

Late blight resistance in wild potato species—Resources for future potato (*Solanum tuberosum*) breeding

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Abstract

Late blight remains the most devastating disease in potato cultivation. The best protection against this disease could be achieved by durably resistant cultivars, but these do not exist at present. To advance resistance breeding, the search for resistant wild potato species and the characterization of their resistance is important. There have recently been a number of new developments in this area. For this reason, all wild potato species known to the authors in which resistance has been found to date are listed in this article with their respective genes and QTL. Lastly, an overview is given, how these new resistance sources can be used for future resistance breeding.

KEYWORDS

late blight, plant breeding, potato, resistance, *Solanum* crop, wild species

1 | INTRODUCTION

With a global production of about 360 million tonnes per year, potato (*Solanum tuberosum* L.) is the fifth most important crop after sugar cane, maize, rice and wheat (FAO, 2020). Potato is vegetatively propagated, which makes it especially susceptible to several pathogens. Infected seed tubers can cause early onset of diseases and promote fast spreading in fields. One of the most severe and best studied diseases is late blight, caused by the oomycete *Pythophthora infestans* (Mont.) de Bary. Ever since the first reported outbreaks in 1843 (Andrison, 1996) leading to the devastating Irish potato famine from 1845 to 1849 (Woodham-Smith, 1962), potato cultivation has suffered from high yield losses caused by this disease. Today, late blight causes annual yield losses with an estimated cost of 6.7 billion dollars worldwide (Haas et al., 2009; USABlight, 2021). At present, potato production relies on fungicides to control the disease. However, registrations for many of these are gradually expiring and few novel

fungicides are coming onto the market. Therefore, new more environmentally friendly alternative control strategies are needed. Even organic farming heavily relies on copper-based fungicides (Nechwatal & Zellner, 2015), which can also have adverse effects on soil microorganisms (Rehman et al., 2019). For both conventional and organic farming, breeding of resistant cultivars is of outstanding importance in order to reduce overall fungicide applications. However, more than 160 years of resistance breeding have not yet resulted in cultivars that can keep their resistance in the long term (Nowicki et al., 2012). Wild relatives of cultivated potatoes have been regarded as a valuable source of resistance for decades. In the middle of the 20th century, the species *S. demissum* bearing 11 major resistance genes became the focus of attention. However, the resistance of these individually incorporated race-specific resistance genes (R genes) were overcome quickly by highly adaptable *P. infestans* strains (Collins et al., 1999; Fry, 2008; Hein et al., 2009). Thus, to date, a primary goal in potato breeding is to establish quantitative resistance against a wide spectrum of races by many quantitative trait loci (QTL) and/or stacking of different R genes to avoid breaking the resistance of only one R gene (Haverkort et al., 2016; Stefańczyk

Short informative: This review compiles the wild potato species in which resistance to Late blight has been found. It also provides ideas for future potato breeding.

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et al., 2020; Zhu et al., 2012). All of these approaches rely on the discovery of new resistances in wild tuber bearing species (section *Petota*) or *S. tuberosum* landraces. A second important aspect is whether the resistance of the wild species is caused by one or more resistance genes or if it is based on QTL effects. In this regard, some new insights have been gained since the last reviews by Tiwari et al. (2013) and Rodewald and Trognitz (2013). Therefore, this review summarizes all currently known *P. infestans* resistance sources in wild potato species and the known loci of respective resistance genes in the genome, in order to inform breeders and researchers on the diversity of possible resistance sources. Only a few *P. infestans* resistant species have been used in the development of commercial cultivars such as *S. bulbocastanum*, *demissum*, *microdontum*, *phureja*, *sparsipilum*, *stoloniferum*, *venturii* and *verrucosum* (Bethke et al., 2017; Bradshaw, 2021; Hawkes, 1994). What further species may have been used in the past remains elusive, because the transition of material from academic breeding research to commercial breeding is rarely documented. Nonetheless, this highlights that there is still a wealth of new resistance sources that can be made accessible for potato cultivar improvement.

2 | LATE BLIGHT RESISTANT WILD RELATIVES OF POTATO

The genus *Solanum* in the family Solanaceae includes about 1500 species (Weese & Bohs, 2007), many of which are tuber bearing (section *Petota*) and are sufficiently closely related to *S. tuberosum* to form hybrids. Thus, their resistance can be introgressed into potato cultivars. Taxonomy is of course always a work in progress and in a large group such as *Petota* the status of many species has been revised and re-revised over the decades. Today, potato scientists rely on two taxonomic systems, one of which was established by Hawkes in 1990 and recognizes 232 species within *Petota*, while the other was published by Spooner et al. (2014) and merges the taxonomy of Hawkes into 107 species using additional molecular data on top of morphological characterization (Spooner et al., 2014, 2018). The system by Hawkes is still used by many scientists and especially by institutions conserving and distributing potato genetic resources, because it is easier to reconcile with their information on the material they collected and catalogued in the past. For listing and comparing the wealth of publications in which resistances against *P. infestans* had been identified in the past, the system by Hawkes may still give the most comprehensive overview and was adapted for this review. Whenever studies used synonyms, the author's original species description is indicated after the accepted name. To ensure comparability to the new taxonomy of Spooner et al. (2014), the new name is included, whenever a species was reclassified. Independent of the applied taxonomy the section *Petota* obviously is large and comprises a wealth of species with potential to provide genetic resources for improving late blight resistance in potato. In the known literature, resistance to *P. infestans* is described in accessions of 85 wild potato species compiled from 74 studies (Table 1) published over the last

four decades. Thus, 33 new species have been discovered in the years since Tiwari's last review in 2013. In most of the papers, resistance was identified by field tests, whole plant testing or detached leaf assays and in some cases by additional tuber slice tests. In about two thirds of the studies, the detached leaf assay was used and in some cases supplemented with greenhouse tests. Accordingly, far fewer field tests were carried out. Vleeshouwers et al. (1999) were able to show that leaf tests are a good alternative to field tests due to a high correlation. An exception is the work of Bachmann-Pfabe et al. (2019), where testing was restricted to small, cut tubers. As it is not yet clear whether foliage and tuber resistance are genetically linked, the results of tuber and tuber slice tests can be compared only to a limited extent to those of studies using the detached leaf assay or field tests (Douches et al., 2002; Mayton et al., 2010; Platt & Tai, 1998). For example Park, Vleeshouwers, Kim, et al. (2005) studied foliage and tuber blight resistance in three populations. In one of them, tuber blight resistance occurred independently of foliage blight resistance. In the second population, tuber and foliage blight resistance were correlated and the third population proved to be completely susceptible, so that no conclusion could be drawn so far (Park, Vleeshouwers, Kim, et al., 2005). Species such as *S. demissum*, *S. bulbocastanum* or *S. microdontum*, whose resistance potential has been known for a long time, are now joined by 25 species, which have only been investigated in recent studies such as those of Khiutti et al. (2015) or Bachmann-Pfabe et al. (2019). For most of these 25 species, there is a lack of studies addressing the genomic localisation of their resistance, as well as for 30 other wild species that have long been known to have resistant accessions. Among the newly discovered resistance sources *S. pampasense* is the exception, two QTL for late blight resistance were discovered on chromosome 5 and 6, respectively. In addition, newly discovered resistances could also turn out to be homologues of already characterized R genes. For instance, among the already known R genes, *Rpi-sto1* and *Rpi-abpt* are homologues of *Rpi-blb1* (Wang et al., 2008) and *R2* (Lokossou et al., 2009). Thus, there is a need for further clarification for the other genes.

3 | RESISTANCE MECHANISMS AGAINST *P. infestans*

Phytophthora infestans evolved in central Mexico, which is also a diversity centre of wild potato species (Grünwald & Flier, 2005). The antagonistic interaction of host species and the pathogen led to the evolution of multiple resistance genes and diverse virulence genes promoting infection and counteracting host resistance (Grünwald & Flier, 2005). The vast majority of hitherto described resistances follows the gene for gene interaction model. In line with the classical R gene and Avr gene nomenclature, R genes are labelled with their respective species abbreviation, for example, *Rpi-sto1* is the first *P. infestans* resistance gene identified in *Solanum stoloniferum*. The corresponding (a)virulence gene, by which the resistant host detects the pathogen, is then called *Avr-sto1*.

TABLE 1 Wild *Solanum* species with resistance against *P. infestans* according to Hawkes, 1990

Species	Accepted by Spooner	Ploidy	EBN	Reference
<i>S. acaule</i> Bitt.		4	2	Bachmann-Pfabe et al. (2019); Budin (2002); Khiutti et al. (2015)
<i>S. agrimonifolium</i> Rydb.		4	2	Karki et al. (2021); Khiutti et al. (2015)
<i>S. ajanhuiri</i> Juz. & Buk.		2	2	Gabriel et al. (2007)
<i>S. alandiae</i> Cárđ.	<i>S. brevicaule</i> Bitt.	2		Bhardwaj et al. (2018); Muratova et al. (2020); Ramsay et al. (1999)
<i>S. albicans</i> (Ochoa) C. Ochoa		6	4	Bhardwaj et al. (2018); Khiutti et al. (2015)
<i>S. albornozii</i> Corr.		2	2	Karki et al. (2021); Khiutti et al. (2015)
<i>S. ambosinum</i> Ochoa	<i>S. candolleianum</i> Berth.	2	2	Zoteyeva et al. (2012)
<i>S. andreanum</i> Baker		2		Budin (2002); Khiutti et al. (2015)
<i>S. arnezii</i> Cárđ.	<i>S. chacoense</i> Bitt.	2		Bhardwaj et al. (2018)
<i>S. astleyi</i> Hawkes & Hjert.	<i>S. boliviense</i> Dun.	2	2	Ruiz De Galarreta et al. (1998)
<i>S. avilesii</i> Hawkes & Hjert.	<i>S. brevicaule</i> Bitt.	2	2	Bhardwaj et al. (2018); Ruiz De Galarreta et al. (1998); Spooner et al. (2001); Verzaux et al. (2011)
<i>S. berthaultii</i> Hawkes		2,3	2	Bhardwaj et al. (2018); Budin (2002); Colon and Budding (1988); Ewing et al. (2000); Khiutti et al. (2015); Manrique-Carpintero et al. (2020); Mayton et al. (2011); Park, Foster, et al. (2009); Ramsay et al. (1999); Rauscher et al. (2006, 2010); Tiwari et al. (2015); Zoteyeva et al. (2012)
<i>S. brevicaule</i> Bitt.		2	2	Bhardwaj et al. (2018); Khiutti et al. (2015)
<i>S. boliviense</i> Dun.		2	2	Budin (2002); Khiutti et al. (2015); Ruiz De Galarreta et al. (1998)
<i>S. brachistotrichum</i> Rydb.	<i>S. stenophyllidium</i> Rydb.	2	1	Bachmann-Pfabe et al. (2019); Hein et al. (2009); Ruiz De Galarreta et al. (1998)
<i>S. brachycarpum</i> Corr.	<i>S. iopetalum</i> Hawkes	6	4	Bachmann-Pfabe et al. (2019); Budin (2002); Ruiz De Galarreta et al. (1998)
<i>S. bulbocastanum</i> Dun.		2,3	1	Bachmann-Pfabe et al. (2019); Budin (2002); Champouret (2010); Helgeson et al. (1998); Khiutti et al. (2015); Lokossou et al. (2009); Naess et al. (2000); Oosumi et al. (2009); Park, Gros, Sikkema, et al. (2005); Song et al. (2003); van der Vossen et al. (2003, 2005);
<i>S. candolleianum</i> Berth.		2,3	2	Khiutti et al. (2015)
<i>S. capsicibaccatum</i> Cárđ.	<i>S. stipuloideum</i> Rusby	2	2	Jacobs et al. (2010)
<i>S. cardiophyllum</i> Lindl. (Including ssp. <i>S. ehrenbergii</i> Bitt.)		2,3,4	1	Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Budin (2002); Karki et al. (2021); Khiutti et al. (2015); Ramsay et al. (1999); Thieme et al. (2010); Tiwari et al. (2015); Zlesak and Thill (2004); Zoteyeva et al. (2012)
<i>S. chacoense</i> Bitt.		2,3	2	Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Budin (2002); Chakrabarti et al. (2014); Khiutti et al. (2015); Monino-Lopez et al. (2021); Ramsay et al. (1999); Tiwari et al. (2015); Vossen et al. (2017); Zoteyeva et al. (2012)
<i>S. chomatophilum</i> Bitt.		2	2	Karki et al. (2021); Khiutti et al. (2015)
<i>S. circaefolium</i> Bitt. (Including <i>S. stipuloideum</i> Rusby)	<i>S. stipuloideum</i> Rusby	2	1	Bachmann-Pfabe et al. (2019); Karki et al. (2021)
<i>S. circaefolium</i> spp. <i>quimense</i> Hawkes & Hjert.	<i>S. stipuloideum</i> Rusby	2	1	Ruiz De Galarreta et al. (1998); Verzaux (2010)
<i>S. commersonii</i> Dun.		2,3	1	Bachmann-Pfabe et al. (2019); Budin (2002); Ramsay et al. (1999); Ruiz De Galarreta et al. (1998)

(Continues)

TABLE 1 (Continued)

Species	Accepted by Spooner	Ploidy	EBN	Reference
<i>S. curtilobum</i> Juz. & Buk.		5		Bachmann-Pfabe et al. (2019)
<i>S. demissum</i> Lindl.		6	4	Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Bormann et al. (2004); Bradshaw, Bryan, Lees, et al. (2006); Budin (2002); Champouret (2010); El-Kharbotly et al. (1994, 1996); Hein et al. (2007, 2009); Huang (2005); Huang et al. (2004, 2005); Jo et al. (2011); Khiutti et al. (2015); Leonards-Schippers et al. (1992); Li et al. (2011); Li et al. (1998); Lokossou et al. (2009); Meksem et al. (1995); Park, Vleeshouwers, Huigen, et al. (2005); van Poppel (2009); Ramsay et al. (1999); Ruiz De Galarreta et al. (1998); Zoteyeva et al. (2012)
<i>S. x edinense</i> Berth.		5	4	Lokossou et al. (2009); Champouret (2010); Park, Vleeshouwers, Huigen, et al. (2005); Verzaux (2010)
		2	1	Karki et al. (2021); Khiutti et al. (2015)
<i>S. fendleri</i> A. Grey	<i>S. stoloniferum</i> Schldtl.	4	2	Bachmann-Pfabe et al. (2019); Ramsay et al. (1999)
<i>S. gandarillasii</i> Cárđ.		2	2	Bhardwaj et al. (2011); Ruiz De Galarreta et al. (1998)
<i>S. gourlayi</i> Hawkes	<i>S. brevicaule</i> Bitt.	2,4	2,4	Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018)
<i>S. guerreroense</i> Corr.		6	4	Zoteyeva et al. (2012)
<i>S. hjertingii</i> Hawkes		4	2	Champouret (2010)
<i>S. hondelmannii</i> Hawkes & Hjert.	<i>S. brevicaule</i> Bitt.	2	Na	Bachmann-Pfabe et al. (2019)
<i>S. hougasii</i> Corr.		6	4	Bachmann-Pfabe et al. (2019); Haynes and Qu (2016); Ramsay et al. (1999); Tiwari et al. (2015)
<i>S. huancabambense</i> Ochoa		2	2	Bhardwaj et al. (2018); Tiwari et al. (2015)
<i>S. hypacrarthrum</i> Bitt.		2	1	Karki et al. (2021)
<i>S. immite</i> Dun.		2	Na	Khiutti et al. (2015)
<i>S. incamayoense</i> Okada & Clausen	<i>S. brevicaule</i> Bitt.	2	Na	Bachmann-Pfabe et al. (2019)
<i>S. infundibuliforme</i> Phil.		2	2	Khiutti et al. (2015)
<i>S. iopetalum</i> Hawkes		6	4	Karki et al. (2021); Khiutti et al. (2015); Ramsay et al. (1999); Tiwari et al. (2015)
<i>S. jamesii</i> Torr.		2	1	Bachmann-Pfabe et al. (2019); Khiutti et al. (2015); Tiwari et al. (2015)
<i>S. juzepczukii</i> Buk.		3	2	Gabriel et al. (2007)
<i>S. kurtzianum</i> Bitt. & Wittm.	<i>S. boliviense</i> Dun.	2	2	Khiutti et al. (2015)
<i>S. leptophyes</i> Bitt.	<i>S. brevicaule</i> Bitt.	2	2	Bachmann-Pfabe et al. (2019); Budin (2002)
<i>S. lesteri</i> Hawkes & Hjert.		2	Na	Khiutti et al. (2015); Tiwari et al. (2015)
<i>S. megistacrolobum</i> Bitt.	<i>S. boliviense</i> Dun.	2	2	Bachmann-Pfabe et al. (2019); Budin (2002)
<i>S. x michoacanum</i> Rydb.		2	1	Jakuczun and Wasilewicz-Flis (2004); Śliwka et al. (2012b); Szczerbakowa et al. (2010)
<i>S. microdontum</i> Bitt. (Including ssp. <i>gigantophyllum</i> or <i>simplicifolium</i>)		2	2	Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Budin (2002); Colon and Budding (1988); Khiutti et al. (2015); Lin et al. (2020); Meade et al. (2020); Ramsay et al. (1999); Sandbrink et al. (2000); Tan et al. (2008); Tiwari et al. (2015); Zoteyeva et al. (2012)
<i>S. mochiquense</i> Ochoa		2	1	Jones et al. (2009); Smilde et al. (2005)
<i>S. morelliforme</i> Bitt. & Muench.	<i>S. boliviense</i> Dun.	2	1	Karki et al. (2021)
<i>S. multidissectum</i> Hawkes	<i>S. brevicaule</i> Bitt.	2	2	Bachmann-Pfabe et al. (2019)

TABLE 1 (Continued)

Species	Accepted by Spooner	Ploidy	EBN	Reference
<i>S. nayaritense</i> Rydb.	<i>S. stenophyllidum</i> Rydb.	2	1	Lokossou et al. (2010)
<i>S. neocardenasii</i> Hawkes & Hjert.		2	2	Karki et al., 2021
<i>S. neorossii</i> Hawkes & Hjert.		2	2	Bachmann-Pfabe et al. (2019); Jones et al. (2009)
<i>S. okadae</i> Hawkes & Hjert.		2	2	Jones et al. (2009); Muratova et al. (2020)
<i>S. palustre</i> Poepp.		2	1	Karki et al. (2021)
<i>S. pampasense</i> Hawkes		2	2	Meade et al. (2020)
<i>S. papita</i> Rydb.		4	2	Bachmann-Pfabe et al. (2019); Ramsay et al. (1999); Ruiz De Galarreta et al. (1998); Vleeshouwers et al. (2008); Wang et al. (2008); Zoteyeva et al. (2012)
<i>S. paucisectum</i> Ochoa		2	2	Villamon et al. (2005)
<i>S. phureja</i> Juz. & Buk.	<i>S. boliviense</i> Dun.	2	2	Costanzo et al. (2005); Ghislain et al. (2001); Śliwka et al. (2006); Trognitz et al. (2002)
<i>S. pinnatisectum</i> Dun.		2	1	Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Budin (2002); Khiutti et al. (2015); Kuhl et al. (2001); Nachtigall et al. (2018); Ruiz De Galarreta et al. (1998); Tiwari et al. (2015); Yang et al. (2017); Zoteyeva et al. (2012)
<i>S. piurae</i> Bitt.	<i>S. brevicaule</i> Bitt.	2	2	Karki et al. (2021); Rietman (2011)
<i>S. polyadenium</i> Greenm.		2	2	Bachmann-Pfabe et al. (2019); Budin (2002); Khiutti et al. (2015); Tiwari et al. (2015)
<i>S. polytrichon</i> Rydb.		4	2	Bachmann-Pfabe et al. (2019); Ramsay et al. (1999); Ruiz De Galarreta et al. (1998); Tiwari et al. (2015); Wang et al. (2008); Zoteyeva et al. (2012)
<i>S. raphanifolium</i> Cárđ. & Hawkes	<i>S. boliviense</i> Dun.	2	2	Bachmann-Pfabe et al. (2019); Khiutti et al. (2015); Ruiz De Galarreta et al. (1998)
<i>S. sanctae-rosae</i> Hawkes		2	2	Budin (2002)
<i>S. schenckii</i> Bitt.	<i>S. brevicaule</i> Bitt.	6	4	Champouret (2010); Jacobs et al. (2010)
<i>S. x semidemissum</i> Juz. (Hawkes, 1990)	<i>S. demissum</i> Lindl.	6	4	Ramsay et al. (1999)
<i>S. sparsipilum</i> Juz. & Buk. (Including <i>S. ruiz-ceballosii</i> Cárđ.)	<i>S. brevicaule</i> Bitt.	2	2	Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Budin (2002); Danan et al. (2009); Śliwka et al. (2012a); Zoteyeva et al. (2012)
<i>S. spegazzini</i> Bitt.		2	2	Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Budin (2002); Danan et al. (2009)
<i>S. stenophyllidum</i> Rydb.		2	Na	Bachmann-Pfabe et al. (2019); Khiutti et al. (2015)
<i>S. stenotomum</i> Juz. & Buk.	<i>S. tuberosum</i> Andigenum group	2	2	Bachmann-Pfabe et al. (2019); Costanzo et al. (2005); Gabriel et al. (2007); Simko et al. (2006)
<i>S. stoloniferum</i> Schltld. & Bouché (Including <i>S. antipovichii</i> Buk. and <i>S. neoantipovichii</i> Buk.)	<i>S. boliviense</i> Dun.	4	2	Bachmann-Pfabe et al. (2019); Budin (2002); Champouret (2010); Khiutti et al. (2015); Ramsay et al. (1999); Ruiz De Galarreta et al. (1998); Tiwari et al. (2015); Vleeshouwers et al. (2008); Wang et al. (2008); Zoteyeva et al. (2012)
<i>S. x sucrensis</i> Hawkes		4	4	Bachmann-Pfabe et al. (2019); Colon and Budding (1988)
<i>S. tarijense</i> Hawkes	<i>S. berthaultii</i> Hawkes	2	2	Bachmann-Pfabe et al. (2019); Budin (2002); Vossen et al. (2017); Zoteyeva et al. (2012)
<i>S. tarnii</i> Hawkes		2	1	Bachmann-Pfabe et al. (2019); Thieme et al. (2008)
<i>S. toralapanum</i> Cárđ. & Hawkes	<i>S. boliviense</i> Dun.	2	2	Budin (2002)
<i>S. trifidum</i> Corr.		2	1	Bachmann-Pfabe et al. (2019); Budin (2002); Karki et al. (2021); Ruiz De Galarreta et al. (1998); Tiwari et al. (2015)

(Continues)

TABLE 1 (Continued)

Species	Accepted by Spooner	Ploidy	EBN	Reference
<i>S. tuberosum</i> subsp. <i>Andigena</i> Hawkes		4	4	Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Budin (2002); Gabriel et al. (2007)
<i>S. tuberosum</i> subsp. <i>tuberosum</i> L.		4	4	Bachmann-Pfabe et al. (2019); Bradshaw, Hackett, Lowe, et al. (2006)
<i>S. tuquerrense</i> Hawkes	<i>S. brevicaula</i> Bitt.	4	2	Bachmann-Pfabe et al. (2019)
<i>S. venturii</i> Hawkes & Hjert.		2	2	Bachmann-Pfabe et al. (2019); Colon and Budding (1988); Foster et al. (2009); Pel (2010); Pel et al. (2009); Rietman (2011)
<i>S. vernei</i> Bitt. & Wittm.	<i>S. boliviense</i> Dun.	2	2	Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Budin (2002); Sørensen et al. (2006); Zoteyeva et al. (2012)
<i>S. verrucosum</i> Schltld		2	2	Bachmann-Pfabe et al. (2019); Budin (2002); Chen et al. (2018); Colon and Budding (1988); Jacobs et al. (2010); Khiutti et al. (2015); Ramsay et al. (1999); Tiwari et al. (2015); Zoteyeva et al. (2012)
<i>S. virgultorum</i> Cárđ. & Hawkes	<i>S. boliviense</i> Dun.	2		Ruiz De Galarreta et al. (1998)
<i>S. violaceimarmoratum</i> Bitt.		2	2	Khiutti et al. (2015)

Most resistance genes from the various *Solanum* species are classical NLR genes, which encode proteins with a nucleotide-binding site and leucine rich repeats (also NB-LRR or NBS-LRR genes) (Witek et al., 2016). They express receptors, which detect pathogen specific effector proteins, thus starting a signal transduction cascade, leading to induced cell death by hypersensitive response (Rodewald & Trognitz, 2013). The current research indicates that all *P. infestans* effectors detectable by host NLRs belong to the RXLR class (Du et al., 2018; Haas et al., 2009; Luo et al., 2021), which are involved in the suppression of plant defence (Whisson et al., 2016; Yin et al., 2017). These effectors show remarkable diversity, with more than 560 RXLR effector genes predicted in the *P. infestans* genome (Haas et al., 2009).

Various host pathogen interaction models have been proposed to explain resistance and susceptibility in more detail than the simplistic gene-for-gene-interaction model. Perhaps the most adapted one is the zigzag model, which explains the interaction as a process with multiple phases in which the pathogen can counteract multiple layers of plant defence (Jones & Dangl, 2006). A detailed description and comparison of the different models was given by Cook et al. (2015), for the scope of this review it may suffice to point out that NBS-mediated detection of RXLR effectors falls in the category of effector-triggered immunity (ETI), which takes place in the cytosol (Schellenberger et al., 2019). ETI represents the host's second line of defence, after the pathogen successfully entered the cell. Recent publications have shown that another resistance mechanism may also be available for *P. infestans* resistance breeding, which enables pathogen detection at an earlier stage. This mechanism detects apoplastic effectors through receptor-like proteins (RLPs) and receptor-like kinases (RLKs), which were found in two accessions of *S. microdontum*, localized on chromosome 9 and 12 (Lin et al., 2020). In the zigzag model context the reaction is classified as the first line of defence MAMP-triggered immunity (MTI), where microbe-associated molecular patterns (MAMPs) are detected

at the cell surface by pattern-recognition receptors (PRRs). Applicability of PRR genes for *P. infestans* resistance breeding in potato remains, though, to be demonstrated.

4 | R GENES AND QTL FOR *P. infestans* RESISTANCE IN WILD POTATO SPECIES

In 32 of the 85 wild species compiled in Table 1, the genetic basis of the resistance has already been described (Table 2). A total of 61 R genes were described in 27 species and 37 QTL in 11 species. In the majority of cases, several genes or QTL were described for one species, in 12 species only one gene or QTL was detected. While the QTL are distributed quite evenly across all chromosomes (Danan et al., 2011), with a slightly higher incidence on chromosomes 10 and 11, the R genes are mainly concentrated on chromosomes 4 (12 R genes), 9 (14 R genes) and 11 (16 R genes). In contrast, there were no R genes at all reported on chromosomes 1–3. In addition to the fact that many genes have homologues, this concentrations on specific genome regions reflects the arrangement of R genes in clusters (Hulbert et al., 2001; Michelmore & Meyers, 1998). According to Park, Vleeshouwers, et al. (2009), there are 12 R gene clusters on 10 chromosomes for late blight resistance. Verzaux (2010) describes three of these as main clusters: One is the R2 cluster on chromosome 4, which mainly contains R2 and corresponding R2 homologues such as *Rpi-abpt* or *Rpi-edn1.1* and *Rpi-blb3*. The second is the R3 cluster on chromosome 11, which contains—among others—the R genes R3, R5-R7 and R9-R11 from *S. demissum*. The last cluster is the N cluster on the northern arm of chromosome 11, which contains, for example, *Rpi-edn3*, *Rpi-avl1* and *Rpi-cap1*. Combining new genes from multiple clusters could be a way to develop more durable resistance in new cultivars, as soon as they have been made accessible for breeding (Zhu, 2014). Detailed information on the identity and position of

TABLE 2 R genes against *P. infestans* of wild potato relatives

Species	R gene/QTL	Chromosome/ position	Phenotypic variance explained (%)	Reference
<i>S. avilesii</i> Hawkes & Hjert.	<i>Rpi-avl1</i>	11/1.8 Mb		Verzaux et al. (2011)
<i>S. berthaultii</i> Hawkes	<i>Rpi-ber</i>	10	56–66	Ewing et al. (2000); Rauscher et al. (2006)
	QTL	1, 3, 7, 8, 11		
	<i>Rpi-ber</i>	10	12–37	Mayton et al. (2011)
			23–42	Rauscher et al. (2010)
	<i>Rpi-ber1</i>	10/54.0 Mb ^a		Park, Foster, et al. (2009)
	<i>Rpi-ber2</i>	10/53.1– 53.2 Mb ^a		
	QTL	5, 10	18; 26.8–71.7	Manrique-Carpintero et al. (2020)
<i>S. brachistotrichum</i> Rydb.	<i>Rpi-bst1</i>	4		Hein et al. (2009)
<i>S. bulbocastanum</i> Dun.	<i>RB/Rpi-blb1</i>	8/50.3 Mb ^a	62	Naess et al. (2000); Song et al. (2003); van der Vossen et al. (2003)
	<i>Rpi-blb2</i>	6/16.8 Mb		van der Vossen et al. (2005)
	<i>Rpi-blb3</i>	4/6.5 Mb		Champouret (2010); Lokossou et al. (2009); Park, Gros, Sikkema, et al. (2005)
	<i>Rpi-bt1</i>	8/50.0 Mb		Oosumi et al. (2009)
<i>S. capsicibaccatum</i> Cárđ.	<i>Rpi-cap1</i>	11		Jacobs et al. (2010)
<i>S. chacoense</i> Bitt.	<i>Rpi-chc1</i>	10/54.05 Mb		Monino-Lopez et al. (2021); Vossen et al. (2017)
	<i>Rpi-chc2</i>	10		Monino-Lopez et al. (2021)
	QTL	9, 10	14.7; 3.4	Chakrabarti et al. (2014)
<i>S. circaefolium</i> spp. <i>quimense</i> Hawkes & Hjert.	<i>Rpi-qum1</i>	11		Verzaux (2010)
<i>S. demissum</i> Lindl.	R1	5/5.0 Mb	4.1–17.4	Bormann et al. (2004); El-Kharbotly et al. (1994); Leonards-Schippers et al. (1992); Meksem et al. (1995)
	R2	4/6.7 Mb		Champouret (2010); Li et al. (1998); Lokossou et al. (2009); Park, Vleeshouwers, Huigen, et al. (2005)
	R3 (a,b)	11		El-Kharbotly et al. (1994); Huang et al. (2004); Huang et al. (2005); Li et al. (2011)
	R4	12		Van van Poppel (2009)
	R5	11		Huang (2005)
	R6	11		Huang (2005); El-Kharbotly et al. (1996)
	R7	11		Huang (2005); El-Kharbotly et al. (1996)
	R8	9		Jo et al. (2011)
	R9	11		Huang (2005)
	R10	11	47.6–56.9	Bradshaw, Bryan, Lees, et al. (2006); Huang (2005)
	R11	11	51.6–63.6	Bradshaw, Bryan, Lees, et al. (2006); Huang (2005)
		<i>Rpi-dmsf1</i>	4	
<i>S. edinense</i> Berth.	<i>Rpi-edn1.1</i>	4		Champouret (2010)
	<i>Rpi-edn2</i>	9		Verzaux (2010)
	<i>Rpi-edn3</i>	11		Verzaux (2010)
<i>S. hjertingii</i> Hawkes	<i>Rpi-hjt1.1</i>	4		Champouret (2010)
	<i>Rpi-hjt1.2</i>			
	<i>Rpi-hjt1.3</i>			
<i>S. michoacanum</i> Rydb.	<i>Rpi-mch1</i>	7	82.7	Śliwka et al. (2012b)

(Continues)

TABLE 2 (Continued)

Species	R gene/QTL	Chromosome/ position	Phenotypic variance explained (%)	Reference
<i>S. microdontum</i> Bitt.	<i>Rpi-mcd1</i>	4	50	Tan et al. (2008)
	QTL	4, 5, 10	30 (QTL on chromosome 4)	Sandbrink et al. (2000)
	QTL	5, 6, 10	21.1–47.4; 20.7–30.8; 20.3	Meade et al. (2020)
<i>S. mochiquense</i> Ochoa		9, 12		Lin et al. (2020)
	<i>Rpi-moc1</i>	9		Smilde et al. (2005)
	<i>Rpi-mcq1</i>	9		Jones et al. (2009)
<i>S. neorossii</i> Hawkes & Hjert.	<i>Rpi-nrs1</i>	9		Jones et al. (2009)
<i>S. okadae</i> Hawkes & Hjert.	<i>Rpi-oka1</i>	9		Jones et al. (2009)
	<i>Rpi-oka2</i>			
	<i>Rpi-oka3</i>			
<i>S. pampasense</i> Hawkes	QTL	11, 12	19–22.6; 16.9–20.8	Meade et al. (2020)
<i>S. papita</i> Rydb.	<i>Rpi-pta1</i>	8/50.36 Mb		Vleeshouwers et al. (2008); Wang et al. (2008)
	<i>Rpi-pta2</i>	8		Vleeshouwers et al. (2008); Wang et al. (2008)
<i>S. paucissectum</i> Ochoa	QTL- <i>pcs10</i>	10		Villamon et al. (2005)
	QTL- <i>pcs11</i>	11	25	Villamon et al. (2005)
	QTL- <i>pcs12</i>	12	7–10	Villamon et al. (2005)
<i>S. phureja</i> Juz. & Buk	<i>Rpi-phu1</i>	9	65–68	Śliwka et al. (2006)
	QTL	7, 11, 12	9.1; 8.0–10.9; 10.3–15.6	Ghislain et al. (2001)
	QTL	3, 12		Trognitz et al. (2002)
	QTL	3, 5, 11	23.4; 17.9; 9.4	Costanzo et al. (2005)
<i>S. pinnatisectum</i> Dun.	<i>Rpi1</i>	7		Kuhl et al. (2001)
	<i>Rpi2</i>	7		Yang et al. (2017)
		7		Nachtigall et al. (2018)
<i>S. piurae</i> Bitt.	<i>Rpi-pur1</i>	11		Karki et al. (2021); Rietman (2011)
<i>S. polytrichon</i> Rydb.	<i>Rpi-plt1</i>	8		Wang et al. (2008)
<i>S. schenckii</i> Bitt.	<i>Rpi-snk1</i>	4/6.5 Mb		Champouret (2010); Jacobs et al. (2010)
	<i>Rpi-snk2</i>	4		Champouret (2010)
<i>S. sparsipilum</i> Juz. & Buk. (Including <i>S. ruiz-ceballosii</i> Cárd.)	QTL	10	29	Danan et al. (2009)
	<i>Rpi-rzc1</i>	10	87.1	Śliwka et al. (2012a)
<i>S. spegazzini</i> Bitt.	QTL	10	29	Danan et al. (2009)
<i>S. stenotomum</i> Juz. & Buk.	QTL	3, 5, 11	23.4; 17.9; 9.4	Costanzo et al. (2005)
	QTL	8, 10	63 (QTL on chromosome 10)	Simko et al. (2006)
<i>S. stoloniferum</i> Schltldl. & Bouché	<i>Rpi-sto1</i>	8/50.03 Mb		Vleeshouwers et al. (2008); Wang et al. (2008)
	<i>Rpi-sto2</i>	11		Champouret (2010)
<i>S. tarijense</i> Hawkes	<i>Rpi-tar1</i>	10/54.05 Mb		Vossen et al. (2017)
<i>S. tuberosum</i> subsp. <i>tuberosum</i> L.	QTL	4	51–78	Bradshaw, Hackett, Lowe, et al. (2006)
<i>S. tuberosum</i> L. cv. <i>Sarpo mira</i>	<i>Rpi-Smira1</i> <i>Rpi-Smira2</i>	11		Rietman et al. (2012)
<i>S. venturii</i> Hawkes & Hjert.	<i>Rpi-vnt1.1</i>	9/65.6 Mb		Foster et al. (2009); Pel et al. (2009)
	<i>Rpi-vnt1.2</i>	9		Foster et al. (2009); Pel et al. (2009)
	<i>Rpi-vnt1.3</i>	9		Foster et al. (2009); Pel et al. (2009)
	<i>Rpi-vnt2</i>	11		Rietman (2011); Pel (2010)

TABLE 2 (Continued)

Species	R gene/QTL	Chromosome/ position	Phenotypic variance explained (%)	Reference
<i>S. vernei</i> Bitt. & Wittm.	QTL	6, 8, 9	15.4; 10.9; 15.7	Sørensen et al. (2006)
<i>S. verrucosum</i> Schldtl.	<i>Rpi-ver1</i>	6		Jacobs et al. (2010)
	<i>Rpi-ver1</i>	9/52.6– 56.98 Mb		Chen et al. (2018)
	<i>Rpi-abpt</i>	4/6.7 Mb		Champouret (2010); Lokossou et al. (2009); Park, Vleeshouwers, Hutten, et al. (2005)

^aBLAST information.

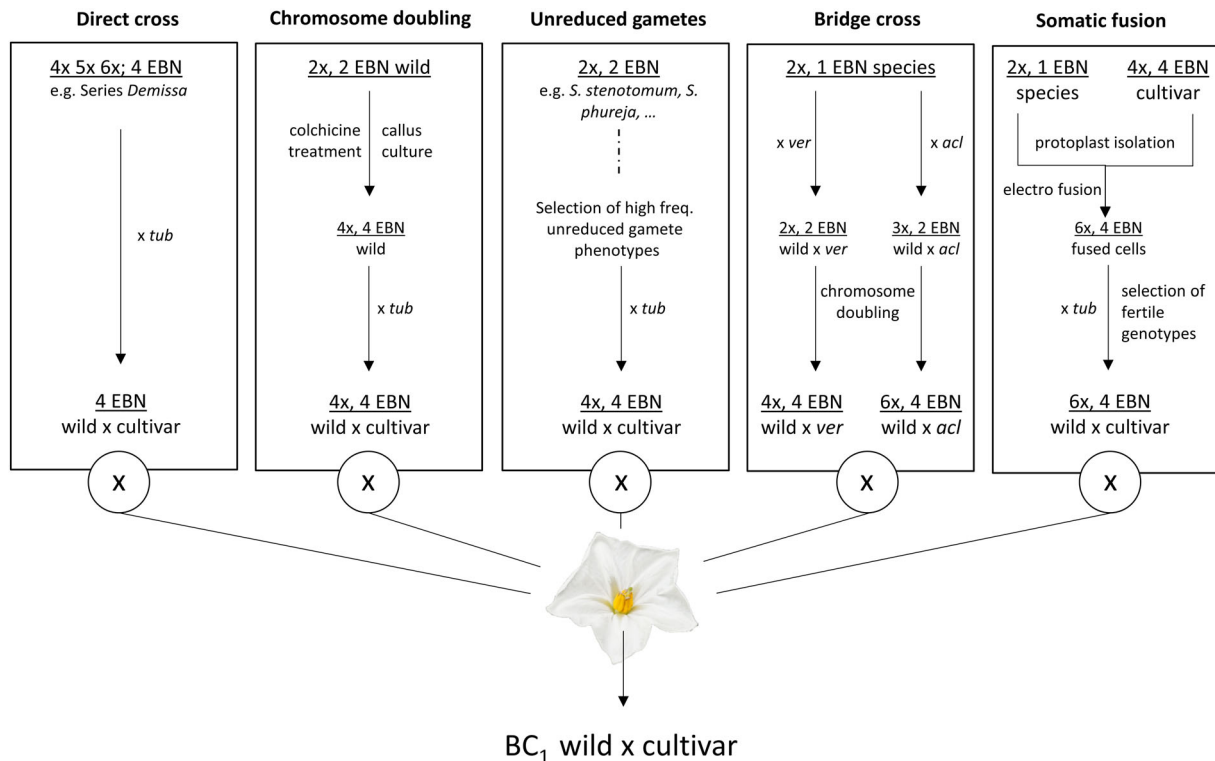


FIGURE 1 Interspecific hybridisation for potato pre-breeding through direct cross, chromosome doubling, unreduced gametes, bridge cross and somatic fusion. EBN = endosperm balance number, *acl* = *acaule*, *tub* = *tuberosum*, *ver* = *vernei*

known *P. infestans* R genes can be derived from RenSeq analysis, which is a NLR gene-targeted enrichment sequencing technology (Jupe et al., 2013). This technology has been proven to be specific enough to discern between functional and nonfunctional alleles of homologous R genes (Van Weymers et al., 2016), hence such analysis can also elucidate if R genes from different species are alleles of the same gene. Although target specific, RenSeq was also successful in identifying new R genes from the NB-LRR gene family (Van Weymers et al., 2016; Duan et al., 2020).

5 | INTERSPECIFIC HYBRIDISATION WITH WILD POTATO SPECIES

The wealth of possible resistance donor species comes in different ploidies, most of them being diploid, some tetraploid and a few are hexaploid. Additionally, there are some species with multiple ploidies,

such as *S. cardiophyllum* ($2n = 2x; 3x; 4x$) as well as natural hybrid species, which can also be triploid (*S. x rechei*, $2n = 3x$) or pentaploid (*S. x edinense*, $2n = 5x$). Crossing compatibilities between species of similar and diverging ploidies have been studied in great detail in the past decades (Jackson & Hanneman, 1999), which resulted in the classification into distinct ploidy and endosperm balance number groups (EBN) (Johnston et al., 1980). Incompatibility between species is most often attributed to insufficient endosperm development, causing the death of the embryo within the seed. According to the EBN theory endosperm development depends on a specific 2:1 ratio of yet undefined maternal:paternal factors (Bethke et al., 2017; Johnston et al., 1980). Almost all potato cultivars fall into the 4x, 4 EBN category, but most tetraploid wild species are 4x, 2 EBN. Diploid species can be 2x, 1 EBN; or 2x, 2 EBN and all hexaploid species are 6x, 4 EBN. Generally, species with similar EBN numbers are compatible, even in some interploidy crosses (Figure 1). That is unless no other factors besides EBN prevent hybridisation, such as male sterility, or insufficient pollen

tube penetration (Jansky, 2006). Even before EBN categories were established, scientists realized that ploidy manipulation can enable hybridisation with otherwise incompatible species (Hanneman & Peloquin, 1968; Swaminathan, 1951). This works either by doubling chromosome numbers and EBN through classical colchicine treatment (Johnstone, 1939), or spontaneous duplication in callus culture (Jacobsen, 1981). A common application for chromosome doubling is to raise diploid (2x, 2 EBN) species to the tetraploid chromosome complement (4x, 4 EBN) to become compatible with tetraploid potato cultivars (Swaminathan, 1951) (Figure 1). Similar to somatic chromosome doubling, diploid species can also produce elevated frequencies of unreduced gametes, through first of second division restitution (FDR, SDR) which are naturally compatible with 4x, 4 EBN species (Mendiburu & Peloquin, 1977). In these cases, 4x-2x cross combinations can be successful. This method is especially relevant for hybridisation with diploid *S. stenotomum* and *S. phureja*. Past research has shown that *P. infestans* resistance can be fixed in *stenotomum* × *phureja* hybrids (Haynes et al., 2014), if the material can be crossed to potato cultivars via unreduced gametes. This may represent another important source of *P. infestans* resistance, especially since such hybrids occasionally show potential for yield increase through heterosis (Graebner et al., 2022). Chromosome number can also be reduced, either by prickle pollination (Hougas & Peloquin, 1958; Marks, 1966), or anther culture (Irikura & Sakaguchi, 1972). This makes it possible to cross dihaploid lines extracted from tetraploid potato cultivars, with 2x, 2 EBN wild species, which is a promising approach to develop diploid cultivars with similar quality to common potato varieties (Jansky & Peloquin, 2006). Another way to achieve hybridisation with tetraploid potato cultivars is through bridge crossing (Figure 1). This is most commonly used to produce hybrids with diploid 1 EBN species (Bethke et al., 2017). Especially *S. verrucosum* (2x, 2 EBN) is known to produce viable seeds when crossed to 2x, 1 EBN species. The resulting offspring can be used afterwards for further crossing to diploid *S. tuberosum* lines, which upon chromosome doubling can be integrated into the gene pool of tetraploid potato cultivars (Jansky & Hamernik, 2009; Yermishin et al., 2014). To a lesser extent, *S. acaule* was used for bridge crosses in a similar way (Dionne, 1963; Hermsen & Ramanna, 1973). Probably the most common method to make 2x, 1 EBN species accessible for potato breeding is the development of somatic hybrids through protoplast fusion (Millam et al., 1995; Pandey et al., 2010).

Eighty-five species of the section *Petota* across all ploidy and EBN groups show resistance against *P. infestans*. Looking at the available gene pool for resistance breeding against *P. infestans*, only a few resistant or partial resistant cultivars and landraces from *S. tuberosum* subsp. *tuberosum* and *andigena* are available in the primary gene pool. The secondary gene pool contains 68 species, but only 11 (4 EBN) show no strong hybridisation barriers and can be directly crossed to potato cultivars with some success. One is *S. demissum* (6x, 4 EBN) which was the first wild species used for resistance introgression on a larger scale since the 1950ies (Bradshaw, Bryan, & Ramsay, 2006). The widely used but broken resistance genes R1 to R11 came from this species. Another 57 species are 2 EBN; these need ploidy

manipulation to be made accessible for resistance breeding. The remaining 22 species are diploid 1 EBN, or are of unknown EBN (*S. lesteri*), they form the tertiary gene pool. In summary, only 13% of the species with some degree of *P. infestans* resistance can be used for resistance breeding in tetraploid potato cultivars, without ploidy manipulation or other ways to circumvent hybridisation barriers.

6 | OPPORTUNITIES OF DIPLOID BREEDING

Potential benefits to breed diploid potato cultivars have been recognized at least since the 1950ies (Hougas & Peloquin, 1958). In general, Mendelian segregation of traits at the diploid level would make it much more feasible to select for recessive alleles (Jansky et al., 2016) and develop superior combinations of the upwards of 40 other important traits for high quality potato cultivars (McCauley, 2021). In the context of *P. infestans* resistance breeding, the fact that 40 of the 85 potential late blight resistance donor species are 2x, 2 EBN (Table 1) and can directly be crossed to diploid potato cultivars makes it even more interesting to attempt potato breeding at the diploid level.

Public and private breeding operations aiming to develop diploid potato cultivars are mostly focusing on the development of high quality inbred lines for hybrid breeding (Birhman & Hosaka, 2000; Hosaka & Sanetomo, 2020; Lieshout et al., 2020), which may express heterosis effects that may match the performance of tetraploid cultivars (Lindhout et al., 2011, 2016). Inbred lines would also enable propagation of uniform potato cultivars from true potato seeds (TPS) (Lindhout et al., 2016), which bears potential to greatly reduce propagation costs of potato cultivars, since true seeds are mostly free of disease which are problematic in seed tuber production (Jansky et al., 2016; Lindhout et al., 2016).

Ultimately, high quality inbred lines could become the ideal vehicle to transfer new resistance genes from diploid wild species into cultivars (Su et al., 2020). This could not only benefit the development of diploid cultivars, because they can easily hybridized with conventional potato cultivars after chromosome doubling. The classical approach for resistance introgression is to double the chromosome number in the wild resistance donor and hybridize directly with potato cultivars. This method, however, has the great disadvantage, that undesirable “wild” traits such as exclusive tuberization under short day conditions, long stolons, irregular tuber shape and bad taste are co-transferred to the generated hybrid (Bethke et al., 2017). Once these traits are present at the tetraploid level, it is very difficult and time consuming to select against these adverse traits, due to linkage drag and the long breeding cycles in conventional potato breeding (Bethke et al., 2017). By the use of elite inbred lines, the “wild” traits however can easily be purged by backcrossing and selfing in a much more controlled manner before crossing with tetraploid cultivars (Su et al., 2020).

However, there are two major obstacles which have hampered advances in the development of diploid cultivars in the past. These are the natural self-incompatibility of the diploid potato species

(Hosaka & Hanneman, 1998) and inbreeding depression, which is especially problematic in diploid lines extracted from tetraploid potato cultivars (De Jong & Rowe, 1971). The inbreeding depression in potato is predominantly caused by unfavourable recessive lethal and sublethal alleles (Bachem et al., 2019; Zhang et al., 2019). These can have negative influences on gamete development, prezygotic and postzygotic embryo development, flower development and plant vigour (Zhang et al., 2019; Zhou et al., 2020). In conventional potato breeding, there is no effective method to select against such alleles, because tetraploid cultivars are propagated vegetatively and breeding commences exclusively by selection among heterozygous F_1 crosses (Jansky et al., 2016; Lian et al., 2019; Lindhout et al., 2011). Even in the diploid wild species, inbreeding depression is observed (De Jong & Rowe, 1971; Lian et al., 2019; Phumichai et al., 2005). Similar to tetraploid cultivars, inbreeding depression is caused by deleterious alleles, which are shared by diploid and tetraploid potatoes and may be ancestral (Zhang et al., 2019). In contrast to tetraploid cultivars, deleterious alleles in diploids tend to persist through strong self-incompatibility rather than through the breeding methodology itself.

Self-incompatibility, which is predominant in diploid species, can be overcome since a self-compatibility inducer has been discovered in accessions of *S. chacoense* (Cappadocia & Cheng, 1986). The self-compatibility induction is linked to the single gene *Sli* (Eggers et al., 2021) which interacts with the self-incompatibility inducing S-locus (Hosaka & Hanneman, 1998). Interestingly, the gene is also relatively common in tetraploid potato cultivars (Clot et al., 2020). Through the use of publically available self-compatibility inducers such as the line M6 (Jansky et al., 2014; Leisner et al., 2018), it became possible to develop the first homozygous diploid potato inbred lines (Hosaka & Sanetomo, 2020; Lieshout et al., 2020). The M6 is self-compatible due to the S-locus inhibitor gene *Sli*, which is inherited dominantly (Hosaka & Hanneman, 1998), so that hybrids with M6 become self-compatible as well. In the future, careful selection and recombination of inbred lines from wild and cultivated diploid species may lead to the development of diploid elite lines. Reciprocal recurrent selection (Ortiz, 2020), in parallel to elite inbred line development, potentially enables selection for allele combinations of significant heterotic potential for the development of diploid F_1 hybrid potatoes (Lindhout et al., 2016). There are also many potential benefits of diploid potato breeding for scientific investigation. M6 derived segregating populations have already been used to locate genes for resistance against Colorado potato beetles (Kaiser et al., 2020), resistance against bacterial rot (Chung et al., 2017) and for investigating the genetic basis of physiological traits such as skin colour, tuber shape and the occurrence of undesirable characteristics like eye tubers and jelly ends (Endelman & Jansky, 2016).

7 | LATE BLIGHT RESISTANCE THROUGH GENETIC ENGINEERING

One way to obtain resistant cultivars is the above mentioned introgression of resistance genes into elite inbred lines for diploid hybrid

breeding. However, the resistances from the wild species summarized here are not only important for conventional breeding but can also be applied through genetic engineering. The use of genetic modified organisms (GMOs) can be problematic due to regional differences in political regulations especially in the EU (Eckerstorfer et al., 2019) and consumer acceptance (McComas et al., 2014), but genetic engineering also brings great advantages due to the significantly faster and more precise application. For example Cis-genesis was used for the development of the cultivar 'Fortuna', which carries the genes *Rpi-blb1* and *Rpi-blb2* from *S. bulbocastanum* through *Agrobacterium*-mediated transformation (Storck et al., 2011). Another example would be the Innate[®] potato cultivars, which carry a late blight resistance gene from *S. venturii* (*Rpi-vnt1*), as well as other quality relevant traits from wild potato species (Richael, 2021). The Cis-genesis approach in particular could considerably minimize problems with disease infestation. It allows fast stacking of several R genes from multiple gene clusters (Zhu et al., 2012) without the significant drawback of linkage drag around introgressed resistance genes, as is often the case in conventional R gene introgression. Quantitative resistance in potato cultivars arises from the interaction of genes that induce some degree of tolerance against pathogens without complete prevention of infection (Poland et al., 2009) but also in combination with R genes both broken and still functional (Stewart et al., 2003). If quantitative and durable resistance can be developed by genetic engineering is still open for debate.

8 | CONCLUSION

As has been shown, there is a wealth of untapped potential for new impulses to *P. infestans* resistance breeding using the newly identified donor species. Future breeding and research should focus on localization and functional analysis of these genes. In order to equip cultivars with durable resistance, it is of vital importance to stack resistance genes from different sources as well as include quantitative resistance, which is generally more durable than individual monogenic resistance genes.

In addition, breeders should focus on finding new ways to implement resistances quickly. One such way could be breeding at the diploid level as has been described above. This method has the potential benefit that segregating populations derived from crosses with improved inbred lines not only help to map and characterize resistance but also already deliver material of higher quality for breeding resistant cultivars. The development of an inbred line based F_1 seed propagated potato crop would also enable fast and easy stacking and exchange of resistance genes. Although there is still much initial research needed for diploid potato breeding, it could become one possible gateway for the development of future cultivars. Thereby, diploid as well as tetraploid cultivars resulting from chromosome duplication could be used. Due to current regulations, genetic modification technologies are not yet an alternative way, even if organic farming could benefit strongly from the merits of Cis-genesis (Gheysen & Custers, 2017). It may be worthwhile to re-evaluate in order to harness the technology for the development of a more sustainable

agricultural practice (Waters et al., 2021). All methods must ultimately serve the same goal to make the cultivars capable for future agriculture with much higher standards in terms of sustainability, carbon-neutrality and reduced input of synthetic pesticides.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHOR CONTRIBUTIONS

JB and RG developed the idea and wrote the manuscript in equal parts. RU and TH read and edited the draft version. All authors read and approved the final version of the manuscript.

DATA AVAILABILITY STATEMENT

All the data we used for this review came from the articles cited correspondingly.

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