protection. *Crop Health* **2024**, *2*, 2. [CrossRef]
146. 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. [CrossRef]