

Breeding Barley for Yellow Rust Resistance: Conventional and Molecular Pursuits

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Article history:

Received: 21 Oct., 2024

Revised: 11 Dec., 2024

Accepted: 23 Dec., 2024

Citation:

Patial M, SK Bishnoi, O Singh, D Pal, KK Pramanick, N Sharma and J Kumar. 2024. Breeding Barley for Yellow Rust Resistance: Conventional and Molecular Pursuits. *Journal of Cereal Research* **16** (3): 225-238. <http://doi.org/10.25174/2582-2675/2024/158532>

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Abstract

Puccinia striiformis f. sp. *hordei* (*Psh*) causing barley stripe or yellow rust is a serious threat to barley production. The most cost-effective and long-lasting strategy for combating this disease is using genetic resistance. Stripe rust resistant genes providing both qualitative and quantitative resistances to *Psh* have been documented and resistance breeding has adeptly developed numerous barley varieties employing both conventional and molecular methods. The creation of high-yielding, disease-resistant cultivars necessitates the identification of resistant sources, comprehension of genetic inheritance, and subsequent hybridization and selection. A significant challenge in barley breeding remains the pyramiding of multiple disease resistance genes into high-yielding germplasm. Historically, barley breeders utilized fundamental genetic approaches, mutation breeding, and hybridization. To hasten resistance breeding advanced methodologies such as doubled haploidy and molecular techniques are also adopted.

Keywords: *Hordeum vulgare*, *Puccinia striiformis* f. sp. *Hordei*, genetic resources, genetics, QTLs

Introduction

Barley (*Hordeum vulgare* L.) an ancient crop, cultivated in more than 100 countries, is the fourth most important cereal crop in the world. Overall, global barley production hovers around 150 million tonnes. The major barley producing areas are Russian Federation, Australia, Europe, North America, Canada UK, and Asia (Harwood, 2019). Barley has diversified uses as livestock feed, food stuffs (sattu/roasted barley, porridge, and chapattis) and religious purpose, besides it is an important industrial crop used for production of malt for brewing and distillation, and in health drinks. The crop is short seasoned, early maturing and is cultivated mostly in neglected areas with low and unstable productivity, where wheat can't be grown, thereby, known as "poor men's crop" (Verma *et al.*, 2010). Barley has several health benefits and has good nutritional

and even medicinal properties due to high content of bioactive compounds such as -d-glucan, tocotrienols, tocopherols, and phenolics such as benzoic and cinnamic acid derivatives, quinones, proanthocyanidins, chalcones, flavonols, and flavones (Holtekjolen *et al.*, 2008).

Climate change, have potential to bring about severe epidemics and affects the agricultural productions adversely thereby, threatening the global food security. According to Oerke (2006), plant diseases and pests could passively deprive humanity for over 50% of the attainable yield. Barley productivity, throughout the world, is affected by economically different diseases; however, yellow rust or stripe rust caused by *Puccinia striiformis* f. sp. *hordei* (*Psh*) severely decreases grain quality and yield thereby curtailing barley production. The most



economical and long-lasting component of yellow rust management is genetic resistance which focus on using resistant cultivars, especially those with durable resistance, to combat yellow rust disease.

Resistance breeding has been very successful in the past, and, many resistant or tolerant barley varieties/lines/genetic stocks have been developed using conventional and molecular breeding approaches (Nelson *et al.*, 2018; Patial *et al.*, 2021; Patial *et al.*, 2023). Marker Assisted Selection (MAS) have been widely used in commercial barley breeding programmes for effective and efficient incorporation of yellow resistance genes derived from adapted and non-adapted germplasm. Moderately dense genetic maps have been constructed (Graner *et al.*, 1991; Kleinhofs *et al.*, 1993) which has led to an increased accuracy of locating QTL to specific chromosomal regions. The identification and introgression of yellow rust resistance genes through MAS leading to pyramiding of different resistance genes into barley cultivars have sustained the disease resistance mechanism. This review provides an insight on conventional and molecular breeding aspects for yellow rust resistance breeding which will be an important for breeders working in barley improvement programme.

Genetic Resources and Pre-breeding for yellow rust resistance in barley

Genetic diversity is an important source of *de novo* beneficial alleles and is paramount for the progress towards a breeding goal. Many of the barley cultivars grown today shares related pedigrees with one-parental inheritance in certain cases (Martin *et al.*, 1991; Wych and Rasmusson, 1983; Sjakste *et al.*, 2003). For example, most of the present-day high yielding Turkish barley cultivars had developed from 'Tokak' landrace (Kilian *et al.*, 2006).

Due to ongoing erosion of resistance genes in cultivation, discovery of novel sources of resistance is crucial. For barley yellow rust resistance, Mathur and Siradhana (1990) screened 700 cultivars under natural epiphytotic of *Puccinia striiformis* of which only fifteen were disease free and 11 showed traces of the rust and considered as resistant. Chen *et al.* (1995) reported barley genotypes - Hor 2926, Hor 1428, Hor 3209, Abyssinian 14, BBA 2890, Stauffers Obersulzer, Grannelose Zweizeilige to be resistant to all barley yellow rust races. Nover and Scholz (1969), Toojinda *et al.* (2000) and Castro *et al.* (2003)

established a number of transiently designated genes for stripe rust resistance from barley germplasm. Gyawali *et al.* (2018) in 336 barley genotypes revealed eleven (AM-14, AM-177, AM-37, AM-120, AM-300, AM-36, AM-103, AM-189, AM-291, AM-275 and AM-274) resistant sources of stripe rust against six races and 89 Adult Plant Resistance (APR) sources for barley yellow rust race. Verma *et al.* (2018) revealed twelve resistant genotypes (ARAMIR/COSSACK, C8806, Astrix, C9430, Gold, CLE 202, Gull, Isaria, Pirolina, Lechtaler, Stirling and Trumpf) at adult-plant and seedling stages. Patial *et al.* (2023) studied genetic variability of yellow rust resistant advanced lines and identified potential lines for yield enhancement. The characterization of sources of yellow rust resistance and the exploitation of the allelic richness of landraces, wild progenitors, and breeding lines in barley has facilitated their utilization in breeding programs.

Gene, genetics and QTLs for yellow rust resistance

In barley, stripe rust can be caused by either the rust that infects wheat (*Puccinia striiformis* f. sp. *tritici*, *Pst*) or barley (*P. striiformis* f. sp. *hordei*, *Psh*). Barley stripe rust/yellow rust can cause yield losses of up to 70% under epidemic conditions (Dubin and Stubbs, 1986) and occurs in cool and wet climate. Resistance is classed as seedling and adult-plant resistance (APR). Seedling resistance is also known as 'all stage resistance'. This type of resistance is expressed at all growth stages, is often race specific and is conferred by a single 'major effect'. On the other hand, APR is expressed in adult plants, controlled by multiple 'minor effect' genes and often polygenic in nature. Because specific genes that provide high levels of resistance are easy to detect and manipulate, most barley breeders have used them in their breeding programs. However, these genes deployment is vulnerable to the changes in the pathogen following boom-bust cycle. Therefore, gene pyramiding involving deployment of multiple seedling resistance genes has been highly effective and widely adopted.

Murty (1942) conducted the first study on the genetics of barley stripe rust resistance in India who reported that stripe rust resistance in the American cultivar "Alpha" was conditioned by two dominant genes. During 1960's a number of studies on the genetics of stripe rust resistance in barley genotypes were done in India and abroad (Bakshi and Bahl, 1965; Luthra, 1966; Nover and Scholz, 1969). In



barley, both dominant and recessive genes are reported for stripe rust resistance by different workers (Table 1). Verma *et al.* (2016) reported adult plant and seedling resistance to stripe rust from ICARDA high-input barley breeding programme and identified 12 sources against five *Psh* races

in India. Patial *et al.* (2016, 2018) studied the gene action studies for grain yield and its component traits in yellow rust advanced breeding lines and reported the potential yield traits and genotypes for yield enhancement.

Table 1: Genetics of stripe rust resistance in barley

S. No.	Reference	Reported work on genetics of stripe rust resistance
1.	Johnson (1968)	Single dominant gene in 'Cambrinus' cultivar.
2.	Nover and Scholz (1969)	Single recessive gene to European race 24 in 'BBA 2890'
3.	Upadhyay and Prakash (1977)	Susceptibility of 'Bigo' to an Indian race 24 and resistance in 'Abyssinian 14' controlled by one or more genes.
4.	Dayani and Bakshi (1978)	Resistance to field infection (predominate races 24 and G) in 'EB1556' controlled by two recessive genes.
5.	Luthra and Chopra (1990)	Cultivar 'Himani' carries the dominant gene <i>Rps1</i> giving resistance to race G.
6.	Chen and Line (1999)	Genotypes BBA 809, Bigo, BBA 2890, Hiproly, and Grannelose Zweizeilige have one recessive gene; Emir, PI I5, PI 548734, 548708, PI 548747, Varunda have two recessive genes; Stauffers Obersulzer and Abyssinian 14 have one dominant gene and one recessive gene against <i>Psh-1</i> .
7.	Chen and Line (2003)	Reported 26 different genes for stripe rust resistance.
8.	Pahalawatta and Chen (2005)	One dominant (<i>RpstS1</i>) and one recessive (<i>rpstS2</i>) gene in cultivar 'Steptoe' for resistance to races <i>PST-41</i> and <i>PST-45</i> .
9.	Yan and Chen (2007)	In BA 2890 F ₈ RILs confirmed the presence of a single recessive gene for resistance.
10.	Prakash and Verma (2009)	The inheritance pattern of yellow rust resistance in four lines (RD 2552, RD 2503, RD 2508 and RD 2634) indicating that resistance was governed by single dominant gene.
11.	Derevnina <i>et al.</i> (2015)	Single resistant gene in 16 Australian and three exotic barley lines.

Although a fairly small number of resistance genes have been formally assigned for barley stripe rust compared to other barley rusts, reports of both qualitative and quantitative resistance to *Psh* have well documented (Nover and Scholz, 1969; Chen and Line, 1999; Dracatos *et al.*, 2019). In the past 40 years, different genes, either catalogued or transiently, have been identified as dominant (*Rps*) and recessive (*rps*) (Clare *et al.*, 2016). However, with the appearance of new races of pathogen, many of these genes have lost the resistance.

Initially, during 1960s, Johnson (1968) and Nover and Scholz (1969) reported *rps1* (*yr1*), *rps2* (*yr2*), *rps3* (*yr3*) and *Rps4* (*Yr4*) genes in differential barley sets used in India. In addition to this Luthra *et al.* (1991) reported *Rps4* (*Yr4*) in EB410; *rps5* (*yr5*) in EB438 and EB 1556; *rps6* (*yr6*) in EB 1556; *rps7* (*yr7*), *rps8* (*yr8*) and *rps9* (*yr9*) in EB1626;

rps1 (*yr1*), *Rps10* (*Yr10*) and *Rps11* (*Yr11*) in Abyssinian 14; and *rps3* (*yr3*), *Rps12* (*Yr12*) and *Rps13* (*Yr13*) in I5 for effective resistance against Indian *Psh* races. Johnson (1968) reported a gene in cultivars 'Europa', 'Cambrinus', and 'Deba Abed' that were designated as *Rps4* (*Yr4*). Chen and Line (1999) described three recessive genes (*rps1*, *rps2* and *rps3*) providing resistance to the stripe rust pathogen. Later, they described a fourth gene, *rps4* in their studies. Kumar *et al.* (2012), did not observe virulence on genotypes 'Helis Franken' (with resistance genes *Rps4* (*Yr4*) and, *rpsHF*), 'Emir' (*rpsEm1* and *rpsEm2*) and 'Asterix' (*Rps4* (*Yr4*), *rpsAst*) and reported these genes to be effective for providing resistance to yellow rust. Safavi *et al.* (2013) in Iran reported no virulence on 12 barley differential sets with race-specific resistance genes *rpsEm1*, *rpsEm2*, *rpsHF*, *Rps4*, *rpsVa1*, *rpsVa2* and *rpsAst* and considered these genes



as effective genes which can be used in pyramiding with race-non-specific resistance genes to attaining durable and highly effective resistance to stripe rust. The resistance genes *rps2*, *Rps1b*, *Rps3*, and *rps15* were deemed ineffective as these genes demonstrated susceptible reaction and virulence. Clare *et al.* (2016) isolated the *RpsHOR1428-5H* locus present in cultivar ‘HOR1428’ in a ‘Manchuria’ genetic background and designate the locus as *Rps9*. The additive nature of *Rps9* suggests that the locus is a semi-dominant resistance gene, which contrasts with the observed recessive nature of *rpsHOR1428-1* and *rpsHOR1428-2* by Chen and Line (1999).

Several QTLs conferring resistance to stripe rust have been found. The first genetic study of barley stripe rust resistance was conducted in the United States by Chen *et al.* (1994) using a doubled haploid population that was developed by crossing a susceptible line (a backcross derivative of ‘Bowman’) with a resistant breeding line (LB1ran/UNA8271/‘Gloria’/‘Come’). Using molecular markers, they mapped two resistant QTL on chromosomes 5H and 4H. Castro *et al.* (2002) in ‘Shyri × Galena’ double haploid population reported two QTLs on chromosomes 4 and 5H conferring resistance to three *Psh* isolates (*Psh-1*, *Psh-13* and

Psh-14). In the doubled haploid population arising from a cross between ‘Franklin’ and ‘Yerong’. Derevnina *et al.* (2015) reported genes that contribute to seedling resistance and mapped them to the long arms of chromosomes 5H and 7H, respectively. The temporary designations *Rpsp-hFranklin* and *Rpsp-hYerong* were applied to these genes. At the adult plant stage, three QTLs were identified in the same population; two were located in the same positions as *Rpsp-hYerong* and *Rpsp-hFranklin*, while the third was mapped to 5HS. Klos *et al.* (2016) highlighted QTL in ‘Lenetah × Grannelose Zweizeilige’ recombinant inbred line cross and reported a major seedling resistance QTL on chromosome 4H in cultivar ‘Grannelose Zweizeilige’. Using *Psh* races from North America and Europe, Klos *et al.* (2016) and Dracatos *et al.* (2016) respectively reported QTL mapping of resistance at the seedling stage. Visionsi *et al.* (2018) observed 18 QTL for resistance to barley stripe rust in adult plant stages and 45 QTL distributed over the seven barley chromosomes for seedlings resistance to five races. Vatter *et al.* (2018) used 5,715 informative SNPs to explore SNP-based nested association mapping in HEB-25. Twelve robust QTL were found to be associated with resistant and eight of these were deemed novel.

Table 2: QTLs conferring resistance to yellow rust in barley

QTLs	Chromosome Location	Markers	Method	References
QYr1H, QYr3H	1H, 3H	RFLP markers	Linkage Mapping	Toojinda <i>et al.</i> , 2000
QYr2H, QYr7H	2H, 7H	AFLP markers	Linkage Mapping	Castro <i>et al.</i> , 2003
QYr5H, QYr6H	5H, 6H	SSR markers	Linkage Mapping	Derevnina <i>et al.</i> , 2015
QYr1H, QYr3H, QYr7H	1H, 3H, 7H	SNP markers	GWAS	Vatter <i>et al.</i> , 2018
QYr2H, QYr5H	2H, 5H	SSR markers	GWAS	Verma <i>et al.</i> , 2018
QYr4H, QYr6H	4H, 6H	SNP markers	GWAS	Visionsi <i>et al.</i> , 2018

Till date, seven *Rps* (Resistance to *Puccinia striiformis*) loci have undergone genetic mapping- *Rps1* on chromosome 3H (Yan and Chen, 2007), *Rps4* on chromosome 1H (Johnson 1968), *rps5* (*rpsGZ*) on chromosome 4H (Klos *et al.*, 2016), *Rps6* on chromosome 7H, *Rps7* and *Rps8* on 1H and 4H, respectively (Bettgenhaeuser *et al.*, 2021); and *Rps9* on 5H (Clare *et al.*, 2016). Chen *et al.* (1994) identified two genes conferring resistance to the barley stripe rust in Mexico and South America germplasm against race 24. These genes were mapped to the M arms of barley chromosomes 7 and 4 in a doubled haploid

population using molecular markers and QTL mapping approach. Two additive effect QTL loci that confer resistance to *P. striiformis* f. sp. *hordei* in ‘HOR1428’ were mapped by Clare *et al.* (2016) which were located on chromosomes 3H and 5H. Li *et al.* (2016) using a high-density mapping population (>10,000 gametes) precisely mapped *Rps6* within a 0.14 cM region (~500 kb contig). An intermediate host resistance gene in barley, also thought to provide resistance against wheat stripe rust, ‘*Rps6*’, was isolated, fine-mapped, and positioned to chromosome 7H by Dawson *et al.* (2016).



Breeding yellow rust resistant barley varieties

Sustainable control of pathogens is possible through the manipulation and deployment of resistance genes in cultivars, thereby providing in-built resistance with no extra cost and avoids the harmful effects of chemicals on environment. The development of high yielding cultivar with enhanced disease resistance is quite challenging which involves identification of resistant sources, understanding of the mode of genetic inheritance of the character, followed by hybridization and selection approach. Different breeding strategies have resulted in the development of several yellow-resistant barley varieties (Kumar *et al.*, 2012, Bishnoi *et al.*, 2022; Kumar *et al.*, 2020). A multitude of varieties, including BHS169, BH393, DL88, NDB1173, and VLB56 have been developed through hybridization and selection methods (Singh *et al.*, 2016). However, sometimes, exotic germplasm are also used for direct release of varieties, for example barley lines LSB2, Dolma, HBL113, BHS400, VLB118, and BHS380 received from ICARDA have been released directly for cultivation in Northern Hill Zone of India (Gangwar *et al.*, 2018). Pyramiding multiple disease resistance genes into high yielding germplasm remains a major challenge in barley breeding. Singh (2008) reported barley cultivars RD2508, RD2035, DWRUB52, RD2552 and RD2624 with multiple disease resistance in India and accessions BCU167 from the indigenous and BCU51, 26 and BCU127 from the exotic collection having multiple resistance (Yadav and Kumar, 1999). The previous, laborious, and time-consuming classical approaches were primarily used by barley breeders which involved simple genetics, selection, mutation breeding, and hybridization. Therefore, barley breeders turned to the more advanced and integrated molecular approaches in order to expedite resistant breeding (Harwood, 2019).

Doubled haploid breeding in barley for yellow rust resistance

Cultivated barley is an inbreeding species so superior lines which are homozygous and true breeding needs to be developed. This when achieved through conventional plant breeding techniques is time consuming (approximately 10 + years) (Patial *et al.*, 2015; Patial *et al.*, 2021; Patial *et al.*, 2022). Therefore, the importance of haploid and doubled haploid (DH) techniques to speed the genetic gain in breeding programs as well as in basic and applied

research cannot be overstated. For cultivated barley improvement programme, plant breeders have used *H. spontaneum* (Thomas *et al.*, 1987) and other wild species as a novel gene source but, the resultant hybrids are sterile or non-viable. Hence, transfer of important and novel traits through conventional approach becomes unrealistic. By applying DH technique, successful hybrid can be rescued and from the early breeding generations, genotypes carrying the trait to be introgressed (Patial *et al.*, 2023; Patial and Verma 2023), as well as having the highest possible proportion of the elite genome, can be selected quickly (Patial *et al.*, 2016; 2017; 2019; 2023b; Patial and Pal 2017).

Clapham (1973) developed first haploid in barley and haploid production mechanism in the crop was investigated by Sunderland (1974). A plethora of *in-vivo* and *in-vitro* protocols exists to accommodate the widely varying degrees of response between species to DH induction in barley (Patial *et al.*, 2022). Initially wide hybridization technique between *H. vulgare* with *H. bulbosum* was available and resulted in development of DH in most genotypes of barley (Kasha and Kao, 1970) and this technique have become routine tools in barley for direct release of cultivars. Later improvement in anther culture (Kao, 1981) and isolated microspore culture (Kasha, 1990) were perfected for barley breeding programmes. However, due to genotypic non-specificity, the *bulbosum* method is the most commonly used to produce barley haploids (Choo *et al.*, 1985). Barley has over 100 direct DH cultivars (Forster and Thomas, 2005; Weyen, 2009) released in Canada (Mingo, Rodeo), New Zealand (Gwylan), the U.K. (Doublet) and other countries. Using anther culture technique, barley cultivars ‘Anthere’ (D, 1995), ‘Henni’ (D, 1995), ‘Sarah’ (D, 1997), ‘Uschi’ (D, 1997), ‘Carola’, ‘Nelly’ (D, 1998) and “Ya/LM94-PC27” resistant to stripe rust (Gomez-Pondo *et al.*, 2009) were released. Gomez-Pondo *et al.* (2009) produced DH barley lines with higher yield, grain quality and resistance to stripe rust from anther culture technique. Due to DH advances, barley is considered the cereal model crop species for haploid production and research.

A number of DH lines have been developed and used for inheritance and breeding studies against different biotic stresses. For triple disease resistance (stem rust, leaf rust and powdery mildew), Steffenson *et al.* (1995) developed



anther culture F_1 population from a cross of accession 'Q21861' and the susceptible line 'SM89010' with reported inheritance of one gene and two genes.

In addition to variety development, DH populations are a significant research tool for mapping single locus genes and QTL controlling traits of interest (Patial *et al.*, 2019; Gandi *et al.*, 2023). Today DH populations are used routinely in mapping. Toojinda *et al.* (2000) outlined the number, location, and function of genes that confer resistance to BYDV, leaf rust, and stripe rust diseases using 94 DH lines. In the same population, they also mapped Resistance Gene Analog Polymorphism loci based on degenerate motifs of cloned disease resistance genes. The DH population has served as a major study material for breeders and geneticist. The technique offers an opportunity to speed up traditional breeding methods, can be applied at any generation thereby allows greater flexibility and allowing rapid response to changing market demands.

Innovative barley breeding approaches: Molecular and Genomics tools for yellow rust resistance

With the development of the modern molecular breeding tools, plant breeding is becoming ever more precise, easier, and faster and offers the opportunity to increase the speed and efficiency. Many barley breeding programs now routinely use molecular technologies, such as marker assisted selection (MAS), virus-induced gene silencing (VIGS), targeted induced local lesions in genome

(TILLING), genomics, recombinant DNA technology, and gene cloning to identify major loci controlling disease resistance. The potential applications of molecular breeding in crop plants for developing disease resilience have been well discussed by many researchers (Diab, 2006; Kota *et al.*, 2001; Varshney *et al.*, 2007).

Marker technology for yellow rust resistance breeding

The use of molecular markers in barley improvement is routinely applied in many breeding programs for major loci controlling disease resistance. Markers have been primarily used in backcross breeding to select lines with a genome composition similar to the recurrent parent and to introgress recessive traits. Markers have shown to be useful in progeny breeding for developing valuable parents and enriching F_1 s with intricate crosses. Earlier, RFLP markers were employed to develop the first comprehensive molecular marker maps in barley (Graner *et al.*, 1991) which led to the mapping of a series of agronomic, quality and disease resistance traits (Friedt and Ordon, 2008). Subsequently, a number of barley genetic maps based on different DNA markers (such as AFLPs, RAPD, RFLPs, STSs, and SSRs) were published (Varshney *et al.*, 2007). Now, SNP markers are rapidly replacing SSRs or Diversity Arrays Technology (DArT) markers because they are more abundant, reproducible, amenable to automation and increasingly cost-effective (Diab, 2006). The shift from RFLP to SSR and SNP markers has been important in facilitating the tracking of resistant genes in

Table 3: Introgression of disease resistance in barley through MAS

Gene (s)/QTLs	Recurrent Line (s)	Donor Line (s)	Marker type (name)	Reference
QTLs on chromosomes 4 (4H) and 7 (5H),	Steptoe	BSR41	106 AFLPs, and eight RAPDs	Toojinda <i>et al.</i> (1998)
QTLs 4, 7 QTL 5	Galena	Accession CI10587 (PI 243183)	SSRs	Castro <i>et al.</i> (2003)
QTL on 1H, 4H, 5H	BCD47 and BCD12	Baronesse	SSR (GMSO21, kO6267, Bmac0213, EBmac0679, HvMLO3, Bmag0337)	Richardson <i>et al.</i> (2006)
QTLs on 1H, 2H, 3H, 5H	Harrington	CIho 3515	SNP (9K iSelect)	Wellings <i>et al.</i> (2011)
QTLs on 1H, 3H, 7H	Chevron	CIho 3515	SSR (HvMLO3, Bmag0337)	Smith <i>et al.</i> (2015)
QTLs on 4H, 5H, 6H	Barke	CIho 3515	SNP (9K iSelect)	Visioni <i>et al.</i> (2018)
QTLs on 2H, 3H, 6H	Morex	CIho 3515	SNP (9K iSelect)	Gyawali <i>et al.</i> (2021)



barley. This systematic development of functional markers was facilitated with Expressed sequence tags (ESTs) using appropriate software tools (Thiel *et al.*, 2004). The ESTs helps to identifying sequence polymorphism (mainly single-nucleotide and small InDels) in the corresponding EST alignments from multiple-genotypes of barley, which have been exploited for the development of markers. A computer algorithm SNiPping for discovery of functional markers (Kota *et al.*, 2001), SNP2CAPS for computational conversion of SNP markers into CAPS markers (Thiel *et al.*, 2003) and consensus maps (Diab, 2006; Varshney *et al.*, 2007) has been developed for barley. Barley's qualitative resistance mechanisms have been thoroughly investigated in terms of genomic location and specificity (Thomas *et al.*, 1995; Giese *et al.*, 1993; Graner and Tekauz, 1996), and in scenarios where a genetic map is unavailable, researchers occasionally employ Bulk Segregant Analysis (BSA) to map resistant genes.

Gene cloning in barley

To provide much needed protection against virulent pathogen strains, cloning of resistance (R) genes from wild or sexually incompatible species is required. Also, when R genes are bred one at a time into crop lines, the protection that they confer is often overcome within a few seasons by pathogen evolution. However, if several cloned R genes were available, it would be possible to pyramid R genes in a crop, which might provide more durable resistance. Dracatos *et al.* (2019) used "MutChromSeq" a recently developed molecular genomics tool for the rapid cloning of genes in plants, to clone the first leaf rust resistance gene, *Rph1* (*Rph1.a*), from cultivated barley.

Next-generation sequencing (NGS) in barley

In barley, NGS methods- reduced-representation libraries (RRLs) (You, 2011; Gompert *et al.*, 2010), complexity reduction of polymorphic sequences (CRoPS) (Mammadov *et al.*, 2010), restriction-site-associated DNA sequencing (RAD-seq) (Baxter, 2011) and low-coverage sequencing for genotyping (Andolfatto *et al.*, 2011; Elshire *et al.*, 2011) are valuable for genome-wide marker development, genotyping and targeted sequencing across the genomes. Recent rapid advances of NGS facilitate the identification of novel rust resistant genes in barley.

Future priorities

Barley, a crop of rainfed agriculture, can serve as an important crop for supplementing the forage and grain demand of the farmers. Apart from developing better varieties for biotic stresses, the variety suitable for brewery, dual purpose and resistant to abiotic stresses will add to the value of the crop. Over the decades, tireless efforts of barley breeders to transfer adaptive traits/genes from landraces to elite genotypes and modern cultivars have met with little success; apparently, due to problems of linkage drag, more residual heterozygosity and complex adaptive gene cassettes involved in metabolic pathways. Emphasis should be placed on increasing the yield potential of barley landraces without altering their adaptation: landraces need to be invariably used as recipient rather than as donor parents. With the advent of marker-assisted and omics-based tools a great opportunity is available to barley breeders for transferring gene(s)/QTLs from landraces to popular cultivars while minimizing problems like linkage drag. Breeding strategy to introgress noble genes from wild genetic resources to the cultivated barley through pre-breeding aided with markers technique is required. The breeding for yellow rust resistance should focus on pyramiding of genes having seedling and adult plant resistance

Barley being highly adaptable can be an excellent source of genes for stress tolerance. An increased adoption of MAS in barley rust resistance breeding programs requires a rapid genomics research, new high-throughput marker genotyping platforms, a large number of markers and parallel development of user friendly software and databases and complete barley genome annotation which will raise the likelihood of finding potential resistance genes underlying various illnesses.

Acknowledgments

The authors acknowledge ICAR-IARI, New Delhi for inhouse project on rust resistance barley breeding at ICAR-IARI, Regional Station, Tutikandi Centre, Shimla (H.P).

Author contributions

The review was written and enriched by MP and SKB. All authors read, edited, and approved the final manuscript.

Conflict of interest

No



Declaration

The authors declare no conflict of interest.

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