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EDITED BY
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Bharathi Raja Ramadoss,
Plenty Unlimited Inc., United States

*CORRESPONDENCE
Shaun J. Clare
shaun.clare@wsu.edu

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Colocalization of genetic regions that confer resistance/susceptibility against *Puccinia* species and association with *Pyrenophora teres* loci within the barley genome

Shaun J. Clare[1]*, Fluturë Novakazi[2], Patrick M. Hayes[3], Matthew J. Moscou[4] and Robert S. Brueggeman[1]

[1]Department of Crop and Soil Sciences, Washington State University, Pullman, WA, United States, [2]Department of Crop Health, University of Rostock, Rostock, Germany, [3]Department of Crop and Soil Science, Oregon State University, Corvallis, OR, United States, [4]United States Department of Agriculture, Agricultural Research Service, Cereal Disease Laboratory, University of Minnesota, St. Paul, MN, United States

Cereal rust diseases, including leaf, stem, and stripe rust, are some of the most devastating and economically important diseases of barley. However, host–pathogen genetic interaction research for each pathosystem is typically conducted independently and in isolation. Examples of host resistance/susceptibility genes functioning sympathetically to multiple pathogens or antagonistically to additional pathogens have been reported. Therefore, consolidation of loci that have been reported in multiple studies and across pathosystems is useful for variety development to maximize resistance to multiple pathogens and avoid inadvertent incorporation of susceptibility loci that act antagonistically to other pathogens. This review summarizes loci reported in three key biotrophic pathosystems of barley, including leaf, stem, and stripe rust. In conjunction with previously consolidated net blotch loci, this review lays the foundation for a wider barley rust resistance/susceptibility atlas. This review aims to inform breeders and researchers in rapidly identifying accessions and loci that need further characterization and which loci would be most useful to introgress into elite varieties.

KEYWORDS

barley, leaf rust, stripe rust, stem rust, net blotch, atlas, *Hordeum*, *Puccinia*

Introduction

Cereals are staple crops the world over, providing calories and protein to the growing global population (Hubbard et al., 2015; Kearney, 2010). Currently, barley ranks as the second most-produced temperate cereal in the world after wheat (Thiel et al., 2021). Barley is primarily used as animal feed yet is the key ingredient in brewing beer and distilling premium whiskey by

providing the necessary nutrients and enzymes for alcohol production (Sayre-Chavez et al., 2022). Beer ranks third for the most consumed beverage worldwide behind water and tea (Salanță et al., 2020), and its consumption plays a major role in the social fabric in many parts of the world. Thus, a secure supply of malting quality barley is essential to support the multibillion-dollar added value industry. Barley is also reemerging as a food crop due to its human health benefits (Tosh and Bordenave, 2020), and efforts are underway to develop modern biofortified and heart-healthy hulless barley varieties.

A major constraint to barley yield and quality is disease outbreaks. Due to climate change, environmental conditions have led to more severe epidemics in important barley production regions, preventing the crops from reaching their full potential and requiring additional inputs for disease management and mitigation (Dean et al., 2012; Xie et al., 2018). Rusts have been a major bane of cereal production and a part of human history since the beginning of agriculture. The Romans performed sacrificial ceremonies of Robigalia to appease the god of cereal rust diseases, Robigus (Saunders et al., 2019). In addition, all rust species mentioned in this review are macrocyclic and heteroecious (Bolton et al., 2008; Jin et al., 2010; Leonard and Szabo, 2005). Thus, countries have performed extensive eradication programs of barberry, the alternative host to multiple rust species, in an attempt to prevent sexual recombination and stabilize rust populations to slow the evolution of new races of rust species (Saunders et al., 2019). Although not calculated for barley, the economic impact of rusts on wheat is estimated to be $4.3–5.0 billion, 3.5% of the $145 billion economic value of worldwide wheat (Figueroa et al., 2018).

Cereal rust species are members of the genus *Puccinia* from the basidiomycota division of fungi that are obligate biotrophs (Bolton et al., 2008; Jin et al., 2010; Jin and Steffenson, 1999; Leonard and Szabo, 2005). There are four primary species of rust known to infect barley (Table 1): *Puccinia coronata* var. *hordei* (*Pch*), the causal agent of crown rust; *Puccinia hordei* (*Ph*), the causal agent of the leaf (brown) rust; *Puccinia striiformis* f. sp. *hordei* (*Psh*), the causal agent of the stripe (yellow) rust; and *Puccinia graminis* f. sp. *tritici* (*Pgt*), the causal agent of the stem (black) rust, all showing close phylogenetic relationships with other cereal rusts (Brueggeman et al., 2020; Dracatos et al., 2019b; Park et al., 2015). The notion of *formae speciales* (ff. spp.) separating specialized forms of a species that infect specific host species was developed by Eriksson (1894). However, this specialization does not hold true for some *formae speciales*, as the wheat stem rust pathogen *Pgt* also infects barley. Depending on local fluctuations in pathogen virulence and the deployment of inadequate resistance loci, leaf, stem, and stripe rust of barley all have the potential to cause incredibly damaging epidemics (Dean et al., 2012; Kleinhofs et al., 2009). In comparison, crown rust does not cause significant yield loss (Jin et al., 1992; Jin and Steffenson, 1999), and therefore is relatively understudied.

Two types of resistance are described within cereal rust pathosystems: seedling/all-stage resistance (ASR) effective throughout the plant's life cycle and adult plant resistance (APR) effective at the postseedling stage. ASR genes are often considered race-specific and associated with the hypersensitive response, whereas APR genes are often incomplete, providing additive resistance (Dracatos et al., 2015a), that can result in near-immunity when sufficiently stacked (Huerta-Espino et al., 2020). Some resistance/susceptibility genes are involved in interactions with multiple pathogens, whether as sympathetic resistance to multiple diseases or antagonistic relationships of resistance/susceptibility to biotrophic and necrotrophic pathogens. Therefore, the ability to report colocalization of newly reported loci currently requires intimate knowledge of respective pathosystems or an extensive and therefore time-consuming literature review. Previously, the Barley Genetics Newsletters provided an excellent resource for this purpose; however, with high-resolution mapping and the sheer abundance of loci reported in the current barley community, this easily becomes unmanageable. Similar consolidations have been achieved for various pathogens of wheat (Amo and Soriano, 2022; Jan et al., 2021; Pal et al., 2022; Peters Haugrud et al., 2022; Soriano and Royo, 2015; Yu et al., 2014; Zheng et al., 2021). This review consolidates resistance/susceptibility loci for the three highly devastating pathogens of barley leaf, stem, and stripe rust and the lesser pathogen crown rust against the Morex V3 reference genome (Mascher et al., 2021) to lay a foundation for a larger resistance/

TABLE 1 Common cereal rust species and their respective hosts.

Species	*Formae speciales*/ variation	Disease	Primary host(s)
Puccinia coronata	*avenae*	Crown	Oats
	hordei	Crown	Barley
Puccinia hordei		Leaf	Barley
Puccinia triticina		Leaf	Wheat
Puccinia graminis	*tritici*	Stem	**Wheat**, **barley**
	secalis	Stem	**Rye**, barley
	avenae	Stem	**Oats**, barley
Puccinia striiformis	*hordei*	Stripe	Barley
	pseudo-hordei	Stripe	Wild barley grass
	secalis	Stripe	Rye
	tritici	Stripe	Wheat

Bold indicates the primary host.

Abbreviations: APR, adult plant resistance; ASR, seedling/all-stage resistance; f., form (different forms of a species with the same host); f. sp., *forma specialis* (same species with different host specificity); ff. spp., *formae speciales* (plural of *f. sp.*); MTA, marker-trait association; *Pch*, *Puccinia coronata* var. *hordei*; *Ph*, *Puccinia hordei*; *Pt*, *Puccinia triticina*; *Psh*, *Puccinia striiformis* f. sp. *hordei*; *Pst*, *Puccinia striiformis* f. sp. *tritici*; *Pga*, *Puccinia graminis* f. sp. *avenae*; *Pgs*, *Puccinia graminis* f. sp. *secalis*; *Pgt*, *Puccinia graminis* f. sp. *tritici*; *Ptm*, *Pyrenophora teres* f. *maculata*; *Ptt*, *Pyrenophora teres* f. *teres*; *Ptr*, *Pyrenophora tritici-repentis*; QTL, quantitative trait locus/loci; *Rpc#*, *Reaction to Puccinia coronata #*; *Rpg#*, *Reaction to Puccinia graminis #*; *Rph#*, *Reaction to Puccinia hordei #*; *Rps#*, *Reaction to Puccinia striiformis #*; *Rpt#*, *Reaction to Pyrenophora teres #*; SNP, single-nucleotide polymorphism; *Spt#*, *Susceptibility to Pyrenophora teres #*; *Spr#*, *Susceptibility to Pyrenophora tritici-repentis #*.

susceptibility atlas incorporating the net blotch consensus maps (Clare et al., 2020).

Genetics to crown rust

Crown rust was first identified in 1991 in the USA (Jin et al., 1992) and designated a variety of *P. coronata* in 1999 (Jin and Steffenson, 1999). Barley crown rust has currently only been documented in the USA, Hungary, and China (Tian et al., 2021). To date, only the *Reaction to Puccinia coronata 1* (*Rpc1*) locus has been reported against *Pch* on chromosome 3H in HOR 2596 (Agrama et al., 2004). *Rpc1* was reported to colocalize with *Rph5*, *Rph6*, and *Rph7* (leaf rust); *Rp1-D* (stem rust); *Run6* (loose smut); *rym4* and *rym5* (barley mild mosaic virus); and *Ryd2* (barley yellow dwarf virus) at the time (Agrama et al., 2004; Jin and Steffenson, 2002). However, refinement of *Rph5*, *Rph6*, and *Rph7* loci has shown that *Rpc1* colocalizes with *Rph10* (Martin et al., 2020). Candidate gene analysis for *Rpc1* is limited due to the use of proprietary markers that encompass a large 314 Mb (175.45 to 489.01 Mb) genomic interval (Supplementary Table 1).

Genetics to leaf rust

Leaf rust is often reported as one of the most devastating barley diseases, with yield losses up to 62% and routinely contributing up to 30% yield loss under conditions conducive to epidemic formation (Cotterill et al., 1992; Griffey et al., 1994; King and Polley, 1976). Despite barley infections primarily being *Ph*, leaf rust can also be caused by *P. triticina* (*Pt*), the causal agent of wheat leaf rust (Kleinhofs et al., 2009). The genetics of leaf rust resistance have been studied since the 1920s (Fazlikhani et al., 2019), with at least 80 *Leaf rust* (*Lr*) (Prasad et al., 2020) and 28 *Reaction to Puccinia hordei* (*Rph*; Table 2) loci (Mehnaz et al., 2021a) identified within wheat and barley, respectively. Additionally, there are a series of *Rphq* partial resistance loci with minor effects (Marcel et al., 2007, 2008; Qi et al., 1998, 1999, 2000; Yeo et al., 2017), not to be confused with the set of *RphQ* loci (Ziems et al., 2014). *Rphq1-10* and *Rphq20-21* were first identified in L94 × Vada, *Rphq11-13* in L94 × 116-5, *Rphq14-15* and *Rphq22-23* in Steptoe × Morex, and *Rphq16-19* in Oregon Wolfe Barley (Marcel et al., 2007, 2008; Qi et al., 1998, 1999, 2000; Yeo et al., 2017).

TABLE 2 Summary information of all designated resistance/susceptibility loci in barley to leaf rust pathogen *Puccinia hordei*.

Locus	Synonym	Alleles	Species	Accession	Stage	Chr.	Pos. (bp)	Mapping	Validation
Rph1	*Pa1*	*Rph1.a*	*H. vulgare*	~ 6 including Sudan, CI9214	ASR	2H	12,389,435–12,394,017	Tuleen and McDaniel (1971)	Dracatos (2019a)
Rph2	*Pa2*, *RphQ*, *RphH1*	*Rph2.b*, *Rph2.j*, *Rph2.k*, *Rph2.l*, *Rph2.m*, *Rph2.n*, *Rph2.q*, *Rph2.r*, *Rph2.s*, *Rph2.t*, *Rph2.u*, *Rph2.y*	*H. vulgare*	~ 20 (see Rothwell et al., 2020) including Halycon, Kaputar, Q21861	ASR	5H	34,077,798–312,743,283	Borovkova et al. (1997), Park et al. (2003); Martin et al. (2020) Additional: Henderson (1945), Zloten (1952), Starling (1955), Moseman and Greeley (1965), Roane and Starling (1967), Reinhold and Sharp (1982), Jin et al. (1995), Miah (2004)	
Rph3	*Pa3*, *RphAl1*, *Rphx*	*Rph3.c*, *Rph3.w*	*H. vulgare*	~ 130 (see Dinh et al. (2022)) including Barke, Estate, Scarlett	ASR	7H	606,973,547–606,996,548	Jin et al. (1993); Toojinda et al. (2000); Park et al. (2003); von Korff et al. (2005); Rossi et al. (2006)	Dinh et al. (2022)
Rph4	*Pa4*	*Rph4.d*	*H. vulgare*	Gold	ASR	1H	76,846–174,305	McDaniel and Hathcock (1969), Tan (1978), Park et al. (2003), Martin et al. (2020)	
Rph5	*Pa5*, *Pa6*, *Rph6*	*Rph5.e*, *Rph5.f*, *Rph5.ai*	*H. vulgare*	Magnif 104, Bolivia, Quinn	ASR	3H	1,053,008–5,498,681	Tuleen and McDaniel (1971), Mammadov et al. (2003), Zhong et al. (2003), Martin et al. (2020)	
Rph7		*Rph7.g*, *Rph7.ac*	*H. vulgare*	Cebada Capa	ASR	3H	6,026,163–6,027,1401	Brunner et al. (2000), Graner et al. (2000),	Chen et al. (2023)

(Continued)

TABLE 2 Continued

Locus	Synonym	Alleles	Species	Accession	Stage	Chr.	Pos. (bp)	Mapping	Validation
								Scherrer et al. (2005), Martin et al. (2020)	
Rph8		*Rph8.h*	*H. vulgare*	Egypt 4	ASR	2H	28,814,087–39,471,633 or 49,001,372–50,000,878	Martin et al. (2020)	
Rph9	*Rph12*, *RphC*	*Rph9.i*, *Rph9.z*, *Rph9.am*	*H. vulgare*	~ 14 (see Dracatos et al. (2014)) including HOR 2596, Triumph, Cantala	ASR	5H	532,570,445–540,071,401	Jin et al. (1993), Borovkova et al. (1998), Park et al. (2003), Dracatos et al. (2014), Martin et al. (2020)	
Rph10		*Rph10.o*	*Hv. spontaneum*	Bar Giyyora 30	ASR	3H	442,259,673–510,344,784	Feuerstein et al. (1990), Martin et al. (2020)	
Rph11		*Rph11.p*	*Hv. spontaneum*	Maalot 17	ASR	6H	542,548,571–552,271,928	Feuerstein et al. (1990), Martin et al. (2020)	
Rph13	*RphPI531849*	*Rph13.x*	*Hv. spontaneum*	PI 531849	ASR	3H	591,731,322–592,805,407	Jin et al. (1996), Martin et al. (2020), Jost et al. (2020)	
Rph14	*RphZhu4*, *Rph1063*	*Rph14.ab*, *Rph14.a*, *Rph14.an*	*H. vulgare*	PI 584760	ASR	2H	40,172,574–49,001,371	Jin et al. (1996), Kicherer et al. (2000), Golegaonkar et al. (2009), Derevnina et al. (2015), Martin et al. (2020)	
Rph15	*Rph16*	*Rph15.ad*, *Rph15.ae*	*Hv. spontaneum*	PI 355447, HS078, HS084, HS680, HS677, Krona (*H. vulgare*)	ASR	2H	43,324,066–43,334,936	Chicaiza (1996), Ivandic et al. (1998), Kicherer et al. (2000), Perovic et al. (2004), Kopahnke et al. (2004), Weerasena et al. (2004), Derevnina et al. (2015), Martin et al. (2020)	Chen et al. (2021)
Rph17		*Rph17.af*	*H. bulbosum*	81882	ASR	2H	11,230,663–33,607,782	Pickering et al. (1998), Derevnina et al. (2015)	
Rph18		*Rph18.ag*	*H. bulbosum*	NGB22900	ASR	2H	655,492,223–665,585,731	Pickering et al. (2000)	
Rph19	*Rphq1*, *RphP*	*Rph19.ah*	*H. vulgare*	Prior, Reka 1	ASR	7H	618,144,019–620,924,895	Qi et al. (1998), Park and Karakousis (2002), Park et al. (2003), Marcel et al. (2007), Ziems et al. (2014), Schnaithmann et al. (2014)	
Rph20	*Rphq4*, *qRphFlag*	*Rph20.ai*	*H. vulgare*	Flagship, Vada, Pompadour	ASR/APR	5H	477,713,965–552,456,002	Qi et al. (1998), Marcel et al. (2008), Hickey et al. (2011), Hickey et al. (2012), Dracatos et al. (2021)	
Rph21	*RphRic*	*Rph21.aj*	*H. vulgare*	Ricardo	ASR	4H	569,191,770–587,482,042	Sandhu et al. (2012)	

(Continued)

TABLE 2 Continued

Locus	Synonym	Alleles	Species	Accession	Stage	Chr.	Pos. (bp)	Mapping	Validation
Rph22	*Rphq2*	*Rph22.ak*	*H. bulbosum*		ASR/ APR	2H	658,097,219–658,992,658	Qi et al. (1998), Marcel et al. (2007), Jafary et al. (2006), Liu et al. (2011), Johnston et al. (2013)	Wang et al. (2019)
Rph23		*Rph23.al*	*H. vulgare*	Yerong	APR	7H	25,493,925–40,364,161	Singh et al. (2015)	
Rph24	*qRphND, Rphq3*	*Rph24.an*	*H. vulgare*	ND24260-1	ASR/ APR	6H	358,564,150–366,401,166	Qi et al. (1998), Marcel et al. (2008), Hickey et al. (2011), Castro et al. (2012), González et al. (2012), Ziems et al. (2014), Ziems et al. (2017), Dracatos et al. (2021)	
Rph25	*RphFT*	N/A	*H. vulgare*	Fong Tein, Yagan	ASR/ APR	5H	N/A	Kavanagh et al. (2017)	
Rph26		N/A	*H. bulbosum*	A17	ASR/ APR	1H	508,419,600–515,212,328	Yu et al. (2018)	
Rph27	*RphCRQ3*	N/A	*H. vulgare*	Quinn	ASR	4H	1,404,433–1,575,580	Rothwell et al. (2020)	
Rph28	*RphHEB*	N/A	*Hv. spontaneum*		ASR/ APR	5H	562,823,935–562,920,797	Mehnaz et al. (2021a)	
$Rph_{MBR1012}$		N/A	*H. vulgare*	MBR1012	ASR	1H	2,101,387–2,601,463	König et al. (2012), Fazlikhani et al. (2019)	

Information includes locus designations, synonyms and alleles, species and accessions, effective stages, chromosomal location, and relevant literature.

Due to the number of reported loci, barley *Rph* loci appear complex; however, further research has revealed multiple *Rph* genes are allelic variants. In addition, *Rphq* loci are often elevated and reclassified into *Rph* loci. Therefore, the true number of *Rph* loci currently stands at 25 (Martin et al., 2020). The *RphD* locus is not assigned to any chromosome (Marcel et al., 2008). Additionally, two collections of diverse barley lines were found to carry uncharacterized leaf rust resistance (Mehnaz et al., 2021b; Verma et al., 2018). There are also three QTL detected within a population between Blenheim and E224/3, but marker intervals were not reported (Thomas et al., 1995).

Chromosome 1H

Rph4 was first mapped to the short arm of chromosome 1H (McDaniel and Hathcock, 1969; Qi et al., 1998; Tan, 1978). Additionally, $Rph_{MBR1012}$, when first mapped, was not suspected to be *Rph4* (König et al., 2012). Further work delimited $Rph_{MBR1012}$ to a 500 kb interval (2.1–2.6 Mb) in close proximity to *Rph4* (Fazlikhani et al., 2019). Subsequent work delimited *Rph4* to a 97-kb interval (0.08–0.17 Mb), distal to $Rph_{MBR1012}$, and therefore is a distinct locus (Martin et al., 2020). *Rph26* was identified in the wild bulbous barley line A17 (Yu et al., 2018), mapping to a 7.2-Mb interval (508.42–515.21 Mb) that was also mapped in previous studies (Gutiérrez et al., 2015; Hickey et al., 2011). Additional loci identified on chromosome 1H include *RphQ1*, *RphQ3*, and *RphQ4* (Ziems et al., 2014); *qGH_PBIC_3.91* (Dracatos et al., 2019b); *Qlr.HeB-5-1H* (Schnaithmann et al., 2014), *Rphq14* (Yeo et al., 2017); *Rphq21* (Marcel et al., 2008); and *Rphq22* (Yeo et al., 2017).

Chromosome 2H

The *Rph1* gene was first reported in the experimental line Minn. II 12.15 and cultivar Sudan (Roane and Starling, 1967; Watson and Butler, 1947) on chromosome 2H (Tuleen and McDaniel, 1971). *Rph1* is highly likely to have been mapped as *qField_PBIC_2016_3.14* (Dracatos et al., 2019b), *QPh.2H-1* (Vatter et al., 2017), and *QRph5* (Ziems et al., 2014). *Rph1* encodes a coiled-coil (CC) nucleotide binding site leucine-rich repeat (NLR) receptor protein (Dracatos et al., 2019a). Phylogenetic classification of RPH1 places the NLR in the C9 clade, which includes the rice NLR Pik-2 that functions with the NLR Pik-1 (C12 clade) to confer resistance to *Magnaporthe oryzae* (Ashikawa et al., 2008; Bailey et al., 2018). Sequencing of *rph1* mutants determined five mutants carry *Rph1* mutations, whereas two mutants lacked mutations in *Rph1* (Dracatos et al., 2019a). This observation supports the hypothesis that additional loci, such as a second NLR, are required for *Rph1*-mediated resistance. *Rph8* was first described in Egypt 4 as an ASR locus (Tan, 1977), despite Egypt 4 previously being used as a susceptible check (Martin et al., 2020). The *Rph8* locus remains elusive and understudied due to the lack of avirulent isolates on *Rph8* (Jin et al., 1996). As Egypt 4 is the only known source of *Rph8*, introgression into Bowman delimited the locus to a 10.6-Mb (28.81–

39.24 Mb) or 1.0-Mb (49.00–50.00 Mb) interval under the assumption that *Rph8* is not allelic to *Rph14/15/16/17* (Martin et al., 2020). This region is highly complex, with current mapping efforts delimiting *Rph8*, *Rph14*, *Rph15*, *Rph16*, and *Rph17* to the same region (Derevnina et al., 2015; Martin et al., 2020). *Rph14* was identified in barley accession PI584760 (Jin et al., 1996) and mapped to an 8.8-Mb interval (40.17–49.00 Mb) (Golegaonkar et al., 2009; Martin et al., 2020). In contrast, *Rph15* was first identified in wild accession PI355447 (Chicaiza, 1996), and *Rph16* in wild accessions HS078, HS084 (Ivandic et al., 1998), HS688 (Perovic et al., 2004), and potentially HS677 (Kopahnke et al., 2004), as well as landrace HOR1063 (Kicherer et al., 2000). Subsequently, *Rph15* and *Rph16* were confirmed to be allelic (Weerasena et al., 2004), whereas *Rph14* was believed to be an independent locus based on segregation ratios (Derevnina et al., 2015). More recent studies dispute this, suggesting *Rph14* may be allelic to *Rph15/16* with the single susceptible individual separating *Rph14* from *Rph15/16* as a potential admixture (Derevnina et al., 2015). Therefore, *Rph14*, *Rph15*, and *Rph16* are predicted to be an allelic series (Derevnina et al., 2015), of which *Rph15/16* has already been validated as encoding a CC-NLR with an integrated zinc finger BED domain (Chen et al., 2021), located at 43.32–43.33 Mb. RPH15 is found in clade C24 within a subclade of related NLRs with N-terminal integrated zinc finger BED domains, including the resistance proteins Xa1, Xo1, Yr5, Yr7, and YrSP (Bailey et al., 2018; Marchal et al., 2018; Read et al., 2020; Yoshimura et al., 1998). These results suggest five potential alleles: *Rph14.ab* and *Rph14.am* (previously *RphZhu4*); *Rph14.an* (previously *Rph1063*) (Kicherer et al., 2000); and *Rph15.ad* and *Rph15.ae* (previously *Rph16*) (Derevnina et al., 2015; Martin et al., 2020). The allele designations.*am* and.*an* had already been applied to *Rph9.am* (Dracatos et al., 2014) and *Rph24.an* (Ziems et al., 2017) and therefore need to be addressed in the future. *Rph17* is confirmed to be independent of *Rph14/15/16* (Derevnina et al., 2015), mapping to a 22.4-Mb interval (11.23–33.61 Mb) using *H. bulbosum* × *H. vulgare* hybrids (Pickering et al., 1998). However, *Rph17* currently encompasses *Rph1* (Dracatos et al., 2019a) and the proximal end of *Rph8* (Martin et al., 2020). Additionally, *Rph17* is known to cosegregate with *Mildew locus* from *Hordeum bulbosum* (*Mlhb*), a powdery mildew resistance locus (Pickering et al., 1998). Lastly, *RphQ7* maps in close proximity to this complex region (Ziems et al., 2014). *Rph18* was also mapped using *H. bulbosum* × *H. vulgare* hybrids; however, it mapped to a 10.1-Mb interval (655.49–665.59 Mb) (Pickering et al., 2000), encompassing the validated *Rph22* gene (Wang et al., 2019). *Rph22* was originally mapped as *Rphq2* (Qi et al., 1998) but was subsequently high-resolution mapped (Johnston et al., 2013) and identified as a lectin receptor-like kinase (Wang et al., 2019). *Rph22* was also most likely mapped by association mapping studies as *QPh.2H-2* (Vatter et al., 2017) and two unnamed QTL (Czembor et al., 2022; Gutiérrez et al., 2015). Both the wild bulbous barley and cultivated barley alleles confer stronger resistance responses to bulbous and cultivated barley leaf rust isolates, respectively (Wang et al., 2019). Additional loci mapping to chromosome 2H include *Qlr.HeB-F23-2H* (Schnaithmann et al., 2014); *Rphq11* and *Rphq12* (Qi et al., 2000; Yeo et al., 2017); *QLr.S42-2H.a* and *QLr.S42-2H.b* (von Korff et al., 2005); and two unnamed QTL (Amouzoune et al., 2022; Castro et al., 2012).

Chromosome 3H

Initially, the loci *Rph5*, *Rph6*, and *Rph7* were believed to be dispersed along chromosome 3H (Zhong et al., 2003); however, *Rph5* and *Rph6* are currently hypothesized to be allelic variants, whereas *Rph7* remains an independent locus. The *Rph5/Rph6* and *Rph7* loci are delimited to 4.5-Mb (1.05–5.50 Mb) and 134-kb intervals (5.98–6.12 Mb), respectively, using introgression mapping (Martin et al., 2020). Subsequently, *Rph7* was identified as a NAC transcription factor at ~ 6.03 Mb (Chen et al., 2023). Four of eight mutants carried mutations in *Rph7*, indicating that additional loci are involved in *Rph7*-mediated resistance (Chen et al., 2023). *Rph10* and *Rph11* were originally mapped to chromosomes 3H and 6H within wild barley accessions Bar Giyyora 30 and Maalot 17, respectively (Feuerstein et al., 1990). *Rph10* was subsequently mapped to an 18.1-Mb (442.26–510.34 Mb) interval (Martin et al., 2020). However, within the *Rph10* backcross accession BW683, there is additional donor DNA in close proximity (~ 5.9 Mb) to *Rph11* on chromosome 6H. Therefore, there is debate as to whether *Rph10* was present in previous mapping studies due to the paucity of marker saturation at the time (Feuerstein et al., 1990) and that resistance may have been contributed by *Rph11* (Martin et al., 2020).

Rph13 was identified in the experimental line PI531849, derived from a wild barley accession backcrossed to the British cultivar Berac (Martin et al., 2020). *Rph13* was confirmed to be distinct from *Rph1-12* (Jin et al., 1996) and mapped to a 1.1-Mb interval (591.73–592.81 Mb) (Jost et al., 2020). Additional loci mapping to chromosome 3H include *qRphFra-3H* (D., Singh et al., 2015), *Qlr.HeB-F23-3H* (Schnaithmann et al., 2014), *qGH_PBIC_3.86* (Dracatos et al., 2019b), and three unnamed QTL (Czembor et al., 2022; Hickey et al., 2011). Lastly, several QTL map to chromosome 3H but have been unanchored, including *Rphq17* and *Rphq20* (Marcel et al., 2007); *Rphq23* (Yeo et al., 2017); *QLr.S42-3H.a* (von Korff et al., 2005); and three unnamed QTL (Castro et al., 2012; Rossi et al., 2006; Thomas et al., 1995).

Chromosome 4H

Rph21 (*RphRic*) was identified in Ricardo (Sandhu et al., 2012), mapping to an 18.2-Mb interval (569.19–587.48 Mb). Unnamed QTL (Hickey et al., 2011) and *QPh.4H-1* and *QPh.4H-2* (Vatter et al., 2017) also map in close proximity to *Rph21*. *Rph27* identified in cultivar Quinn provides limited value, only being effective against two pathotypes. In addition, due to the fact that DArTseq markers without sequence or positions were utilized, *Rph27* was positioned using the gene *HORVU.MOREX.r3.4HG0331680* and the full-length cDNA clone AK250035.1 (Rothwell et al., 2020) to a 350-kb interval between 1.40 and 1.76 Mb. As 20 DArTseq markers were determined to be in complete linkage with *Rph27* (Rothwell et al., 2020), the *Rph27* region is most likely larger, and further high-resolution mapping will be required before validation. Additional loci mapping to chromosome 4H include *Qlr.HeB-5-4H* and

Qlr.HeB-F23-4H (Schnaithmann et al., 2014); *Rphq10* (Qi et al., 1999); *Rphq19* (Marcel et al., 2007); *Rphq20* (Marcel et al., 2008); and *QLr.S42-4H.a* (von Korff et al., 2005). Lastly, two loci map to chromosome 4H but remain unanchored in *Rphq5* (Qi et al., 1998) and *Rphq8* (Ziems et al., 2014).

Chromosome 5H

Rph2 (*RphQ*) was first identified in Halycon, Kaputar, and Q21861 (Borovkova et al., 1997; Park et al., 2003) and is currently delimited to a large 278-Mb interval (34.07–312.74 Mb) (Martin et al., 2020). Currently, there are at least 12 allelic variants of the *Rph2* locus present in at least 20 barley accessions (Table 2). However, as this locus is further refined, allelic variants may in fact be independent genes separating *Rph2* into multiple loci due to the paucity of markers and small population size. Due to the large interval currently encompassing *Rph2*, it may also correspond to *qField_PBIC_2018_rep1_11.79*, *qField_PBIC_2016_3.99*, *qField_PBIC_2018_rep2_17.45*, and *qGH_PBIC_9.67* (Dracatos et al., 2019b); *RphQ9* (Ziems et al., 2014); and two unnamed QTL (Czembor et al., 2022; Schnaithmann et al., 2014).

The *Rph9* locus identified in Ethiopian landrace HOR 2596 was designated after allelism tests with *Rph1-8* donor accessions (Tan, 1977). The *Rph12* locus was subsequently mapped to chromosome 5HL using Triumph and believed to be distinct from *Rph9* based on both different reaction types and segregation with allelism tests with HOR 2596 (*Rph9*) (Jin et al., 1993). However, using a population of 3,858 F_2 lines of Triumph × HOR 2596, no segregation could be identified and determined *Rph9* (*Rph9.i*) and *Rph12* (*Rph9.z*) to be allelic (Borovkova et al., 1998). *Rph12* has also been identified in Franklin and Tallon (Park et al., 2003). The cultivar Cantala was subsequently identified to have an additional allele of *Rph9* (*Rph9.am*) (Dracatos et al., 2014). The *Rph9/12* locus is delimited to a 7.5-Mb interval (532.57–540.07 Mb) using introgression mapping within Bowman (Martin et al., 2020).

Rph20 (*qRphFlag*) and *Rph24* (*qRphND*) were simultaneously mapped (Dracatos et al., 2021; Hickey et al., 2011); however, since intervals were not reported, determining the localization is troublesome. In addition, the DArT markers mapping *Rph20* do not have significant homology to chromosome 5H and align to chromosome 4H in all Morex assemblies (Mascher et al., 2017, 2021; Monat et al., 2019). However, using lower-quality BLAST hits, *Rph20* could be anchored to a 74.7-Mb interval (477.71–552.46 Mb) on chromosome 5H. *Rph20* is believed to have been sourced from *H. laevigatum* or Gull that is subsequently present in derived accession Vada (Golegaonkar et al., 2009; Hickey et al., 2011; Hickey et al., 2012) and previously mapped as *Rphq4* (Liu et al., 2011; Qi et al., 1998). Diagnostic markers developed to track *Rph20* (Dracatos et al., 2021), map to chromosome 4H in all Morex assemblies (Mascher et al., 2017, 2021; Monat et al., 2019), which also may explain the inability to locate markers used by Hickey et al. (2011). Whether this region is misassembled in all Morex versions or other phenomena have occurred, such as a translocation relative to Morex, should be investigated. Based on this current information, *Rph20* may also correspond to *QPh.5H-1* (Vatter et al., 2017), *RphQ10* (Ziems et al., 2014), and an unnamed QTL (Gutiérrez et al., 2015).

Rph25 (*RphFT*) was identified in the Chinese cultivar Fong Tein and Australian cultivar Yagan (Kavanagh et al., 2017). However, due to the use of reporting cM positions within a population and lack of sequence availability, *Rph25* cannot be anchored to the Morex assembly. *Rph28* (*RphHEB*) identified in wild barley was the most recently designated locus (Mehnaz et al., 2021a), mapping to an ~ 100-kb interval (562.28–562.92 Mb). *Rph28* was most likely previously identified as an unnamed QTL (Schnaithmann et al., 2014).

Chromosome 6H

Rph11 was mapped to a 9.7-Mb interval (542.55–552.27 Mb) using introgression mapping but may also be allelic to *Rph10* currently assigned to chromosome 3H (Martin et al., 2020), which was previously discussed. *Rph24* (*qRPhND*) was mapped to a large 351 Mb region (Hickey et al., 2011) and subsequently, a 7.9-Mb region (358.56–366.40 Mb) using DArT markers (Ziems et al., 2017). *Rph24* was also previously mapped as *Rphq3* (González et al., 2012); *QPh.6H-2* and *QPh.6H-3* (Vatter et al., 2017); *RphQ11* (Ziems et al., 2014); *qRphYer2-6H* (D., Singh et al., 2015); and multiple unnamed QTL (Castro et al., 2012; Czembor et al., 2022; González et al., 2012; Gutiérrez et al., 2015; Hickey et al., 2011; Qi et al., 1998; Ziems et al., 2014). Diagnostic markers targeting indels were subsequently developed to track *Rph24* (Dracatos et al., 2021) in close proximity to the distal flank of the 7.9 Mb region. However, the fact that three distinct loci, *QPh.6H-2*, *QPh.6H-3*, and *QPh.6H-4* (Sallam et al., 2017), were identified within the previously 351 Mb *Rph24* interval (Hickey et al., 2011), suggests there may be additional resistance loci along the chromosome. Further investigation will be required to determine the true number of resistance loci in the region. Additional loci mapping to chromosome 6H includes *QLr.S42-5H.a* (von Korff et al., 2005), *Rphq16* (Yeo et al., 2017), *QPh.6H-1* (Vatter et al., 2017), *qRphYer1-6H* (Singh et al., 2015), three unanchored QTL (Castro et al., 2012), and unanchored *Rphq15* (Marcel et al., 2007).

Chromosome 7H

The *Rph3* gene was first reported in the cultivar Aim and subsequently Estate (Henderson, 1945; Roane and Starling, 1967). *Rph3* was mapped to chromosome 7HL (Jin et al., 1993) and cloned as a small, unique, avirulence-dependent inducible membrane protein, reminiscent of TALE-activated executor resistance genes (Dinh et al., 2022). *Rph3* exhibits increased diversity in wild accessions compared to domesticated germplasm (Dinh et al., 2022), most likely due to *Rph3* being sourced from a wild accession. *Rph3* can confer a strong hypersensitive response or incomplete resistance in the cultivar Ribari and barley accession L94, respectively (Martin et al., 2020). *Rph19* was first identified in cultivar Prior, exhibiting the same resistance specificity as Reka 1 and mapped to a 2.8-Mb interval (618.14–620.92 Mb) (Park and

Karakousis, 2002). *Rph23* (*qRphYer-7H*) was identified within the Australian cultivar Yerong and believed to have originated from Russian landrace LV-Taganrog (D., Singh et al., 2015), mapping to a 14.9-Mb interval (25.49–40.36 Mb). Additional loci mapping to chromosome 7H include *Rphq1*, *Rphq8*, *Rphq9*, *Rphq13*, and *Rphx* (Qi et al., 1998); *RphP/RphQ15* (Park and Karakousis, 2002; Ziems et al., 2014); *RphQ2*, *RphQ12*, *RphQ13*, and *RphQ14* (Ziems et al., 2014); *QPh.7H-1*, *QPh.7H-2*, and *QPh.7H-3* (Vatter et al., 2017); *Qlr.HeB-F23-7H* (Schnaithmann et al., 2014); and *QLr.S42-7H.a* (von Korff et al., 2005). Furthermore, five unnamed QTL map to chromosome 7H (Czembor et al., 2022; Gutiérrez et al., 2015; Rossi et al., 2006; Thomas et al., 1995), and one unnamed QTL remains unanchored to chromosome 7H (Hickey et al., 2011).

Association mapping

There have been six association mapping studies identifying leaf rust loci. The first association mapping study was conducted on 360 elite barley lines from Australia. A total of 11 of the 15 reported QTL were previously identified loci and four deemed novel (Ziems et al., 2014). The second association mapping study was performed in the Halle Exotic Barley (HEB)-5 nested association mapping (NAM) panel (Schnaithmann et al., 2014). At the time, only one novel QTL was identified with remaining loci corresponding to previously characterized *Rph* loci (Schnaithmann et al., 2014). The third association mapping study was conducted in Latin American barley, identifying two novel QTL out of six loci detected (Gutiérrez et al., 2015). The fourth was conducted with the HEB-25 NAM panel, a significant expansion of the HEB-5 population, identifying a total of two novel loci out of 11 (Vatter et al., 2018). The fifth association mapping study identified six QTL (Czembor et al., 2022), with the most significant marker-trait association (MTA) mapping within 1.2 Mb of *RphQ11* identified on chromosome 6H (Ziems et al., 2014) and therefore is unlikely to be novel. The last association mapping conducted ASR and APR, claiming 58 MTA, 32 of which were novel. However, based on the low LOD thresholds utilized, it could be argued that all but seven of the MTA detected should be considered significant. In addition, these seven MTA are within a 7-Mb interval, suggesting all markers may form a single locus (Amouzoune et al., 2022).

Genetics to stem rust

The stem rust pathogen *Pgt* contains the largest host range within *Puccinia* with 28 hosts and is the primary cause of barley and wheat stem rust (Dracatos et al., 2015b). Stem rust is unique in that a barley-specific ff. spp. has not been identified. In addition, other ff. spp. are known to infect barley, including *Puccinia graminis* f. sp. *secalis* (*Pgs*), *Puccinia graminis* f. sp. *avenae* (*Pga*) (Brueggeman et al., 2020; Dracatos et al., 2015b), and a *Pgt* × *Pgs* hybrid known as Scabrum rust arising on triticale (Park, 2007). Barley stem rust epidemics in North America during the 1920s–1930s resulted in yield losses between 15% and 20% (Steffenson, 1992); however, 100% yield loss has been reported in wheat to the Digalu (*Pgt* race TKTTF) lineage (Singh et al., 2015). Due to the widespread deployment of *Rpg1*, barley stem rust epidemics were largely controlled until the late 1980s when *Pgt* race QCCJB overcame *Rpg1* (Sharma Poudel et al., 2018). In addition, the Ug99 (race TTKSK) lineage of *Pgt* isolates overcame *Sr31* in wheat and is seen as a major threat to global food security with 80%–95% of worldwide acreage of wheat considered susceptible (Singh et al., 2015). In addition, over 95% of barley cultivars and wild accessions surveyed are considered susceptible (Hatta et al., 2021; Prins et al., 2020; Steffenson et al., 2017). Due to effective resistance gene deployment and adequate disease management over the past 75 years, stem rust was not considered a major threat despite its enormous potential to devastate barley and wheat crops (Singh et al., 2011). The first reported epidemics in over 60 years in the UK and the first in decades across Germany and Sicily have caused devastating damage (Edae and Rouse, 2020; Lewis et al., 2018). Reports have also found *Pgt* isolates becoming more aggressive at both warmer and cooler temperatures (Lewis et al., 2018). Alarmingly, the first isolates with virulence on *Rpg1* and *rpg4/Rpg5* when stacked together in barley line Q21861 were recently reported in the Pacific Northwestern region of North America (Upadhaya et al., 2021).

Genetic studies describing stem rust resistance have been reported since the 1930s (Powers and Hines, 1933). Over 60 *Stem rust* (*Sr*) resistance loci have been designated within wheat, with at least nine identified and validated (Chen et al., 2018; Hatta et al., 2021). Multiple wheat stem rust resistance genes can remain functional in a susceptible barley background to provide resistance against *Pgt*. For example, the wheat genes *Sr22*, *Sr33*, *Sr35*, and *Sr45* all provide resistance to the *Pgt* race TTKSK when transformed into the susceptible barley background of Golden Promise (Hatta et al., 2021). In comparison, only nine *Reaction to Puccinia graminis* (*Rpg*, Table 3) loci have been identified within barley (Hatta et al., 2021). *Rpg1-rpg4*, *rpg6-Rpg7*, and *RpgU* were first identified against *Pgt*, whereas *Rpg5* and *rpgBH* were identified against *Pgs* (Zhou et al., 2014). The *RpgU* locus was identified in Peatland, Husky, and Diamond (Fox and Harder, 1995) and potentially SB90585 (Harder and Legge, 2000); however, the locus was never mapped. Based on segregation ratios, *RpgU* is not *Rpg1*, and most likely not *Rpg2* or *Rpg3* (Fox and Harder, 1995). However, further investigation is required to determine the location of *RpgU* and whether *RpgU* is allelic to any other *Rpg* loci. The recessive locus *rpgBH* was identified in Black Hulless, effective against *Pgs* (Steffenson et al., 1984). As allelism tests or mapping experiments have not been conducted, it cannot be ruled out that *rpgBH* is not a different and/or less effective allele of previously mapped *Rpg* loci. Up to two other loci were reported in Purple Nudum and Skinless (Babriwala, 1954; Luig, 1957), but were not investigated further. A total of nine loci were identified against *Pga* (*Rgpaq1-9*); however, only *Rpgaq7* and *Rpgaq9* did not colocalize with previously reported *Rpg* loci and were considered novel (Dracatos et al., 2016a). Lastly, a total of 17 *required for P. graminis resistance* (*rpr*) mutants have been obtained using fast neutron irradiation of Morex (*Rpr1-7*) and Q21861 (*Rpr8-17*), three of which have been mapped as *Rpr1*, *Rpr2*, and *Rpr9* (Gill et al., 2016; Solanki et al., 2019; Zhang et al., 2006).

TABLE 3 Summary information of all designated resistance/susceptibility loci in barley to stem rust pathogen *Puccinia graminis*.

Locus	Synonym	Alleles	Modifier[a]	Species	Accession	Stage	Chr.	Pos. (bp)	Mapping	Validation
Rpg1		*Rpg1.a*, *Rpg1.e*, *Rpg1.f*		*H. vulgare*	Morex, Q21861	ASR	7H	3,737,286–3,742,527	Powers and Hines (1933), Shands (1939), Steffenson (1992), Kilian et al. (1994), Kilian et al. (1995), Kilian et al. (1997), Mirlohi et al. (2008)	Brueggeman et al. (2002); Rostoks et al. (2004); Nirmala et al. (2006); Brueggeman et al. (2006)
Rpg2		*Rpg2.b*		*H. vulgare*	Hietpas-5	APR	2H	533,271,411–555,123,559	Patterson et al. (1957), Case et al. (2018a)	
Rpg3		*Rpg3.c*		*H. vulgare*	GAW-79	APR	5H	448,616,105–451,961,626	Jedel et al. (1989), Case et al. (2018a)	
rpg4/Rpg5	*rpg4*, *Rpg5*, *Rpg-TTKSK*, *RpgQ*, RMRL1	*rpg4.d*, *Rpg5.g*, *Rpg5Xx*		*H. vulgare*	Q21861	ASR	5H	562,864,623–562,924,851	Jin et al. (1994), Borovkova et al. (1995), Sun et al. (1996), Han et al. (1999), Steffenson et al. (2009), Moscou et al. (2011); Arora et al. (2013); Hernandez et al. (2019), Hernandez et al., (2020a)	Brueggeman et al. (2008); Wang et al. (2013)
rpg6		*rpg6.h*		*H. bulbosum*	212Y1	ASR	6H	76,567–25,545,426	Fetch et al. (2009); Turuspekov et al. (2016)	
Rpg7		*Rpg7.i*		*Hv. spontaneum*	WBDC094, WBDC238	ASR	3H	606,104,732–615,920,424	Sallam et al. (2017); Henningsen et al. (2021)	
rpgBH		N/A		*H. vulgare*	Black Hulless	ASR	N/A	N/A	Steffenson et al. (1984)	
RpgU		N/A		*H. vulgare*	Peatland	APR	N/A	N/A	Fox and Harder (1995), Harder and Legge (2000)	
Rrr1		N/A	*Rpg1*, *rpg4/Rpg5*	*H. vulgare*	Q21861	ASR	5H	560,962,951–561,491,740	Sharma Poudel et al. (2018)	
Rrr2		N/A	*Rpg1*	*H. vulgare*	Q21861	ASR	7H	6,199,573–6,872,945	Sharma Poudel et al. (2018)	
Rpr1		N/A	*Rpg1*	*H. vulgare*	Morex	ASR	4H	145,528,383–411,428,738	Zhang et al. (2006)	
Rpr2		N/A	*Rpg1*	*H. vulgare*	Morex	ASR	6H	68,281,626–111,536,027	Gill et al. (2016)	
Rpr9		N/A	*Rpg1*, *rpg4/Rpg5*	*H. vulgare*	Q21861	ASR	3H	502,399,383–503,169,804	Solanki et al. (2019)	
Rme1	RMRL2	N/A	*rpg4/Rpg5*	*H. vulgare*	Q21861	ASR	5H	562,972,164–562,986,906	Wang et al. (2013)	
Rme2	2H.16	N/A	*rpg4/Rpg5*	*H. vulgare*	SM89010	APR	2H	41,616,566–54,561,715	Moscou et al. (2011)	
QTL-SR		N/A		*H. vulgare*	Woodies	APR	5H	469,558,062–470,373,345	Hernandez et al. (2020a), Massman et al. (2024b)	

Information includes locus designations, synonyms and alleles, species and accessions, effective stages, chromosomal location, and relevant literature.
[a]Loci with entries are modifiers and/or required for the specific resistance locus to function.

Chromosome 1H

Currently, only association mapping studies have identified stem rust resistance loci on chromosome 1H. These include *Rpgaq1* (Dracatos et al., 2016a), *Rpg-qtl-1H-11_11277* and *Rpg-qtl-1H-12_20613* (Case et al., 2018b), and 10 unnamed QTL (Czembor et al., 2022; Sallam et al., 2017; Turuspekov et al., 2016). Current evidence suggests the 10 unnamed QTL do not overlap and therefore chromosome 1H may harbor untapped potential for stem rust resistance.

Chromosome 2H

Rpg2 was first described in Heitpas-5 (Patterson et al., 1957) and mapped within a 21.9-Mb interval (533.27–555.12 Mb) (Case et al., 2018a); however, it remains largely under investigation due to the low level of resistance it provides (Kleinhofs et al., 2009). Additionally, a *trans*-eQTL regulator hotspot was identified that results in the suppression of hundreds of genes after *Pgt* inoculation and is colocalized with an enhancer of *rpg4/Rpg5*-mediated resistance to *Pgt* race TTKSK at the adult stage (Moscou et al., 2011). Both the enhancer and regulator are hypothesized to be the same gene, and therefore for this manuscript, this locus has been designated *Rpg4-modifier element 2* (*Rme2*) and mapped to a 12.9-Mb interval (41.6–51.6 Mb). Additional loci mapping to chromosome 2H include *Rpg-qtl-PH-PI38-2H* (258.46–264.39 Mb) nested within *Rpg-qtl-HH-Hie-2H.1* (221.89–26830 Mb) (Case et al., 2018a) that was also identified with association mapping (Hernandez et al., 2020a). Other loci include *Rpg-qtl-HH-Hie-2H.2*, *Rpg-qtl-HH-Hie-2H.3*, and *Rpg-qtl-HH-Hie-2H.4* (Case et al., 2018a); *Rpg-qtl-2H-12_11278* (Case et al., 2018b); *Rpg-qtl-2H_SCRI_RS_115905* and *Rpg-qtl-2H_SCRI_RS_109266* (Mamo, 2013); *Rpgaq9* and unanchored *Rpgaq2* (Dracatos et al., 2016a); and nine unnamed QTL (Czembor et al., 2022; Sallam et al., 2017).

Chromosome 3H

Rpg7 is the most recently designated *Rpg* locus identified in wild barley accessions WBDC094 and WBDC238, mapping to a 9.8-Mb interval (606.10–615.92 Mb) (Henningsen et al., 2021). Association mapping identified the MTA *Rpg-qtl-3H_SCRI_RS_180847* approximately 0.98 Mb from the boundary of *Rpg7* (Mamo, 2013). *Rpr9*, which was a gene identified by mutant analysis of line Q21861, is required for both *Rpg1*- and *rpg4/Rpg5*-mediated resistance, and mapped to a 770-kb interval (502.40–503.17 Mb) (Solanki et al., 2019). *Rpr9* is hypothesized to function by facilitating ubiquitination and degradation of proteins required for resistance, based on previous research on *Rpg1* (Solanki et al., 2019). In addition, *rpr9* mutants resulted in a stunted root phenotype due to the hypothesis that *Rpr9* is involved in hormone signaling (Solanki et al., 2019). *Rpr9* appears to be encompassed by *Rpg-qtl-HH-Hip-3H* (Case et al., 2018a) and potentially mapped in association mapping (Czembor et al., 2022). Additional loci mapping to chromosome 3H include *Rpg-qtl-PH-Hip-3H* and *Rpg-qtl-HH-Hip-3H* (Case et al., 2018a); *Rpg-qtl-3H-SCRI_RS_199887* (Case et al., 2018b); and *qGH_PBIC_3.11* (Dracatos et al., 2019b). A total of 11 unnamed QTL have also been mapped to chromosome 3H (Hernandez et al., 2020a; Mamo et al., 2014; Sallam et al., 2017; Turuspekov et al., 2016), whereas *Rpgaq6* remains unanchored (Dracatos et al., 2016a). *Rpg-qtl-PH-Hip-3H* and *Rpg-qtl-HH-Hip-3H* show partial overlap and encompass six MTA identified via association mapping (Czembor et al., 2022; Mamo et al., 2014; Sallam et al., 2017), suggesting less unique loci on chromosome 3H and will require further investigation.

Chromosome 4H

The *Rpr1* locus was mapped to a 265.9-Mb interval (145.53–411.43 Mb) in the Morex V3 genome (Zhang et al., 2006). *Rpr1* was identified as a suppressor of *Rpg1* and therefore required for *Rpg1*-mediated resistance; however, *Rpr1* is not involved in *rpg4/Rpg5*-mediated resistance (Zhang et al., 2006). Six MTA were reported within the *Rpr1* region using association mapping (Sallam et al., 2017; Turuspekov et al., 2016); however, considering the size of the *Rpr1* region, it may encompass different resistance loci. Additional loci mapped to chromosome 4H include *Rpg-qtl-PH-PI38-4H*, *Rpg-qtl-HH-Hie-4H* (Case et al., 2018a), *Rpg-qtl-4H_12_30995* (Mamo, 2013), seven MTA that most likely form a single QTL based on cM positions (Sallam et al., 2017), and a further four unnamed QTL (Czembor et al., 2022; Turuspekov et al., 2016).

Chromosome 5H

Rpg3 was first reported in GAW-79 (Jedel et al., 1989) and mapped to chromosome 5H (Case et al., 2018a). Using markers reported to be significant, *Rpg3* maps to a 323.5-Mb interval (94.22–417.72 Mb) using Morex V3. However, these significant markers are not present within the linkage map reported. Utilizing the genetic marker information of the map, *Rpg3* maps to a 2.3-Mb interval (448.62–450.88 Mb) (Case et al., 2018a), outside of the original *Rpg3* interval. *Rpg3* is more likely to be located within the 2.3-Mb interval based on *Rpg3* being localized to chromosome 5HL and the higher-quality genome assembly of Morex V3. However, as *Rpg3* remains under investigated due to low-level resistance (Kleinhofs et al., 2009), this discrepancy should be addressed for both tracking *Rpg3* for breeding purposes and future validation.

The *rpg4* locus was first identified as providing resistance to *Pgt* isolates, whereas *Rpg5* provided resistance to *Pgs* isolates and later *Pga* isolates (Dracatos et al., 2015b; Sun et al., 1996; Sun and Steffenson, 2005). The *rpg4* gene was originally suspected as *HvAdf2* (Brueggeman et al., 2009; Kleinhofs et al., 2009), whereas the *Rpg5* gene was validated as *HvRga2*, encoding an NLR with an integrated protein kinase (functional haplotype) or protein phosphatase 2C domain (PP2C, nonfunctional haplotype) (Brueggeman et al., 2008). However, increasing evidence found that *rpg4*-mediated resistance was not a result of *HvAdf2* and required *Rpg5* (*HvRga2*) and two additional genes located at the locus, *HvRga1* and *HvAdf3*, to be functional (Arora et al., 2013;

Wang et al., 2013). The *HvAdf3* gene within the locus was also deemed to be a candidate susceptibility gene (Moscou et al., 2011). Therefore, the *rpg4/Rpg5* complex was renamed to the *rpg4*-Mediated Resistance Locus (RMRL) that includes RMRL1 containing *HvRga1*, *Rpg5* (*HvRga2*), and *HvAdf3*; and RMRL2 containing the yet unidentified *Rpg4-modifier element 1* (*Rme1*), which is required for *rpg4*-mediated *wheat* stem rust resistance but not required for *Rpg5*-mediated *rye* stem rust resistance (Wang et al., 2013). RPG5 (HvRGA2) and HvRGA1 belong to MIC1 (C16) and C7 clades, respectively (Bailey et al., 2018). NLRs in the MIC1 and C7 clades were found to be in head-to-head orientation in grasses such as the paired NLRs RGA5/RGA4 in rice that confer resistance to *M. oryzae* through recognition of the effectors AVR-Pia and AVR1-CO39 (Bailey et al., 2018; Cesari et al., 2013). The MIC1 clade is unique in the grasses, as NLRs in the clade have diverse C-terminal integrated domains with RGA5 carrying an integrated heavy metal-associated domain (Bailey et al., 2018; Cesari et al., 2013).

Using six highly diverse barley accessions, only one allele of *rpg4/Rpg5* was identified, suggesting cultivated barley could be extremely vulnerable to a lack of diversity at *rpg4/Rpg5* (Mamo et al., 2014). In addition, the *rpg4/Rpg5* complex was found to be present in nearly every resistant landrace from Switzerland when assessing resistance to *Pgt* races TTKSK and QCCJB (Steffenson et al., 2016). Additional studies mapped *rpg4/Rpg5* using association mapping, identifying a novel allele of *rpg4/Rpg5* designated *Rpg5Xx* (Hernandez et al., 2019, 2020a). Previous work found that the region containing *Rme1* is approximately 220 kb in size, proximal to RMRL1, containing a heat shock protein, a zinc finger SEC14 protein, and an actin depolymerization-like protein (*HvAdf1*) (Wang et al., 2013). Further investigation into the Morex V3 found that *Rme1* encompasses 321 kb. Leaf-expressed candidate genes include those previously identified as well as a PP2C protein. Further work is needed to establish sequence and structural variation within the *Rme1* region relative to diverse barley accessions.

The *rpg4/Rpg5* locus was the only locus to provide resistance to *Pgt* race TTKSK in barley (Brueggeman et al., 2009); however, an additional locus, required for *rpg4*-mediated resistance 1 (*Rrr1*), is required to facilitate *rpg4/Rpg5*-mediated resistance when stacked with *Rpg1* (Sharma Poudel et al., 2018). The *Rrr1* locus was mapped to a 529-kb interval (560.96–561.49 Mb) on chromosome 5H (Sharma Poudel et al., 2018). Similar phenomena were observed with *Rpr9* (required for *Rpg1*- and *rpg4/Rpg5*-mediated resistance) described earlier on chromosome 3H (Solanki et al., 2019), and the identification of two novel loci on chromosomes 5H (not *Rrr1*) and 7H that were additive to *Rpg4/Rpg5* resistance, i.e., *rpg4/Rpg5* is required for resistance but not sufficient (Hernandez et al., 2019). These complex interactions have made the introgression of *rpg4/Rpg5*-mediated resistance to elite cultivars more complicated than originally anticipated (Hernandez et al., 2019).

For further complexity, the recently released Woodies germplasm (Woody-1, DH160733 and Woody-2, DH160754) designed to systematically stack stripe and stem rust resistance have a null allele of *Rpg5*, yet remain highly resistant to stem rust (Hernandez et al., 2020a, b; Massman et al., 2024a). The high level of resistance present in the Woodies has been attributed to the *QTL-SR* locus, encompassing a 1.8-Mb region (469.6–470.4 Mb) in close vicinity to the *rpg4/Rpg5* complex (Massman et al., 2024b). Candidate gene analysis of the Morex V3 region revealed 10 candidate genes within the region of interest, and a further three NLR genes within 10 Mb that may underlie *QTL-SR* due to structural rearrangements. Further comparative analysis revealed that large regions of Morex are absent from the Woody-1 genome assembly (Massman et al., 2024b). Therefore, instead, the Woodies may lack a susceptibility gene that is present in the susceptible barley accession Morex. The identification of this novel locus further complicates the resistance puzzle; however, Woody-2 has been identified to be highly amenable to transformation, which will aid in gene validation.

Additional loci mapping to chromosome 5H include *Rpg-qtl-PH-PI38-5H* (Case et al., 2018a), *Rpg-qtl-5H-11_11355* (Case et al., 2018b; Zhou et al., 2014), *Rpg-qtl-5H-SCRI_RS_10929* (Mamo, 2013), and three unnamed QTL (Czembor et al., 2022; Sallam et al., 2017). Multiple MTA are deemed to delimit *Rpg-qtl-5H-11_11355* as a QTL due to linkage disequilibrium (Case et al., 2018b; Zhou et al., 2014) and were also mapped in earlier and subsequent association mapping studies (Hernandez et al., 2020a; Mamo, 2013). The boundary of *Rpg-qtl-5H-11_11355* is approximately 14 Mb distal to *Rpg3* and therefore is likely to be a distinct locus.

Chromosome 6H

The *rpg6* locus is the only locus identified within *H. bulbosum* to stem rust, providing recessive resistance (Fetch et al., 2009) and located within a 25.5-Mb interval (0.08–25.55 Mb). The *rpg6* locus has also been mapped in three association mapping studies (Czembor et al., 2022; Sallam et al., 2017; Turuspekov et al., 2016). *Rpr2* mapped to a 43.3-Mb (68.28–111.54 Mb) interval and hypothesized to function as a stabilizer of *Rpg1*, as the RPG1 protein was degraded faster than that of highly resistant stem rust-resistant lines (Gill et al., 2016). An MTA embedded within the *Rpr2* interval was also reported in association mapping (Czembor et al., 2022). Additional loci that map to chromosome 6H include a further eight unnamed QTL (Czembor et al., 2022; Sallam et al., 2017), eight MTA that most likely form a single QTL (Turuspekov et al., 2016), and unanchored *Rpgaq3, Rpgaq7*, and *Rpgaq8* (Dracatos et al., 2016a).

Chromosome 7H

Rpg1 was the first *Rpg* locus identified and provided durable, broad-spectrum resistance to *Pgt* against all North American *Pgt* isolates for approximately 70 years (Roelfs et al., 1993). *Rpg1* was first reported in 1933, with sources found in Peatland, Chevron, and Kindred (Powers and Hines, 1933; Shands, 1939; Steffenson, 1992). Cloning of *Rpg1* identified a gene encoding a protein with two tandem serine/threonine protein kinase domains (Brueggeman et al., 2002, 2006) located at 3.74 Mb. Transcript analysis found that *Rpg1* has the highest expression in leaf epidermal cells (Rostoks

et al., 2004) and is predominantly located in the cytosol (Nirmala et al., 2006). Both protein kinase domains are required for resistance; however, the second kinase domain is required for autophosphorylation (Nirmala et al., 2006). In addition, two effectors are required for autophosphorylation with RIN4, and subsequent degradation of RPG1 is required for resistance (Chai et al., 2012; Gill et al., 2012; Horvath et al., 2003; Nirmala et al., 2007, 2010, 2011). Either *Rrr1* or another locus designated required for *Rpg1*-mediated resistance 2 (*Rrr2*) is required for *Rpg1*-mediated resistance in the presence of *rpg4/Rpg5* (Sharma Poudel et al., 2018). *Rrr2* was mapped to a 673-kb interval (6.20–6.87 Mb) (Sharma Poudel et al., 2018), but is not the 7H locus reported by Hernandez et al. (2019). Additional loci mapping to chromosome 7H include *Rpg-qtl-PH-PI38-7H* and *Rpg-qtl-HH-Hie-7H* (Case et al., 2018a); *qGH_BPIC_4.6* (Dracatos et al., 2019b); 19 unnamed QTL (Czembor et al., 2022; Hernandez et al., 2020a; Sallam et al., 2017; Zhou et al., 2014); and unanchored *Rpgaq4* and *Rpgaq5* (Dracatos et al., 2016a).

Association mapping

To date, there have been eight association mapping studies used to characterize stem rust resistance. The first identified up to 15 MTAs in wild barley, two of which were associated with *rpg4/Rpg5* (Steffenson et al., 2007). The second association mapping study was conducted in US breeding material against *Pgt* race TTKSK effectively identifying two novel QTL on chromosomes 5H and 7H, respectively (Zhou et al., 2014). These were both mapped again in subsequent association mapping studies (Case et al., 2018b; Hernandez et al., 2020a). In the third association mapping study, 17 MTAs were reported using Kazakh spring barley in two environments (Turuspekov et al., 2016). However, one marker misassigned to chromosome 2H and four markers assigned to unknown chromosomal loci can be consolidated with other MTAs into a total of eight distinct loci. After consolidating these loci, only markers located at the proximal end of chromosome 6H colocalize with the previously identified locus *rpg6* (Fetch et al., 2009). While the other loci can be deemed novel within stem rust, four colocalize with the leaf rust resistance loci *Rph13*, *Rph20*, *Rph21*, and *Rph26*. The fourth association mapping study was conducted in wild barley, identifying 45 MTAs, many of which were novel at the time (Sallam et al., 2017). The fifth association mapping study identified seven QTL from the barley core collection; one locus of notable interest was on chromosome 5H, as it provided APR not conferred by the *rpg4/Rpg5* complex (Case et al., 2018b). The sixth and seventh association mapping studies were conducted on a double haploid population designed to increase resistance to stem rust race TTKSK (Hernandez et al., 2019, 2020a). These association mapping studies identified eight and six MTAs, respectively (Hernandez et al., 2019, 2020a), none of which were claimed to be novel; however, a new allele of *rpg4/Rpg5* was identified as *Rpg5Xx* (Hernandez et al., 2020a). The last association mapping study identified 48 significant MTAs using European barley accessions (Czembor et al., 2022).

Genetics to stripe rust

Barley stripe rust is predominantly caused by *Psh*; however, barley can also be infected by *P. striiformis* f. sp. *tritici* (*Pst*), the causal agent of wheat stripe rust. Yield losses exceeding 70% have been reported but typically cause approximately 40% yield loss under environmental conditions conducive to disease in a susceptible variety (Marshall and Sutton, 1995). *Psh* is therefore potentially the most damaging rust, despite arguably being the most understudied of the three major barley rusts. Barley stripe rust was first described by European workers in the late 1800s, causing particular issues in winter barley in the UK and the Netherlands (Wellings, 2011). Subsequently, *Psh* was first reported in Columbia in 1975, spreading throughout South America by 1982 (Dubin and Stubbs, 1986), Mexico by 1987, and in the USA by 1991 (Chen et al., 1995; Marshall and Sutton, 1995). Due to stripe rust prevalence in colder, wetter climates, often at higher altitudes, stripe rust is often regarded as cold-temperature rust (Dracatos et al., 2019b). Around 88% of worldwide wheat production is susceptible to stripe rust (Beddow et al., 2015) and is considered a major pathogen of barley, with 60%–70% of Australian barley considered susceptible (Dracatos et al., 2019b; Gyawali et al., 2021).

The genetics of stripe rust resistance have been studied since the 1940s (Murty, 1942). To date, there are 78 *Yellow rust* (*Yr*) loci (Jamil et al., 2020) and at least 50 *Resistance to Puccinia striiformis* (*Rps*; Table 4) loci identified in wheat and barley, respectively (Bettgenhaeuser et al., 2021; Chełkowski et al., 2003; Chen and Line, 1999, 2001, 2003; Nover and Scholz, 1969; Pahalawatta and Chen, 2005). However, only 10 *Rps* loci have been formally designated within the barley-*P. striiformis* pathosystem (Clare et al., 2016), and even fewer have been mapped. Earlier mapping efforts made use of restriction fragment length polymorphisms, simple sequence repeats, amplified fragment length polymorphisms, and resistance gene analog polymorphisms, which make anchoring loci to the Morex V3 troublesome (Castro et al., 2002, 2003a, 2003b; Chen et al., 1994; Thomas et al., 1995; Toojinda et al., 1998, 2000; Vales et al., 2005).

Another caveat is that these loci are functional against *P. striiformis sensu lato*, meaning they can function against both or only *Psh* or *Pst* isolates. The first four *Rps* loci were originally designated *Yr* loci; however, *Rps4* has only been associated with chromosome 1H, and *rps3* was never mapped (Johnson, 1968; Nover and Scholz, 1969). In addition, *Yr4* through *Yr13* were identified in India but were not consistent with international nomenclature (Verma et al., 2018). There were also at least eight additional loci with *Puccinia striiformis* (*Ps*) nomenclature (Chen and Line, 1999; Luthra and Chopra, 1990). Many of the original *Rps* loci function under a recessive mode of inheritance, with only five out of 26 under a dominant mode of inheritance (Chełkowski et al., 2003; Chen and Line, 1999). The first loci identified to govern nonadapted resistance to *Pst* were *RpstS1* and *RpstS2* in Steptoe (Pahalawatta and Chen, 2005). More recently, nonadapted resistance to *Pst* has seen a renewed research focus with the mapping of *Rps6* (Dawson et al., 2016; Li et al., 2016) and subsequent cloning of *Rps7* and *Rps8* (Bettgenhaeuser et al., 2021; Holden et al., 2022).

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TABLE 4 Summary information of all designated resistance/susceptibility loci in barley to stripe rust pathogen *Puccinia striiformis*.

Locus	Synonym	Alleles[a]	Species	Donor	Stage	Chr	Pos. [bp]	Mapping	Validation
rps1	*yr*	*rps1.a*, *rps1.b*, *rps1.c*	*H. vulgare*	Abyssinian 14, BBA2890, Bigo, HOR2926, Mazurka	ASR	3H	~ 578,337,609	Chen and Line (2001); Yan and Chen (2007a)	
rps2	*yr2*	N/A	*H. vulgare*	Abed Binder 12	ASR	2H	658,698,853–662,067,020	Nover and Scholz (1969), Dawson (2015)	
rps3	*yr3*	N/A	*H. vulgare*	I5	ASR	N/A	N/A	Nover and Scholz (1969)	
Rps4	*Yr4*	*Rps4.d*	*H. vulgare*	Cambrinus, Heils Franken, Astrix, Deba Abed, Europa	ASR	1H	N/A	Nover and Scholz (1969), Johnson and Finch (1976)	
rps5	*rpsGZ*	N/A	*H. vulgare*	Grannelose Zweizeilige	ASR	4H	587,747,633–591,696,752	Yan and Chen (2006); Esvelt Klos et al. (2016)	
Rps6	*Rpst2*, *YrpstY1*	*Rps6.i*	*H. vulgare*, *Hv. spontaneum*	Abed Binder 12, PI 466050, Bowman, Baronesse, Golden Promise, Tamalpais, Y12	ASR	7H	613,769,487–613,932,998	Dawson et al (2016); Li et al. (2016); Bettgenhaeuser et al. (2021)	
Rps7	*Rpst1*	*Rps7.a*, *Rps7.b*, *rps7*	*H. vulgare*	CI 16153, Golden Promise	ASR	1H	9,126,973–9,294,177	Bettgenhaeuser et al. (2021)	Bettgenhaeuser et al. (2021)
Rps8	*Rpst3*	*Exo.a-Pur1.a (Rps8)*, *Exo.a-Pur1.r (rps8)*, *Exo.a-Pur1.s (rps8)*, *Exo.a-Pur1.t (rps8)*, *Exo.b-Pur1.a (rps8)*, *Exo.c-Pur1.b*, *Exo.c-Pur1.d*, *Exo.c-Pur1.l*, *Exo.c-Pur1.n*, *Exo.d-Pur1.a (rps8)*, *Exo.d-Pur1.m*, *Exo.e-Pur1.b*, *Exo.e-Pur1.g*, *Exo.f-Pur1.b*, *Exo.f-Pur1.p*, *Exo.g-Pur1.c (Rps8)*, *Exo.h-Pur1.e*, *Exo.i-Pur1.f*, *Exo.j-Pur1.h*, *Exo.k-Pur1.i*, *Exo.l-Pur1.j*, *Exo.m-Pur1.k*, *Exo.n-Pur1.c*, *Exo.o-Pur1.o*, *Exo.p-Pur1.q (Rps8)*, *Exo.q-Pur1.a (rps8)*, *Deletion (rps8)*	*H. vulgare*	Abed Binder 12, Baronesse, Duplex, Golden Promise, HOR1428, Morex, Sultan 5, Baronesse	ASR	4H	579,763,645–579,928,699	Bettgenhaeuser et al. (2021)	Holden et al. (2022)
Rps9	*RpstHOR1428-2*, *RpsHOR1428-5H*	N/A	*H. vulgare*	HOR1428	ASR	5H	533,163,089–544,701,772	Clare et al. (2016)	
Rps10		N/A	*H. vulgare*	WBDC085	ASR	5H	554,804,523–570,835,138	Clare (2016)	
Rpsx		N/A	*H. vulgare*	CI10587	ASR	7H	597,285,158–611,723,570	Castro et al (2003a)	

Information includes locus designations, synonyms and alleles, species and accessions, effective stages, chromosomal location, and relevant literature.
[a]*Rps8* loci are currently listed as a two-gene complex with *Rps8* as functional alleles, *rps8* as nonfunctional alleles, and blank as undetermined.

Chromosome 1H

Rps7 was the first *Rps* gene to be identified and validated within the barley-*P. striiformis* pathosystem (Bettgenhaeuser et al., 2021). *Rps7* encodes an NLR that was previously identified as the barley immune receptor *Mildew locus a* (*Mla*), conferring resistance to *Blumeria graminis* f. sp. *hordei*, and *M. oryzae* (Brabham et al., 2023; Inukai et al., 2006), and susceptibility to *Cochliobolus sativus* (Leng et al., 2018). The authors warned that due to different haplotypes of *Mla* providing different specificities, often to different pathogens, breeders should be careful not to inadvertently remove resistance to nonadapted pathogens (Bettgenhaeuser et al., 2021). *Rps7* was also mapped as *QPsh-DP-2R-1.1* and *QPsh-rM-6R-1.1* (Gyawali et al., 2021); *qGH_WUR_rep1_3.26* and *qGH_WUR_rep2_5.78* (Dracatos et al., 2019b); *RPsh-1H* (Belcher et al., 2018); and unnamed QTL (Hernandez et al., 2020a). The genetic mapping of *Rps4* using protein and phenotypic markers placed the gene ~ 6.2 cM proximal to *Mla* (Johnson et al., 1969). Additional loci mapping to chromosome 1H include *qField_Mex2015_3.30* and *qGH_PBIC_5.29* (against *Psph*, Dracatos et al., 2019b); *QPsh-r24-6R-1.1*, *QPsh-rQ-6R-1.2*, *QPsh-r24-6R-1.2*, and *QPsh-DP-2R-1.2* (Gyawali et al., 2021); *QPs.1H-1* (Vatter et al., 2018); *QPsh.FW6-1H* (Belcher et al., 2018); and two unnamed QTL (Belcher et al., 2018; Dracatos et al., 2016b). Furthermore, eight unnamed unanchored MTA/QTL are present on chromosome 1H (Thomas et al., 1995; Visioni et al., 2018).

Chromosome 2H

The *rps2* locus was originally identified as a recessive resistance locus against *Psh* in Abed Binder 12 (Nover and Scholz, 1969); however, it is currently only one of two *Rps* loci to be functional against *Psh* and *Pst*. Subsequent high-resolution mapping determined that *rps2* was additive rather than completely recessive and localizing to a 3.4-Mb (658.7–662.1 Mb) interval (Dawson, 2015). Additional loci mapping to chromosome 2H include *QPs.2H-1*, *QPs.2H-2*, and *QPs.2H-3* (Vatter et al., 2018); *Qpsh.316A.2Ha* and *Qpsh.316A.2Hb* (Esvelt Klos et al., 2020); *QPsh-rQ-6R-2.1*, *QPsh-r7S0-2R-2.1*, *QPsh-DP-6R-2.1*, *QPsh-DP-6R-2.2*, and *QPsh-DP-2R-2.1* (Gyawali et al., 2021); *qField_Mex2015_5.13*, *qField_Mex2015_5.30*, and *qField_Ecuad2017_3.97* (Dracatos et al., 2019b); and *QPsh.FW6-2H.1* (Belcher et al., 2018). Furthermore, a total of four unnamed QTL from 10 MTA (Belcher et al., 2018) and three unnamed QTL (Dracatos et al., 2016b; Gutiérrez et al., 2015) were mapped to chromosome 2H, while 15 MTA/QTL remain unanchored (Rao et al., 2007; Rossi et al., 2006; Visioni et al., 2018).

Chromosome 3H

The recessive *rps1* resistance locus was identified in Bigo and Abyssinian 14 and mapped in BBA2890 using resistance gene analog polymorphisms (RGAP); however, due to the use of these markers, an interval cannot be reported (Nover and Scholz, 1969; Yan and Chen, 2007a). One marker used to track *rps1* places the causal gene in the vicinity of 578.33 Mb (Yan and Chen, 2007b). Loci with markers in close proximity to *rps1* have included *Qpsh.316A.3H* (Esvelt Klos et al., 2020); *RPsh-3H*, *QPsh.FW6-3H.2*, and two unnamed QTL (Belcher et al., 2018); *QPs.3H-2* and *QPs.3H-3* (Vatter et al., 2018); and *QPsh-rQ-6R-3.1* (Gyawali et al., 2021). Additional loci mapping to chromosome 3H include *QPsh-rQ-2R-3.1*, *QPsh.FW6-3H.1*, *QPsh-r7S0-6R-3.1*, *QPsh-DP-6R-3.1*, and *QPsh-r57-2R-3.1* (Gyawali et al., 2021); *QPs.3H-1* and *QPs.3H-4* (Vatter et al., 2018); *RpsHOR1428-3H*, also mapped by association mapping (Clare, 2016; Gutiérrez et al., 2015); and *qGH_PBIC_3.14* (Dracatos et al., 2019b). A further three unnamed QTL were mapped to chromosome 3H (Belcher et al., 2018; Gutiérrez et al., 2015), while 11 MTA/QTL remain unanchored (Rao et al., 2007; Rossi et al., 2006; Visioni et al., 2018).

Chromosome 4H

The rps5 (*rpsGZ*) locus identified in Grannenlose Zweizeilige was mapped to chromosome 4H using RGAPs (Yan and Chen, 2006) and subsequently to a 3.9-Mb interval (587.75–591.70 Mb) (Esvelt Klos et al., 2016). The nonadapted *Rps8* resistance locus, functional against *Pst*, was the second validated *Rps* locus as a two-gene complex encoding a receptor kinase and an Exo70. Both the receptor kinase and Exo70 are required for resistance (Holden et al., 2022) and are located within a 170-kb interval (579.76–579.92 Mb). Due to the two-gene complex of *Rps8*, there are at least 27 unique alleles/haplotypes currently reported (Holden et al., 2022). *Rps8* was first mapped by Bettgenhaeuser et al. (2021); however, it was also most likely mapped with association mapping as *QPsh-rQ-2R-4.1* and *QPsh-rM-6R-4.1* (Gyawali et al., 2021) and an unnamed MTA (Hernandez et al., 2020a). Additional loci mapping to chromosome 4H include *QPsh-r57-6R-4.1*, *QPsh-r57-6R-4.2*, *QPsh-r57-6R-4.3* *QPsh-rG-2R-4.1*, *QPsh-rG-2R-4.2*, *QPsh-DP-6R-4.1*, *QPsh-DP-6R-4.2*, *QPsh-r7S0-2R-4.1*, *QPsh-r7S0-6R-4.1*, and *QPsh-rG-2R-4.3* (Gyawali et al., 2021); *Qpsh4Ha* and *Qpsh4Hb* (Esvelt Klos et al., 2020); and *qGH_WUR_rep1_3.86* and *qGH_WUR_rep2_3.28* (Dracatos et al., 2019b). A further three unnamed QTL (Belcher et al., 2018; Dracatos et al., 2016b; Gutiérrez et al., 2015) and 10 unanchored MTA/QTL (Rao et al., 2007; Rossi et al., 2006; Visioni et al., 2018) are mapped to chromosome 4H.

Chromosome 5H

The final two most recently designated nonadapted resistance loci are *Rps9* and *Rps10*. *Rps9* was identified as the second locus functional against *Psh* and *Pst*, utilizing a backcrossing scheme to isolate the locus from HOR 1428 in a Manchuria background and delimited to an 11.5-Mb interval (533.16–544.07 Mb) (Clare et al., 2016). *Rps9* has also been identified as *QPs.5H-1* (Vatter et al., 2018), *QPsh-r57-2R-5.1* (Gyawali et al., 2021), and an unnamed QTL (Gutiérrez et al., 2015). The same strategy was used to isolate *Rps10*, functional against *Pst*, from WBDC085. A marker in complete coupling with *Rps10* was not found; however, using the

two peak markers at the BC_2 and BC_2F_2 stages, *Rps10* maps to a 16-Mb interval (554.80–570.84 Mb) (Clare, 2016). *Rps10* was also mapped as *QPsh-DP-2R-5.1* and *QPsh-DP-2R-5.2* (Gyawali et al., 2021) and in close proximity to *QPsh.FW6-5H.2* (Belcher et al., 2018) and *QPsh-rM-6R-5.1* (Gyawali et al., 2021; Vatter et al., 2018) on the proximal flank and *QPsh-r24-6R-5.2*, *QPsh-DP-2R-5.3*, *QPsh-rG-6R-5.2*, and *QPsh-rG-2R-5.1* (Gyawali et al., 2021) on the distal flank. Additional loci were mapped to chromosome 5H including the following: *QPsh-rG-6R-5.1*, *QPsh-r24-6R-5.1*, *QPsh-r7S0-6R-5.1*, *QPsh-rM/Q-2R-5.1*, *QPsh-rM/Q-2R-5.2*, *QPsh-rM-2R-5.1*, and *QPsh-r24-2R-5.1* (Gyawali et al., 2021); *QPsh.FW6-5H.1*, *QPsh.FW6-5H.3*, six MTA most likely forming a single unnamed QTL, and another MTA (Belcher et al., 2018); one unnamed MTA (Hernandez et al., 2020a); *qGH_PBIC_4.26* effective against *Psph* (Dracatos et al., 2019b); *Qpsh.316A.5H* (Esvelt Klos et al., 2020); five MTA that may form a single QTL (Dracatos et al., 2016b); and 14 unanchored MTA/QTL (Rao et al., 2007; Thomas et al., 1995; Visioni et al., 2018).

Chromosome 6H

Currently, only association mapping studies have identified stripe rust resistance loci on chromosome 6H. These include *QPsh-rM-6R-6.1*, *QPsh-rM-6R-6.2*, *QPsh-rM-6R-6.3*, *QPsh.FW6-6H.4*, *QPsh-r57-6R-6.2*, *QPsh-DP-6R-6.1*, *QPsh-r7S0-6R-6.1*, *QPsh-r7S0-6R-6.2*, *QPsh-r7S0-6R-6.3*, *QPsh-r7S0-6R-6.4*, *QPsh-r24/57-6R-6.1*, *QPsh-rQ-6R-6.1* (Gyawali et al., 2021), *QPsh.FW6-6H.1*, *QPsh.FW6-6H.2*, *QPsh.FW6-6H.3*, one unnamed QTL (Belcher et al., 2018), *Qpsh6H* (Esvelt Klos et al., 2016), *Qpsh.316A.6H* (Esvelt Klos et al., 2020), and *QPs.6H-1* (Vatter et al., 2018). Furthermore, seven MTA/QTL remain unanchored to chromosome 6H (Rao et al., 2007; Rossi et al., 2006; Visioni et al., 2018).

Chromosome 7H

Rps6 is functional only against *Pst* and was concurrently high-resolution mapped by two independent studies to a 267.6-kb (613.67–613.94 Mb) and 163.5-kb (613.77–613.93 Mb) interval (Dawson et al., 2016; Li et al., 2016). *Rps6* was mapped in wild barley accessions and the German barley accession Abed Binder 12 (Dawson et al., 2016; Li et al., 2016) and potentially mapped in Franklin (Dracatos et al., 2016b). *Rps6* was also identified using association mapping (Dracatos et al., 2016b; Gutiérrez et al., 2015). *Rpsx* was mapped to a 14.4-Mb (597.28–611.72 Mb) interval using CI10587 (Castro et al., 2003a). *Rpsx* has also been mapped as *QPsh.FW6-7H* (Belcher et al., 2018), two unnamed MTA forming a single QTL (Dracatos et al., 2016b), *qGH_PBIC_4.51* against *Psph* (Dracatos et al., 2019b) and *QPs.7H-1* (Vatter et al., 2018). Additional loci mapped to chromosome 7H include *QPsh-r24/G-2R-7.1*, *QPsh-r24-2R-7.2*, *QPsh-rQ-6R-7.1*, *QPsh-r57-2R-7.1*, *QPsh-r7S0-2R-7.2*, *QPsh-rG-6R-7.1*, and *QPsh-rG-6R-7.2* (Gyawali et al., 2021); *Rpsh-7H* (Belcher et al., 2018); *Qphs7H* (Esvelt Klos et al., 2016); and *Qpsh.316A.7H* (Esvelt Klos et al., 2020). A single unnamed QTL also maps to chromosome 4H (Gutiérrez et al., 2015), whereas a further 10 MTA/QTL (Rao et al., 2007; Rossi et al., 2006; Visioni et al., 2018) remain unanchored to chromosome 4H.

Association mapping

To date, six association mapping studies have been used to characterize resistance to stripe rust in barley. The first used a Latin American barley population and identified a total of seven QTL, three of which were deemed novel (Gutiérrez et al., 2015). The second study, using the HEB-25 NAM panel, identified eight novel loci out of the 12 identified (Vatter et al., 2018). The third association study assessed Oregon and Minnesotan breeding material, identifying three ASR and 14 APR QTL, respectively, five of which were novel (Belcher et al., 2018). The fourth study assessed a global population of 261 barley accessions identifying 45 ASR and 18 APR QTL (Visioni et al., 2018); however, this cannot be verified as the DaRTseq markers could not be anchored to the Morex genome. The fifth study identified four QTL, none of which were novel; however, one locus was mapped for both stem and stripe rust (Hernandez et al., 2020a) in close proximity to *Rph9*. The last association mapping study assessed 336 ICARDA accessions with 42 ASR and 13 APR MTA identified, 33 of which were deemed novel (Gyawali et al., 2021).

Notable changes to net blotch consensus map

Marker positions for consolidated net blotch loci were identified using the Morex V3 genome assembly, further refining multiple loci after incorporating additional studies (Adhikari et al., 2020; Afanasenko et al., 2022; Alhashel et al., 2021, 2023; Clare et al., 2021; Czembor and Czembor, 2023; Esmail et al., 2023; Mazinani et al., 2020; Muria-Gonzalez et al., 2023; Skiba et al., 2022) and additional unanchored markers (Table 5; Supplementary Table 2). The total number of consensus loci for net blotch has been lowered from 73 to 72, despite the separation of *SPN1* from *Rpt5/Spt1*, the identification of *Rpt9* (Franckowiak and Platz, 2021), and the addition of two novel MTA (Czembor and Czembor, 2023). As noted, a major change in the net blotch consensus maps was the identification of *Rpt9* (598.8–611.7 Mb), dividing *Rpt4* (now 415.1–596.6 Mb) (Franckowiak and Platz, 2021) into two loci on the long arm of chromosome 7H. The *Rpt4/Rpt9* region has been subsequently further characterized with two overlapping resistance loci identified at 592.2–602.0 Mb (Alhashel et al., 2021) and 587.1–598.8 Mb (Skiba et al., 2022), and therefore potentially mapping the same underlying gene of either *Rpt4* or *Rpt9*. However, within this interval, a susceptibility locus was identified and high-resolution mapped (592.6–593.0 Mb) with the proposed name of *Sptm1* (Alhashel et al., 2023). Whether *Sptm1* is *Rpt4*, *Rpt9*, or a separate locus is currently unknown and requires further investigation. This is further supported by association mapping that identified two significant markers within the region (596.7 and 611.7 Mb) separated by multiple insignificant SNPs (Clare et al., 2021). Further work will

TABLE 5 Summary information of all designated resistance/susceptibility loci in barley net blotch to net blotch pathogen *Pyrenophora teres*.

Locus	Synonym	Alleles	Species	Accession	Stage	Chr.	Pos. (bp)	Mapping
Rpt1	*Pt_1*, *Pt_2*, *Pt1a/Rpt1a*, *Pt2b/Rpt1b*, *Pt,a*, *QRpts3L*, *QRpts3Lb*, *QRpts3H-2*, *QNFNBSLR.Ar/F-3Ha*, *QNFNBAPR.Ar/F-3Hb*, *QNFNBAPR.Al/S-3H*, *QNFNBAPR.W/Al-3H*, *QNFNBSLR.Al/S-3H*, *QNFNBSLR.W/Al-3H*, *QRpta3H*, *QRpt-3H.3*, *SFNB-3H-117.1*, *QRptta-3H-144.65*, *QRptts-3H-106.96*, *QTLPHs-3H*, *QPt.3H-5*	*Rpt1.a*, *Rpt1.b*	*H. vulgare*	Tifang, Ming, Manchurian, Harbin, Igri, Arapiles, Alexis	ASR/ APR	3H	541,697,453–574,517,190	Mode and Schaller (1958), Bockelman et al. (1977), Graner et al. (1996), Richter et al. (1998), Raman et al. (2003), Cakir et al. (2003), Manninen et al. (2006), Lehmensiek et al. (2007); König et al. (2014); Tamang et al. (2015); Burlakoti et al. (2017); Martin et al. (2018); Adhikari et al. (2019); Novakazi et al. (2019); Mazinani et al. (2020); Clare et al. (2021); Czembor and Czembor (2023)
Rpt2	*Pt2c/Rpt2c*, *Rpt-1H-5-6*, *NBP_QRptt1-1*	*Rpt2.c*	*H. vulgare*	Canadian Lake Shore, CI4922	ASR	1H	25,680,656–78,914,349	Bockelman et al. (1977), Steffenson et al. (1996), Yun et al. (2005), Manninen et al. (2006), Wonneberger et al. (2017); Adhikari et al. (2019)
Rpt3	*Pt_3*, *QRpts2L*, *Pt.d/Pt3d/Rpt3d*, *QRpts2L*, *QNFNBSLR.Ar/F-2Hb*, *QRptts2*, *QRptta2*, *QRptms2*, *QTL_{UH}-2H*, *QRptma2-3*, *Qrpts2L.1*, *Qrpts2L.2*, *QRptta-2H-92.21*, *QRptta-2H-114-117*, *QRptta-2H-126.77*, *QRptta-2H-143.13*, *QRptt.2H-132.15*, *QRptm-2H-126-137*, *QRptm-2H-141-152*, *Qnfnb-2H.1*, *QRptts-2H-114.00*, *NB-1*	*Rpt3.d*	*H. vulgare*	Tennessee Awnless D22-5, TR251, Steptoe, Kaputar, Franklin, ND11213	ASR/ APR	2H	601,806,948–663,579,155	Mode and Schaller (1958), Bockelman et al. (1977), Ho et al. (1996), Steffenson et al. (1996), Molnar et al. (2000), Raman et al. (2003), Cakir et al. (2003), Emebiri et al. (2005), Manninen et al. (2006), Lehmensiek et al. (2007), Grewal et al. (2008), Grewal et al. (2012), König et al. (2013), Wonneberger et al. (2017); Vatter et al. (2017); Amezrou et al. (2018); Daba et al. (2019), Rozanova et al. (2019), Adhikari et al. (2019); Esmail et al. (2023); Muria-Gonzalez et al. (2023)
Rpt4/ Rpt3	*QRpt7*, *QRptm7-4*, *QRptm7-5*, *QRptm7-6*, *Qrptts-7HL.1*, *NBP_QRptt7-2*, *QRptts-7H-74.29*, *Qns-7H.2*, *QRptm-7H-92-95*, *QRptm-7H-119-137*, *QRptm-7H-34-38*, *QRptm-7H-96-107*, *Sptm1*	*Rpt4.e*	*H. vulgare*	Galleon, CI9214, Keel, Tilga, Chebec, PI67381, PI84314, TR251	ASR	7H	415,052,764–596,654,688	Spaner et al. (1998), Williams et al. (1999), Williams et al. (2003); Lehmensiek et al. (2007), Grewal et al. (2008), Cakir et al. (2011); Tamang et al. (2015), Wang et al. (2015), Richards et al. (2017); Wonneberger et al. (2017); Amezrou et al. (2018); Daba et al. (2019); Tamang et al. (2019); Alhashel et al. (2021); Skiba et al. (2022); Alhashel et al. (2023)
Rpt5/ Spt1	*Pt_a*, *Pt,d*, *QRpts6L*, *QRpt6*, *6H-bin6*, *rpt5*, *QPt.6H-1*, *QPt.6H-2*, *NBP_QRptt6-1*, *QRptt.6H-54-55*, *Qns-6H.5*, *Qnfnb-6H.1*, *Qnfnb-6H.2*, *Qnfnb-6H.3*, *Qnfnb-6H.4*, *Qsfnb-6H*, *QRptm-6H-55-64*, *QRptts-6H-59.01*, *QRptts_6H_57.64-60.21*, *QRptts_6H_62.91*, *QRptts_6H_64.29-65.68*	*Rpt5.f*, *Spt1.k*, *Spt1.r*	*H. vulgare*	CI5791 (*Rpt5.f*), CI9819 (*Rpt5.f*), Kombar (*Spt1.r*), Rika (*Spt1.k*), Halycon, TR251, Lavrans, Nomini, CIho2291, Steptoe, HOR9088, Kaputar, ND11213, Chevron, SM89010, M129, Baudin, WPG8412, Pompadour, Stirling, Falcon, H02, UVC8	ASR	6H	362,339,026–376,997,079	Khan and Boyd (1969), Metcalfe et al. (1970), Graner et al. (1996), Steffenson et al. (1996), Spaner et al. (1998), Richter et al. (1998), Read et al. (2003), Cakir et al. (2003), Ma et al. (2004), Emebiri et al. (2005), Manninen et al. (2000), Manninen et al. (2006), Friesen et al. (2006), Abu Qamar et al. (2008), Grewal et al. (2008), St. Pierre (2010), Cakir et al. (2011), Gupta et al. (2011), Grewal et al. (2012), Shjerve et al. (2014), O'Boyle et al. (2014), Liu et al. (2015); Tamang et al. (2015), Wang et al. (2015), Richards et al. (2016), Koladia et al. (2017), Islamovic et al. (2017); Richards et al. (2017), Hisano et al. (2017), Wonneberger et al. (2017); Vatter et al. (2017); Martin et al. (2018); Amezrou et al. (2018); Tamang et al. (2019); Daba et al. (2019), Rozanova et al. (2019), Adhikari et al. (2019); Novakazi et al. (2019); Adhikari et al. (2020); Mazinani et al. (2020); Muria-Gonzalez et al. (2023); Czembor and Czembor (2023)
Rpt6	*QRptta5*, *QTL_{PH}-5H-1*, *QTL_{PHs}-5H*, *QRptm-5H-12-21*	*Rpt6.g*	*H. vulgare*	CI9819	ASR	5H	2,224,211–16,620,817	Manninen et al. (2006), König et al. (2013), König et al. (2014); Alhashel et al. (2021); Czembor and Czembor (2023)

(Continued)

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TABLE 5 Continued

Locus	Synonym	Alleles	Species	Accession	Stage	Chr.	Pos. (bp)	Mapping
Rpt7	*QRpts4*, *Rpt-4H-5-7*, *QNFNBAPR.Al/S-4Ha*, *AL_QRptt4-1*, *NBP_QRptt4-2*, *Qrpts4*, *QPt.4H-3*, *Qns-4H.2*, *Qns-4H.3*, *QRptm-4H-58-64*, *QRptts_4H_53.87*, *QRptts_4H_59.32*, *QRptm-4H-43-57*	*Rpt7.h*	*H. vulgare*	Halycon, Steptoe, Sloop, TR251, OUH602, Arena/HOR9088, PostxViresa/HOR9484, Harrington/TR306, Falcon	ASR/APR	4H	81,923,870–447,260,061 (29,319,685–562,782,042)	Steffenson et al. (1996), Spaner et al. (1998), Read et al. (2003), Yun et al. (2005); Lehmensiek et al. (2007), Grewal et al. (2008), Afanasenko et al. (2015), Tamang et al. (2015); Islamovic et al. (2017); Wonneberger et al. (2017); Wonneberger et al. (2017); Richards et al. (2017); Daba et al. (2019); Novakazi et al. (2019); Adhikari et al. (2020); Alhashel et al. (2021); Muria-Gonzalez et al. (2023)
Rpt8	*QNFNBAPR.W/Al-4H*, *QNFNBAPR.Al/S-4Hb*, *QRptms4*, *QPt.4H-4*, *QPt.4H-5*, *QRptts-4H-97.66*, *Qnfnb-4H.2*, *QRpt-4H.1*	*Rpt8.j*	*H. vulgare*	Q21861	ASR/APR	4H	572,471,001–592,225,675	Friesen et al. (2006), Lehmensiek et al. (2007), Grewal et al. (2012), Tamang et al. (2015); Vatter et al. (2017); Amezrou et al. (2018); Martin et al. (2018); Daba et al. (2019); Clare et al. (2021)
Rpt9/Spt3	*QNFNBAPR.Al/S-7Hb*, *QNFNBAPR.W/Al-7Hb*, *QRptm7-6*, *NBP_QRptt7-2*, *NBP_QRptt7-3*, *QPt.7H-3*, *QRptm-7H-119-137*, *QRptm-7H-138-160*, *QRptm-7H-34-38*, *QRptm-7H-96-107*, *QRpt-7H.2*, *QRpt-7H.3*, *Sptm1*	N/A	*H. vulgare*	Sloop, W2875-1, Hockett (*Spt3*), tradition (*Spt3*)	ASR/APR	7H	587,141,289–632,035,801	Lehmensiek et al. (2007), Wang et al. (2015), Wonneberger et al. (2017); Vatter et al. (2017); Tamang et al. (2019); Clare et al. (2021); Alhashel et al. (2021), Franckowiak and Platz (2021), Skiba et al. (2022); Alhashel et al. (2023); Muria-Gonzalez et al. (2023)
Rpt10/Spt2	*NBP_QRptt5-1*, *QRpt-5H.2*	N/A	*H. vulgare*	CI5791 (*Spt2*), Golden Promise (*Spt2*), Tifang (*Spt2*)	ASR	5H	437,052,384–455,455,300	Wonneberger et al. (2017); Clare et al. (2021); Czembor and Czembor (2023); Clare et al. (2024)
Rpt11/Spt4	*QNFNBAPR.Ar/F-1H*, *Spm1*	N/A	*H. vulgare*	Arapiles (*Rpt11*), Baudin (*Spt4*)	ASR	1H	2,604,525–14,662,483	Lehmensiek et al. (2007); Amezrou et al. (2018); Martin et al. (2018); Mazinani et al. (2020); Muria-Gonzalez et al. (2023)
SPN1	*QRpt*, *6H-bin6*, *QRptm6-2*, *NBP_QRptt6-1*, *QPt.6H-1*, *QRptta-6H-49.79*, *QRptm-6H-55-64*, *QRptts_6H_51.94-52.20*, *NB-12*	N/A	*H. vulgare*	NDB 112	ASR	6H	30,133,310–94,956,289	Steffenson et al. (1996), Cakir et al. (2003), Emebiri et al. (2005), Freisen et al. (2006), St. Pierre et al. (2010), Cakir et al. (2011); Tamang et al. (2015); Liu et al. (2015), Wang et al. (2015), Richards et al. (2017); Wonneberger et al. (2017); Vatter et al. (2017); Amezrou et al. (2018); Novakazi et al. (2019); Adhikari et al. (2020); Esmail et al. (2023)

Information includes locus designations, synonyms and alleles, species and accessions, effective stages, chromosomal location, and relevant literature.

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be required to tease apart the true number of loci present in the *Rpt4/Rpt9/Sptm1* region.

The most broad and effective resistance gene, *Rpt5*, against *Pyrenophora teres* f. *teres* (*Ptt*) has been validated as a RLP at 364.7 Mb, whereas *Spt1* remains under investigation (Effertz, 2023; Effertz et al., 2024). Due to the centromeric location of *Rpt5/Spt1*, the majority of markers identified on chromosome 5H are most likely in linkage disequilibrium currently spanning from 111.9 to 466.6 Mb. However, this separates the *SPN1* locus originally delimited to 46.0–90.3 Mb (Liu et al., 2015). Additionally, further work will be required to determine if any additional loci are present within the large linkage block that currently delimits *Rpt5/Spt1*. Unfortunately, *Rpt5* has been broken by Canadian (Akhavan et al., 2016), French (Arabi et al., 1992), Turkish (Çelik Oğuz and Karakaya, 2017), and Moroccan isolates (Li et al., 2023; Richards et al., 2024). Interestingly, an association mapping study into Egyptian germplasm did not identify *Rpt5*, instead identified seven significant markers on 3H (Esmail et al., 2023). These are reported as seven separate MTA; however, *NB-2*, *NB-3*, *NB-4* colocalize with *Rpt3H-4* (Afanasenko et al., 2022; Clare et al., 2021; Daba et al., 2019; Islamovic et al., 2017; König et al., 2014; Lehmensiek et al., 2007; Novakazi et al., 2019; Richards et al., 2017; Tamang et al., 2015, 2021; Wonneberger et al., 2017; Yun et al., 2005), and *NB-5*, *NB-6*, *NB-7*, and *NB-8* colocalize with *QRpts3La* (Burlakoti et al., 2017; Cakir et al., 2011; Daba et al., 2019; Lehmensiek et al., 2007; Raman et al., 2003; Richards et al., 2017; Tamang et al., 2015, 2019; Vatter et al., 2017; Wonneberger et al., 2017).

Lastly, multiple susceptibility loci have been identified in the barley-*P. teres* f. *maculata* (*Ptm*) pathosystem, including *Sptm1*, described earlier. Firstly, *Spt2* was been high-resolution mapped to a single pentatricopeptide repeat-containing protein candidate gene on chromosome 5H in two independent mapping populations that share CI5791 as a common parent (Clare et al., 2024). The *Spt2* locus is unique in that all parents are considered resistance to the *Ptm* isolate 13IM8.3; however, all F_1 individuals are considered hypersusceptible. This locus was previously mapped as resistance loci: *NBP_QRptt5-1* (Wonneberger et al., 2017), *QRpt-5H.2* (Clare et al., 2021), and potentially an unnamed QTL (Clare et al., 2020; Williams et al., 2003) raising interesting questions about whether the locus can function as a resistance and/or susceptibility target. Another locus designated *Spm1* was identified within a 190-kb interval (9.12-9.31 Mb) on chromosome 1H (Muria-Gonzalez et al., 2023), that has previously been identified as resistance loci: *QRptta-1H-4.11* (Amezrou et al., 2018), *QRpta1H-2* (Mazinani et al., 2020), *QNFNBAPR.Ar/F-1H* (Lehmensiek et al., 2007) and a QTL identified between 19.4 and 25.7 cM (Martin et al., 2018). The *Susceptibility to P. tritici-repentis 1* (*Spr1*) locus facilitates susceptibility to the pathogen *P. tritici-repentis* (*Ptr*), which primarily causes tan spots of wheat (Wei et al., 2020). The *Spr1* locus to 9.4–12.0 Mb has also been included in the *P. teres* maps (Figure 1) and colocalizes with *SFNB-2H-8-10* (Burlakoti et al., 2017), *NBP_QRptt2-1* (Wonneberger et al., 2017), *QRptts-2H-7.44* (Amezrou et al., 2018), *QRptts-2H-9.00*, *QRptts-2H-161.70* (Adhikari et al., 2019), and unnamed QTL (Liu et al., 2015; Skiba et al., 2022; Tamang et al., 2015, 2019).

A trend of identifying susceptibility loci within the barley-*P. teres* pathosystem appears to be common after the initial identification of the *Spt1* susceptibility locus (Richards et al., 2016), followed by *Spt2* (Clare, 2022; Clare et al., 2024), *Sptm1* (Alhashel et al., 2023), *Spm1* (Muria-Gonzalez et al., 2023), and resistant accessions contributing susceptibility alleles at *QRptm-3H-*

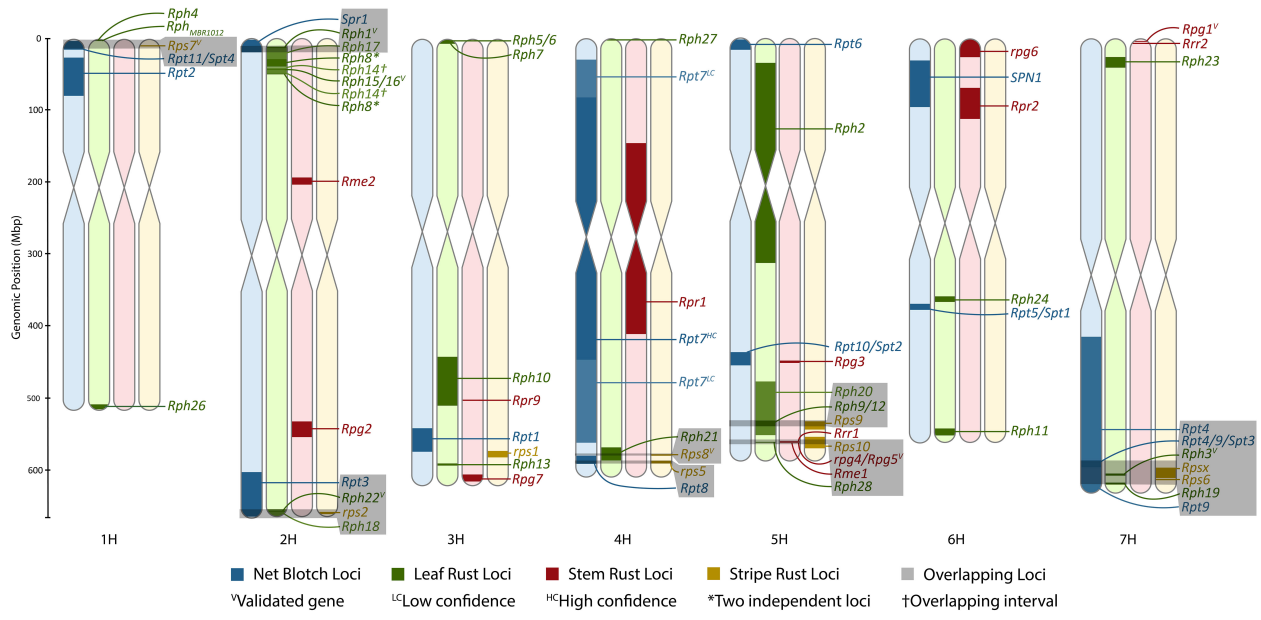

FIGURE 1
Karyotype density map of all rust pathosystems in comparison to previously anchored net blotch loci. The figure was made using Rideogram and restricted to only formally designated loci that could be anchored to the Morex V3 genome. The size of intervals may be increased to allow for visualization if an interval is sufficiently refined.

45-52, *QRptm-5H-12-21*, *QRptm-5H-81-88*, and *QRptm-6H-60-64* (Alhashel et al., 2021). Loci nomenclature needs to be addressed urgently, considering multiple loci are identified to be effective against *Ptt* and *Ptm*. Despite recent research suggesting incipient speciation between *Ptt* and *Ptm* (Yuzon et al., 2023), there is considerable overlap (Clare et al., 2020) and the custom of utilizing three letters and numbers to designate barley loci (Bockelman et al., 1977). The designations *Rpt* and *Spt* provide no discrimination between *Ptt* and *Ptm*, unlike *Sptm* and *Spm*, which suggest these loci are only implicated within *Ptm* interactions, despite the fact these have been previously identified within the *Ptt* interaction but not formally designated. We therefore propose *Sptm1* is renamed to *Rpt4/Rpt9/Spt3* and *Spm1* to *Rpt11/Spt4*. In addition, with the increased number of alleles being discovered at identified designated loci, e.g., *Rph2* and *Rps8* with 12 and 27 alleles, respectively, we also propose the removal of the current convention to designate alleles with a letter across all loci within the pathosystem and instead restart with each locus, i.e., *Rpt2.b* becomes *Rpt2.a*.

Genomic resources and locus colocalization

Currently, there are over 25 full pseudomolecule chromosome assemblies of barley to assess for allelic diversity, ranging from wild accessions, landraces, and cultivars (Jayakodi et al., 2020; Jiang et al., 2022; Mascher et al., 2021; Sakkour et al., 2022; Sato et al., 2021; Schreiber et al., 2020; Xu et al., 2021), that will no doubt expand with the ever-decreasing cost of long-read sequencing. These resources will allow for the rapid identification of new alleles once genes underlying resistance or susceptibility loci have been validated. In summary, chromosomes 6H and 5H contain the least and most amount of formally designated rust resistance genes, respectively (Figure 1; Table 6); however, this may not hold true as additional loci are added to the portfolio. A limitation of this atlas is that frequently raw data are not readily available to determine the nearest insignificant markers, to precisely delimit the MTA/QTL interval, and ultimately identify overlaps between loci. This is particularly a problem with association mapping studies and would therefore implore all marker data to be published in the future. With numerous studies remapping the same locus and the dearth of novel loci, research should focus on refining the genomic intervals underlying these intervals and gene validation.

A total of eight colocalizations of formally designated loci were identified, including *Rps7* with *Rpt11/Spt4*; *Spr1* with *Rph1* or *Rph17*; *rps2* with *Rph18 or Rph22* and potentially *Rpt3*; *Rps8* and *Rph21*; *Rpt8* and *rps5*; *Rph20* with *Rph9/12* and *Rps9*; *rpg4/Rpg5* with *Rps10* and *Rph28*; and *Rpt4/Rpt9/Spt3* with *Rph3*, *Rph19*, *Rps6*, and/or *Rpsx* on chromosomes 1H, 2H, 2H, 4H, 4H, 5H, 5H, and 7H, respectively (Figure 1). *Rpg3* appears to colocalize with *Rpt10*/Spt2; however, the refined *Spt2* region does not overlap with *Rpg3*, and therefore further investigation will be required to determine if *Rpt10* colocalizes with *Rpg3*. The most notable colocalization is *Rph28* and *Rps10* with *rpg4/Rpg5* on chromosome 5H. The *Rph28* locus encompasses two of the three genes within the validated *rpg4/Rpg5* complex, including the two NLRs of *rpg4/Rpg5*, *Adf2*, and two additional zinc fingers. In addition, *Rps10* colocalizes with *rpg4/Rpg5* and *Rph28*, although with a larger overlapping interval. Therefore, there is a high likelihood that the validated dual NLR genetic architecture of *rpg4/Rpg5* and/or novel alleles of the *rpg4/Rpg5* complex is functional against leaf, stripe, and stem rust. Both reports of *Rph28* and *Rps10* lack mention of the *rpg4/Rpg5* complex, despite being validated over a decade ago and providing the most widespread resistance to stem rust, therefore showcasing the importance of high-resolution genetic mapping and developing a barley gene atlas.

Conclusion

This work was initiated due to the fact plant defense responses are highly coordinated and interconnected, with recent research showcasing sympathetic or antagonistic relationships of pathogen recognition mechanisms. Therefore, without a comprehensive resource collating all known resistance/susceptibility loci, identifying previously reported loci within additional accessions against different pathogens, or both, becomes burdensome. We

TABLE 6 Formally designated loci distribution for each pathosystem across the barley genome.

Chr.	Crown rust	Leaf rust	Stem rust	Stripe rust	Net blotch
1H		*Rph5*, *Rph26*, $Rph_{MBR1012}$		*Rps4*, *Rps7*	*Rpt2*, *Rpt11/Spt4*
2H		*Rph1*, *Rph8*, *Rph14*, *Rph15/16*, *Rph17*, *Rph18*, *Rph22*	*Rpg2*, *Rme2*	*rps2*	*Rpt3*
3H	*Rpc1*	*Rph5/6*, *Rph7*, *Rph10*, *Rph13*	*Rpg7*, *Rpr9*	*rps1*	*Rpt1*
4H		*Rph21*	*Rpr1*	*rps5*, *Rps8*	*Rpt7*, *Rpt8*
5H		*Rph2*, *Rph9/12*, *Rph25*, *Rph28*	*Rpg3*, *rpg4/Rpg5*, *Rrr1*, *Rme1*	*Rps9*, *Rps10*	*Rpt6*, *Rpt10/Spt2*
6H		*Rph11*, *Rph24*	*rpg6*, *Rpr2*		*Rpt5/Spt1*, *SPN1*
7H		*Rph23*	*Rpg1*, *Rrr2*	*Rps6*, *Rpsx*	*Rpt4/Rpt9/Spt3*
Unknown			*RpgBH*, *RpgU*	*rps3*	

therefore began the process of consolidating loci that confer resistance or susceptibility to three of the most important diseases of barley in leaf, stem, and stripe rust. In addition, previously reported net blotch loci were updated and included in the colocalization analysis. There is often difficulty determining which loci colocalize with each other due to asynchronous marker technologies and the larger mapping intervals of early mapping studies. However, researchers will be able to use this resource to quickly identify previously reported loci without intimate knowledge of these pathosystems, as we show with *rpg4/Rpg5*, *Rph28*, and *Rps10* loci. Ideally, this atlas will be expanded to include additional fungal diseases as well as bacterial and viral diseases to identify conserved resistance mechanisms or pathogen-specific resistance to inform breeders in the development of highly resistant cultivars.

Author contributions

SC: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing, Project administration. FN: Data curation, Investigation, Writing – original draft, Writing – review & editing, Formal analysis, Validation. PH: Writing – review & editing, Formal analysis, Validation. MM: Formal analysis, Investigation, Methodology, Resources, Writing – original draft, Writing – review & editing, Data curation, Software, Validation. RB: Funding acquisition, Resources, Supervision, Writing – review & editing, Validation.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fagro.2024.1451281/full#supplementary-material

SUPPLEMENTARY TABLE 1
All markers reported as intervals of surrounding barley disease resistance genes for cereal rust and their inferred loci designation based on consolidation.

SUPPLEMENTARY TABLE 2
Upgraded marker positions for all reported net blotch resistance markers and their new loci consolidation.

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