



Potential Breeding Strategies for Developing Disease-Resistant Barley: Progress, Challenges, and Applications

9

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Abstract

There is a pressing call for enhancing world food production by at least 60% by 2050 using the same acreage. Barley (*Hordeum vulgare* L.), considered to be a risk-avoidance crop, is the fourth-most important grain crop in the world in terms of production after maize, wheat, and rice. The major barley producing countries are the Russian Federation, Germany, Canada, France, Spain, and Ukraine. Cultivated barley is an annual self-pollinating, true diploid ($2n = 2x = 14$) cereal, primarily grown for its grain and mainly used as feed for livestock. The rest of the barley grain is used as malted barley, as well as for human food and health food. Barley also yields valuable forage that can be grazed; cut for green forage, hay or silage while still green; cut for dual purpose (green forage and grain); or cut for straw after grain harvest. Cultivated barley is adapted to stress-prone environments, marginal and waste lands. Its wider adaptability, however, exposes the barley crop to different biotic stresses such as insects, phytopathogens, and weeds. Among them, plant pathogens are the most important constraints for the quality production of barley. Although more than 250 different plant pathogens infect barley, only a few of them cause considerable economic yield loss. In commercial barley production, disease management relies heavily on fungicide applications around the globe, which leads to higher production costs. Further, the heavy doses of fungicides create residue problems in fodder and grain and also lead to the development of resistant races or pathotypes. Hence, the best approach for managing barley diseases is by developing disease-resistant varieties. Earlier, the classical breeding approaches were followed to develop resistant varieties, but this approach provides only short-term relief, and the

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163

breakdown of resistance occurs very fast. To overcome these challenges, researchers changed their aim to advance breeding strategies with new molecular approaches like marker-assisted selection (MAS); marker-assisted backcrossing (MABC); targeting induced local lesions in genomes (TILLING); RNA interference (RNAi); virus-induced gene silencing (VIGS); genome editing; and RNA-dependent DNA methylation (RdDM) to breed disease-resistant barley varieties.

Keywords

Disease resistance · Molecular breeding · Powdery mildew · Rusts · Spot blotch · Stripe disease · Smut disease

9.1 Introduction

Cultivated barley, botanically known as *Hordeum vulgare* (L.), is the earliest domesticated coarse cereal (Zohary and Hopf 2000; Harwood 2019) in the Poaceae family, grown during the winter season. It is the fourth most important grain crop grown in the world after maize, rice, and wheat, with a share of 7% of global cereal production (Gangwar et al. 2018; Reddy et al. 2014). Barley is primarily grown for its grain, which is mainly used as animal feed. The second use of barley grain is as malted barley for alcoholic beverages, particularly beer. Barley grain is used as human food as well as healthy food. The main type of fiber found in whole grains is beta-glucan. It is also commonly used in the preparation of bread, soups, cakes, and other healthy products. Almost 70% of total barley production is used for cattle and poultry feed, 25% for malt and malt extract, and 5% for human consumption (Gangwar et al. 2018; Singh et al. 2016). Barley produces valuable forage in addition to grain, which can be grazed, cut for green forage, hay, or silage while still green in the field, cut for dual purpose (first for green forage at vegetative stage and then regenerated for grain), or cut for straw after grain harvest. Barley straw is used as fodder for ruminants and as bedding material. Cultivated barley is a self-pollinating, diploid ($2n = 2x = 14$), annual temperate grass capable of growing in various stress conditions like salinity, drought, higher altitude, and low fertilization. Hence, this characteristic makes barley grow in marginal and waste lands, so it is also known as the poor man's crop (Verma et al. 2012).

On the basis of spike morphology, barley is grouped into two types: two row and six row, while on the basis of growth habit into three types: winter, spring, and facultative (Poehlman 1994). It is also classified into hulled and hullless barley on the basis of grain type. The lemma and palea are fused to the pericarp in hulled barley, whereas chaff is easily separated from the grain in hullless type. Hullless barley is used for human consumption due to its higher nutritive value. Barley grain consists of 20% of dietary fiber and 3–7% of β -glucan (Oscarsson et al. 1996). The β -glucan of barley has significant blood cholesterol-lowering effects (Martinez et al. 1991). Moreover, Barley-glucan and non-starch polysaccharide increase the viscosity of

food material in the intestine which decreases its rate of digestion and absorption (Anderson et al. 1990; Newton et al. 2011), thus useful to people with diabetes (Gosain 1996). Because of its multifarious utilities, nutritive value, and increased industrial demand, sustainable yield gains will be needed over future decades. However, biotic stresses are the most serious constraints to barley production in which phytopathogens cause total crop loss to the tune of about 20–45% (Bellard et al. 2012; Savary et al. 2012). Barley is infected by more than 80 different plant pathogens which cause diseases like yellow and brown rust, covered smut, powdery mildew, net blotch, spot blotch, barley stripe, barley yellow dwarf, and molya diseases which are economically important in a global context (Mathre 1997). Disease resistance has been the second highest priority after grain yield in barley breeding. Here, we are trying to highlight the major diseases of barley along with their major symptoms and disease developmental conditions. We are also including various molecular techniques that have been utilized in the discovery and classification of disease-resistant genes in barley.

9.2 Major Diseases of Barley

The wider adaptability exposes the barley crop to different biotic stresses such as insects, phytopathogens, and weeds. Among them, diseases are the most important constraint for the production of quality barley (Pessaraki 2016). Phytopathogens include fungi, bacteria, plant parasitic nematodes, and viruses that cause infection in cultivated barley. The most important diseases responsible for considerable losses are mentioned below.

9.2.1 Powdery Mildew

It's a common disease of cultivated barley, caused by fungal pathogen *Blumeria graminis* f. sp. *hordei*. Early infection can cause yield loss to the tune of 25%, while infection at later stages affects yield loss by 10%. The disease incidence is more during the early crop growth stage, but symptoms are first noticed at tillering stage (Fig. 9.1). Both winter and spring barley varieties are susceptible to powdery mildew disease. *Blumeria graminis* f. sp. *hordei* is a biotrophic pathogen and disease is favored by cool (15–25 °C) and humid weather, but can also occur in warmer and semiarid environments. The important symptoms of the disease are whitish, fuzzy fungal mycelium seen on the surface of leaves. Later, powdery or fluffy white pustules of conidial chain are noticed on the leaves. The entire spikes of plants can be infected with powdery mildew in addition to the leaves and leaf sheaths.

Fig. 9.1 Powdery mildew in barely



9.2.2 Rusts

Rusts are the most devastating diseases of barley (Duplessis et al. 2011), and these pathogens have evolved further into many distinct physiological races or pathotypes. Barley is infected by four different rusts, i.e., stem, leaf, yellow, and crown rust, all caused by members of the genus *Puccinia*, family Pucciniaceae, order Pucciniales, class Pucciniomycetes, subphylum Pucciniomycotina, Phylum Basidiomycota, kingdom Fungi, and domain Eukarya (Bauer et al. 2006).

9.2.2.1 Black Stem Rust

Black stem rust of barley caused by *Puccinia graminis* f. sp. *tritici* is the most important disease. It infects the crop late in the season; therefore, the losses are minimal. The symptoms that develop predominantly occur on the leaf, blade, sheath, and stem. Severe infections with many stem lesions may weaken plant stems and result in the breaking of stems at the point of infection. Initially, rust pustules are reddish-brown and later turn into black telia containing teliospores (Bhardwaj et al. 2017). Favorable conditions for infection require a temperature range of 15–28 °C with 6–8 h of free moisture on the leaf surface. Secondary infection occurs if wet weather persists and the temperature remains in the range of 26–30 °C. Several cycles of uredospore production occur during the growing season.

9.2.2.2 Crown Rust

Crown rust of barley is caused by *Puccinia coronata* f. sp. *hordei*. Outbreak of crown rust disease on barley was seen during 1991 in south central Nebraska, U.S.A. (Jin and Steffenson 1999). Pathogen infects leaf blades, leaf sheaths, peduncles, and awns. Symptoms starts on leaf blades; uredial pustules are linear, oblong with orange to yellow color, followed by chlorosis.

9.2.2.3 Yellow (Stripe) Rust

Yellow rust is an important foliar disease of barley caused by *Puccinia striiformis* f. sp. hordei. Early infection of yellow rust causes severe yield loss and also prevents spike emergence or grain formation/development (Prakash and Verma 2009). In cooler climates (2–15 °C), the disease is more severe, followed by prolonged leaf wetness (8–10 h). Uredial pustules are seen on leaves as narrow stripes that are orange to yellow in color, and as disease progresses, the yellow stripes continue to enlarge because of the partial systemic nature of pathogens. Black telia readily develops from uredia as infected barley plants approach maturity. The uredial and telial spore stages of *P. striiformis* f. sp. hordei occur on barley and various *Hordeum* spp. (Marshall and Sutton 1995).

9.2.2.4 Leaf (Brown) Rust

Leaf rust, or brown rust, is a sporadic and most common disease of barley, caused by the basidiomycota fungi *Puccinia hordei*. Small orange or brown uredial pustules are mainly scattered on the upper surface of the leaf. Infection is also seen on the leaf sheath. Uredial pustules are surrounded by chlorotic halos, or green islands. Secondary spread occurs by urediospore, which is formed within 7 to 10 days after infection. A temperature ranging from 20 to 25 °C and prolonged wet weather are prerequisites for the faster spread of the disease.

9.2.3 Spot Blotch

Spot blotch, caused by the fungus *Bipolaris sorokiniana* (teleomorph: *Cochliobolus sativus*), is a major foliar disease of barley (Arabi and Jawhar 2004). It occurs in the warmer and more humid regions of the world. Yield losses in susceptible varieties range from 10% to 30%. Spot blotch disease development is favorable when temperatures are 15–22 °C and relative humidity is greater than 90%. Hence, the spot blotch disease of barley is considered to be one of the major threats to barley production under climate change (Singh et al. 2014a, b). Infection is characterized by small, dark brown lesions. As disease progresses, lesions are restricted in width by leaf veins and turn dark brown with a chlorotic margin. Heavily infected leaves dry out and die prematurely. If inoculum is available and the environmental conditions are conducive to infection, the kernel blight phase (black point) of this disease may develop.

9.2.4 Stripe Disease

Stripe disease of barley is caused by *Drechslera gramineae*, and the fungal pathogen causes systemic infection only in barley. Symptoms start as small lesions on seedlings and the most characteristic symptoms are long, narrow, and straw-colored streaks or stripes that appear on the leaves. Later, parallel stripes may extend the entire length of the leaf blade. The light straw-colored streaks soon turn to brown,

which leads to the drying out and splitting of the leaf blade. Severely infected plants shrivel and die prematurely. Infected plants are severely stunted with few tillers and the spikes fail to emerge. The ears that do emerge are greyish brown, withered, twisted, erect, and often barren. The fungal pathogen remains alive for 3 years.

9.2.5 Net Blotch

The fungal pathogen fungi *Pyrenophora teres* causes barley net blotch, an important and destructive disease of barley. Under favorable environmental conditions, the disease can be prevented (Murray and Brennan 2010). Disease has the potential to cause yield losses of 10–44% in susceptible cultivars. Small dark brown lesions are seen on leaves, sheaths, and glumes, which later develop into short brown stripes or irregular blotches. Lesions may be surrounded by a yellow area. The ear can also be infected, but lesions do not usually appear. The infection is more severe in humid periods lasting for 10 or more hours at an optimum temperature of 15–20 °C.

9.2.6 Smut Diseases

9.2.6.1 Loose Smut

Loose smut, an internally seed-borne disease of barley, is caused by *Ustilago tritici*. When an infected seed germinates, the dormant mycelium inside the seed begins to grow and causes systemic infection. The smut pathogen shows host specialization, i.e., isolates that attack wheat do not attack barley and vice versa. The most obvious symptoms occur only after the emergence of spikes. Infected ear heads emerge earlier than normal, and grains are replaced with a mass of dark brown to black teliospores. Disease spread is by wind-blown teliospores from smutted ears to adjacent healthy flowering ears of barley. The teliospores grow and invade the female parts of barley flowers. They then spread to the developing embryo.

9.2.6.2 Covered Smut

Covered smut of barley is one of the most common diseases caused by *Ustilago hordei*. Smutted ear heads emerge at the same time or slightly later than healthy plants. All the grains in the diseased spike and the entire spikes in the diseased plants are infected. All the infected grains in the diseased spike are transformed into masses of teliospores and these teliospores are held by tough greyish white membrane. The membrane is the glume that usually remains intact until harvest or threshing.

9.2.7 Barley Yellow Dwarf Disease

It is caused by the *Barley Yellow Dwarf Virus* (BYDV), a member of the Luteovirus group. The virus causes a 100% yield loss if infection occurs at an early stage of growth (Mathre 1997). Initial symptoms are seen in plants randomly scattered in the

field. The most common noticeable symptoms are yellowing of leaves and a reduction in the growth of plants, which appear either singly or in small patches. Discoloration in shades of yellow, red, or purple is observed in the leaves of infected plants, which typically starts at the tip or margin and moves towards the downside or midrib, respectively. Leaves stand upright and rigid with rough leaf margins along with less tillering, flowering, and sterile florets, which results in fewer filled and smaller kernels with corresponding yield losses.

9.3 Sources of Disease-Resistant Genes

In the absence of genetic resistance, crop production is highly dependent on chemical control of pathogens. Barley disease management depends on repeated application of chemical fungicides, but use of resistant varieties offers both an economical and an environmentally sound method of management. The development of resistant varieties is complicated and needs time, besides being broken by different pathotypes of the pathogen. Bovill et al. (2010) attempted to identify the source of resistance against spot blotch disease of barley caused by *Bipolaris sorokiniana* (teleomorph: *Cochliobolus sativus*). Australian barley cultivars are highly susceptible to spot blotch disease, and hence, resistance sources have been identified in North American two-row barley lines. In adult plants, spot blotch-resistant QTL were found on chromosomes 3HS and 7HS, but seedling resistance is controlled by a locus on chromosome 7HS. A total of 124 accessions of two-row barley were screened for spot blotch resistance for 3 years under natural epiphytotic conditions (Singh et al. 2014a, b). Accessions, viz. BCU422, BCU1204, and BCU5092, are identified as resistant sources against the spot blotch pathogen, while BCU711, K603, and RD2506 are noted as the most susceptible fungal pathogens to *Bipolaris sorokiniana*. Several resistance genes (Mla1-Mla31 except Mla4, and Mlmr) are identified against powdery mildew disease in barley and many more specific resistances have been detected in cultivars, landraces, and wild barley. Dreiseitl (2011) described three specific powdery mildew-resistant genes (Ml (Ro), MlaLv, and Ml (Ve)); they are widely used in commercial cultivars. In 20 barley accessions, 39 powdery mildew-resistant genes are identified (Mastebroek et al. 1995). Dreiseitl and Bockelman (2003) screened 1383 accessions collected from United States Department of Agriculture (National Small Grains Collection). Among 1383 accessions, 123 accessions were resistant to 22 isolates.

9.4 Breeding Approaches for Disease Resistance

Durable resistance offers great prospective for global food security and sustainability. Developing high-yielding barley varieties with enhanced resistance to biotic and abiotic stresses and improved quality for feed, malt, food, and fodder is imperative. Presently, researchers are trying to bring two or more desirable traits together, like, for example, higher yield with enhanced resistance towards different

Table 9.1 Various approaches for disease resistance breeding in barley

S. No.	Approaches
1	Conventional breeding <ul style="list-style-type: none"> • Introduction of exotic lines • Selection • Hybridization • Backcrossing • Mutagenesis using chemicals and radiations
2	Marker-assisted breeding <ul style="list-style-type: none"> • Marker-assisted selection • Marker-assisted backcrossing • Genome-wide association mapping • Genomic selection
3	Targeting induced local lesions in genome <ul style="list-style-type: none"> • Eco-TILLING • DEco-TILLING
4	Transgenics <ul style="list-style-type: none"> • Agrobacterium-mediated transformation and regeneration protocols • RNA interference • Virus-induced gene silencing • Genome editing tools • Overexpression of genes • Tissue or developmental stage-specific expression of genes • Constitutive expression of genes • Promoter trap • Enhancer trap

biotic and abiotic factors and improved dietary value of grain and fodder. Classical, genetic, molecular, and new breeding approaches/technologies against diseases in barley are mentioned in Table 9.1.

The modern high-yielding barley varieties and breeding lines developed worldwide are found to have a restricted genetic base in contrast to their natural ancestors as most of the breeding objectives were mainly restricted to fewer traits (Caldwell et al. 2005). Due to narrow genetic diversity, cultivated barley gene pool is vulnerable to various diseases. The gene pool of cultivated barley was defined and the wild progenitor, *H. vulgare* subsp. *Spontaneum*, is classified in the primary, *H. bulbosum* in the secondary, while all other species in the tertiary gene pool. Crop wild relatives are bestowed with desirable agronomic and stress-(biotic and abiotic) resistant traits which could be useful for plant breeding initiatives. Due to limited variability of resistant genetic resources in the cultivated gene pool of barley, significant attempts have been made to introduce promising alleles from natural ancestors and landraces into current breeding populations (Schmalenbach et al. 2008; Friedt et al. 2011).

Globally, around 4,66,531 accessions of barley gene pool are conserved, mainly by Canada and USA (FAO 2010). In order to increase the utilization of conserved barley germplasm for breeding programme, Knüpfper and van Hintum (2003) formed two core collections of wild barley (one with 70 accessions and another 144 accessions), while Steffenson et al. (2007) established Wild Barley Diversity

Collection (WBDC) with 318 accessions. These core subsets are presently preserved at the International Centre for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria. Fu and Horbach (2012) developed a core subset of 269 accessions representing 16 countries from the collection of 3782 accessions. Neupane et al. (2015) assessed 2062 accessions and identified 15 of them to have effective resistance against four diverse isolates of *Pyrenophora teres maculata* collected worldwide. Cope et al. (2021) analyzed 131 heritage cultivars and landrace lines of barley against four diverse isolates of Barley ‘Scald’ and three lines with new source of resistance were identified. The disease resistance against leaf stripe (*Drechslera graminea*) was reported in wild barley (*Hordeum spontaneum*) and barley landraces (Oğuz 2019). Fetch et al. (2003) reported high frequency of resistance for septoria speckled leaf blotch, leaf rust, net blotch, powdery mildew; intermediate for spot blotch; and low for stem rust in *Hordeum spontaneum*. They also reported two *H. spontaneum* accessions (Shechem 12–32 and Damon 11–11) having resistance for all the six diseases as mentioned. *Hordeum bulbosum* L. ($2n = 4x = 28$) belongs to the secondary gene pool of cultivated barley and has long been searched for novel disease-resistant alleles (Pickering et al. 2006; Fetch et al. 2009). The quantitative barley leaf rust resistance gene, Rph26, was fine-mapped within a *H. bulbosum* introgression on barley chromosome 1HL for pyramiding with other resistance genes (Xiaohui et al. 2018).

In barley, chromosome substitution lines (CSL) (Matus et al. 2003; Inostroza et al. 2008), nested association mapping (NAM) panels (Schnaithmann et al. 2014), advanced backcross lines (Pillen et al. 2003; Nice et al. 2016), and multi-parent segregating populations (MAGIC) (Sannemann et al. 2015) are being utilized for the identification of QTLs/genes responsible for disease resistance. Leng et al. (2018) identified, fine-mapped, and physically anchored a dominant spot blotch susceptibility gene *Scs6* to a 125 kb genomic region containing the *Mla* locus on barley chromosome 1H against pathotype 2 isolate (ND90Pr) of *C. sativus* in barley cultivar Bowman. Leng et al. (2020) also mapped genetic loci controlling spot blotch and powdery mildew diseases of barley using 138 recombinant inbred lines (RILs). They recognized two QTLs, QSbs-1H-P1 and QSbs-7H-P1, responsible for spot blotch on chromosomes 1H and 7H, respectively. Hickey et al. (2017) applied a novel modified backcross strategy for rapid trait introgression to the European two-rowed barley cultivar, Scarlett. Hautsalo et al. (2021) used four Multi-parent Advanced Generation Inter-Cross (MAGIC) populations in Genome-Wide Association Studies (GWAS) and identified nine areas on chromosomes 1H, 3H, 4H, 5H, 6H, and 7H associated with resistance, in which three of these regions are putatively novel resistance sources. Pogoda et al. (2020) assessed the severity of powdery mildew infection on detached seedling leaves of 267 barley accessions using two poly-virulent isolates and identified four candidate genes against powdery mildew attack. Therése et al. (2017) performed a genome-wide association study in a Nordic spring barley panel consisting of 169 genotypes and identified a total of four QTLs, one located on chromosome 4H and three on chromosome 6H.

Amouzoune et al. (2021) compared the Generation Challenge Program Reference set (GCP) with 188 accessions against the Focused Identification of Germplasm

Strategy (FIGS) with 86 accessions for identifying new sources of resistance against leaf rust of barley, and they reported FIGS as a better approach than GCP in yielding higher percentages of resistant accessions at adult plant-resistant stage. Bilgic et al. (2005) identified a gene (Rcs5) on chromosome 7H conferring seedling resistance to pathotype I (ND85F) whereas in another study, Bilgic et al. (2006) used a doubled haploid (DH) mapping population to identify a gene (designated as Rcs6) on chromosome 1H conferring resistance to pathotype 2 (ND90Pr) of *Bipolaris sorokiniana*.

9.5 Molecular Breeding Approaches for Disease Resistance

Barley production is harshly affected by a range of biotic stresses. Usually, breeding for disease-resistant genotypes involves manual inoculation of the pathogen into the host at the right stage along with the desirable conditions for disease development, but this technique is very cumbersome and can also lead to false negatives (Figs. 9.2 and 9.3). Therefore, use of advanced breeding approaches like Marker-Assisted Selection (MAS), Genome-Wide Association Studies (GWAS), QTL mapping, and high throughput molecular techniques like sequencing and genomics has been utilized in accelerating breeding programs for various qualitative and quantitative traits (Figs. 9.1 and 9.2). Long-lasting resistance requires combinations of several resistance genes and QTLs in a genome.

Host-based resistance is one of the most feasible and eco-friendly approaches for controlling disease-related losses in crop plants, and a diverse genetic base is one of



Fig. 9.2 Advanced breeding approaches for disease resistance

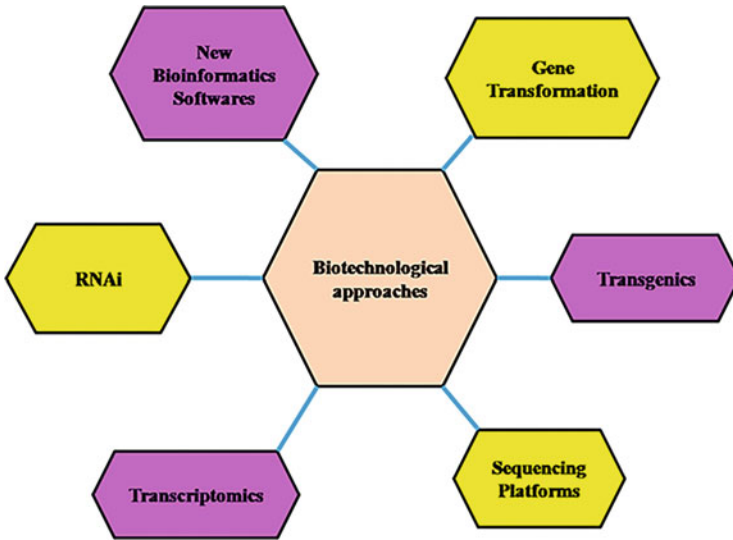


Fig. 9.3 Biotechnological approaches for disease resistance

the primary requisites for it. Barley has one of the oldest cultivated crops and has a rich genetic base, having geographically diverse wild accessions, landraces, and cultivars. The genome of barley has already been mapped, and there are many genomic resources available in public databases. These include expressed sequence tags, full length cDNA (FL-cDNA) sequences, genome sequences, and pan genomic data for 20 varieties of barley that include landraces, cultivars, and wild races (Zhang et al. 2004; Sato et al. 2009; Mayer et al. 2012; Jayakodi et al. 2020). Barley has a haploid genome size of nearly 5.1 Gigabases (gb) with nearly 26,000 highly confident genes as supported by transcript and homology data. The International Barley Genome Sequencing Consortium attempted sequencing of barley cv. Morex in 2012 using a hierarchical shotgun sequencing approach (Mayer et al. 2012). Molecular markers have served extensively in barley breeding programs for tracking useful genes and in their isolation (Stein and Graner 2005; Perovic et al. 2018). Single nucleotide polymorphism (SNP) markers are currently the most chosen markers due to their high throughput detection employing NGS (Ganal et al. 2018). With the advent of the 9 K Illumina iSelect chip and the 50 K Illumina Infinium array, the number of existing SNP markers has improved to 44,040 SNPs (Stein et al. 2007; Close et al. 2009; Bayer et al. 2017). Zang et al. (2015) tried to fine map the candidate gene responsible for loose smut resistance in barley by utilizing dense linkage map saturated with various useful markers like RFLP, microsatellite, and SNPs. They were able to enrich the genomic region associated with loose smut resistance. Sayed and Baum (2018) screened two groups (homozygous-resistant and susceptible), each comprising of 10 plants for barley scald disease caused by *Rhynchosporium commune* from the recombinant inbred line (RIL) population at F₇ generation with the help of 25 markers which lie close to scald-resistant genes.

Out of the 25 markers, only 5 markers showed clear discrimination between resistant and susceptible plants. They reported that most of these markers reside near to the centromeric region of the long arm of 3H chromosome. They anticipated that presence of polymorphic markers will be extremely helpful in discriminating breeding material in barley. Brueggeman et al. (2002) cloned *Rpg1* (Resistant to *Puccinia graminis* 1) gene against stem rust, caused by *Puccinia graminis* f. sp. *tritici* (*Pgt*) through high-resolution map-based cloning. The *Rpg1* gene encodes a receptor kinase-like protein with two tandem protein kinase domains. In Northern America, *Rpg1* gene offered strong resistance to barley varieties for nearly 40 years, but with the appearance of a new race of *Puccinia graminis* f. sp. *tritici* (*Pgt*) TTKSK, an alternative to *Rpg1*-resistant gene was needed. Jin et al. (1994) identified, cloned, and characterized the *rpg4*, a recessive gene against the same. The *rpg4* gene was later found on the chromosome 5H in barley (Borovkova et al. 1995). Fusarium head blight (FHB) is another devastating malady of barley which results in the reduction of grain yield and accumulation of deoxynivalenol (DON) mycotoxin in grains. It has been reported that the morphological and developmental characters of the host plant, e.g., earliness and plant height, are linked with pathogen infection and its severity. Ogrodowicz et al. (2020) investigated 100 recombinant inbred lines (RILs) by employing a barley Illumina 9 K iSelect platform and found a set of 70 quantitative trait loci (QTLs). They suggested tight association of yield-related traits with FHB-associated QTLs should be followed while designing a barley breeding programme for FHB resistance. Powdery mildew of barley is caused by *Blumeria graminis* f. sp. *hordei*. Recessive allelic form (*mlo*) of the barley *Mildew resistance locus o* (*Mlo*) locus provides broad spectrum resistance to the fungal pathogen, *Erysiphe graminis* f. sp. *hordei*. Büschges et al. (1997) utilized RFLP and AFLP marker systems for the purpose of gene isolation. Later, Hoseinzadeh et al. (2019) did high-resolution genetic and physical mapping of major powdery mildew-resistant locus in barley through GBS approach. Vatter et al. (2018) followed SNP-based nested association mapping (NAM) to map stripe rust and leaf rust resistance QTL in barley. They reported 8 new QTLs for stripe rust and 2 new QTLs for leaf rust. Hu et al. (2019) identified new major QTL on chromosome 5H along with two minor QTLs on chromosome 7H providing tolerance against barley yellow dwarf infection in barley. Visoni et al. (2020) employed High Input Association Mapping (HI-AM) panel comprising 261 spring barley genotypes (including released varieties, breeding material from ICARDA, and germplasm from GenBank) to map spot blotch-resistant QTLs at seedling and adult plant stages in barley by utilizing genome-wide association mapping (GWAM) approach. It was reported that expression of wheat Lr34 gene in transgenic barley lines imparted resistance against multiple fungal pathogens (Risk et al. 2013; Chauhan et al. 2015). Its constitutive expression in transgenic barley lines caused upregulation of senescence and pathogenesis-related genes, resulting in leaf tip necrosis in general and reduced height and total gain weight in extreme cases which can be overcome through regulated expression.

Host-delivered RNA interference (HD-RNAi) approach has been effectively used in various crop species to impart resistance, especially against viral diseases and

insect-pests damage (Tiwari et al. 2017; Joshi et al. 2020). In barley, there are few reports where researchers have used RNAi against phytopathogens, e.g., Kis et al. (2016) designed and expressed a polycistronic cassette of artificial microRNAs in barley against wheat dwarf virus and found higher level of resistance at low temperature conditions which are highly favorable for the insect vector to survive and spread disease. In contrast to HD-RNAi approach, RNA-spray-mediated approach has been also attempted, similar to pesticide application. Koch et al. (2016) sprayed 791 nt long noncoding dsRNA molecule (*CYP3*-dsRNA) targeting three essential genes of ergosterol biosynthesis pathway of *Fusarium graminearum*. Their study revealed increased level of resistance in the sprayed as well as non-sprayed portion of the detached leaves of barley. Acquired resistance observed in the non-sprayed areas of the leaves indicated systemic movement of interfering RNA from applied to adjacent non-applied areas through plant conducting tissues. Moreover, their research also enlightened the role of fungal RNAi machinery like fungal DICER-LIKE 1 (*FgDCL-1*) in spray-based RNAi approach. As per their study, mutant form of *FgDCL-1* was found to be nonfunctional against same insecticidal dsRNA. Recently, Werner et al. (2020) also used spray-based RNAi approach for silencing *ARGONAUTE* and *DICER* genes of *Fusarium graminearum* (*Fg*). They also observed enhanced resistance in barley leaves. Genome editing technologies have been deployed in various crop plants for imparting disease resistance. But, in barley very few attempts have been made due to lack of enough knowledge on techniques like gene transformation and tissue culture. Moreover, success of transformation is highly genotype-dependent. CRISPR-Cas9 technology has been employed in deciphering role of orthologous disease-related genes in barley by using model organisms in which protocols of genetic transformation are well-standardized (Low et al. 2020). Golden Promise is one such cultivar of barley which is highly amenable for genetic transformation and shows higher regenerability. Its genome has been recently sequenced and assembled through illumina-based next-generation sequencing platform (NGS), which could be definitely useful for entire barley research groups especially through CRISPR-Cas 9 platform (Schreiber et al. 2020). Kis et al. (2016) utilized CRISPR platform to enhance viral resistance in Golden Promise cv. of barley against *wheat dwarf virus*. Due to its successful transformation and regeneration ability, Golden Promise cv. was extensively used for transgenic research. Recently, Han et al. (2021) developed a highly efficient and genotype-independent gene editing technique based on anther culture. They found that their platform can generate a greater number of transgenic plants within a similar time frame along with high editing efficiency as compared to immature embryo protocols. This technology may play a crucial role in imparting disease resistance trait in commercial cultivars of barley as well as in functional validation of disease-related genes.

9.6 Conclusion

Barley, one of the oldest crops primarily grown for its grain, has the largest single use in feeding livestock throughout the world. Despite the overall decline in barley acreage, total production has increased due to the continuous improvement in barley productivity (yield per hectare). But no breeding program can develop varieties with acceptable levels of resistance to all diseases under all conditions. Moreover, the climate is constantly changing owing to various anthropogenic activities, which may further affect host and pathogen relationships. Therefore, our primary focus after higher grain yield is to impart broad spectrum resistance to the crop species with long-lasting impact. Traditional breeding methods (introduction of exotic lines, selection, hybridization, backcrossing, gene pyramiding) and modern breeding methods have been used to bring and improve resistance to biotic stresses in barley. Modern breeding approaches overcome the problems of traditional breeding strategies like more effort, more labor, transfer of non-desirable genes along with resistant genes, short-term relief, limited resistance sources, breakdown of existing resistance due to continuous evolution of new pathogen races, and being time-consuming. Advanced breeding and biotechnological methods like QTL mapping, gene mapping, MAS, MABC, TILLING, transgenics, RNA interference (RNAi)-mediated gene silencing, gene and genome editing using CRISPR-Cas9, along with bioinformatics and high throughput computational technologies, can enable us to engineer durable resistance in cultivated barley. The ability of the CRISPR platform to provide a transgene-free crop with desirable attributes is getting sincere applause among the scientific community. The availability of various bioinformatics tools will help us in the identification of pathogen-inducible promoters, key transcription factors, and noncoding RNAs pertaining to pathogen attack and disease development. They also allow us to decipher the actual biochemical roles of various disease-related genes in the disease signaling pathways, as gene annotation has become a major challenge in understanding their role. Global expression profiling techniques like suppression subtractive hybridization, microarray, serial analysis of gene expression (SAGE), and RNA seq. will allow us to capture the expression status of several genes in resistant and susceptible genotypes, which will definitely help us to focus on key or vital disease-related genes that could be used in the future. Whatever the approach (conventional or molecular breeding), our main concern is to increase productivity and minimize yield loss due to phytopathogens. It is very certain that advancements made in the science of molecular biology will become important pillars towards successful breeding methods in barley.

References

- Amouzoune M, Amri A, Benkirane R, Kehel Z, Al-Jaboobi M, Moulakat A, Abderrazek J, Rehman S (2021) Mining and predictive characterization for resistance to leaf rust (*Puccinia hordei* Oth) using two subsets of barley genetic resources. *Genet Resour Crop Evol.* <https://doi.org/10.1007/s10722-021-01268-4>

- Anderson JW, Deakins DA, Floore TL, Smith BM, Whitis SE (1990) Dietary fibre and coronary heart disease. *Crit Rev Food Sci Nutr* 29:95–147
- Arabi MIE, Jawhar M (2004) Identification of *Cochliobolus sativus* (Spot Blotch) isolates expressing differential virulence on barley genotypes in Syria. *J Phytopathol* 152:461–464
- Bauer R, Begerow D, Sampaio JP, Weib M, Foberwinkler (2006) The simple-septate basidiomycetes: a synopsis. *Mycol Prog* 5:41–66
- Bayer MM, Rapazote-Flores P, Ganal M, Hedley PE, Macaulay M, Plieske J, Ramsay L, Russell J, Shaw PD, Thomas W, Waugh R (2017) Development and evaluation of a barley 50k iSelect SNP array. *Front Plant Sci* 8:1792
- Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. *Ecol Lett* 15:365–377
- Bhardwaj SC, Gangwar OP, Prasad P, Khan H, Kumar S (2017) Understanding wheat rusts and managing them strategically. In: Gautam HR, Gupta SK (eds) *Diseases of commercial crops in India*. Neoti BookAgency Pvt. Ltd., New Delhi, pp 9–29
- Bilgic H, Steffenson BJ, Hayes P (2005) Differential expression of seedling and adult plant resistance to spot blotch in different genetic backgrounds of barley. *Theor Appl Genet* 111: 1238–1250
- Bilgic H, Steffenson B, Hayes P (2006) Molecular mapping of loci conferring resistance to different pathotypes of the spot blotch pathogen in barley. *Phytopathology* 96:699–708
- Borovkova IG, Steffenson BJ, Jin Y, Rasmussen JB, Kilian A, Kleinhofs A, Rosnagel BG, Kao KN (1995) Identification of molecular markers linked to the stem rust resistance gene rpg4 in barley. *Pythopathology* 85:181–185. <https://doi.org/10.1094/Phyto-85-181>
- Bovill J, Lehmensiek A, Sutherland M, Platz GJ, Usher T, Franckowiak J, Mace E (2010) Mapping spot blotch resistance genes in four barley populations. *Mol Breed* 26(4):653–666
- Brueggeman R, Rostoks N, Kudrna D, Kilian A, Han F, Chen J, Druka A, Steffenson B, Kleinhofs A (2002) The barley stem rust-resistance gene Rpg1 is a novel disease-resistance gene with homology to receptor kinases. *Proc Natl Acad Sci* 99(14):9328–9333
- Büsches R, Hollricher K, Panstruga R, Simons G, Wolter M, Frijters A, Van Daelen R, Van der Lee T, Diergaarde P, Groenendijk J, Töpsch S (1997) The barley Mlo gene: a novel control element of plant pathogen resistance. *Cell* 88(5):695–705
- Caldwell K, Russell J, Langridge P, Powell W (2005) Extreme population-dependent linkage disequilibrium detected in an inbreeding plant species, *Hordeum vulgare*. *Genetics* 172:557–567
- Chauhan H, Boni R, Bucher R, Kuhn B, Buchmann G, Sucher J, Selter LL, Hensel G, Kumlehn J, Bigler L, Glauser G (2015) The wheat resistance gene Lr34 results in the constitutive induction of multiple defense pathways in transgenic barley. *Plant J* 84(1):202–215
- Close TJ, Bhat PR, Lonardi S, Wu Y, Rostoks N, Ramsay L, Druka A, Stein N, Svensson JT, Wanamaker S, Bozdag S (2009) Development and implementation of high-throughput SNP genotyping in barley. *BMC Genomics* 10:582
- Cope JE, Norton GJ, George TS, Newton AC (2021) Identifying potential novel resistance to the foliar disease ‘Scald’ (*Rhynchosporium commune*) in a population of Scottish Bere barley landrace (*Hordeum vulgare* L.). *J Plant Dis Prot* 128:999–1012
- Dreiseitl A (2011) Resistance of ‘Roxana’ to powdery mildew and its presence in some European spring barley cultivars. *Plant Breed* 130:419–422
- Dreiseitl A, Bockelman HE (2003) Sources of powdery mildew resistance in a wild barley collection. *Genet Resour Crop Evol* 50:345–350
- Duplessis S, Cuomo CA, Lin YC, Aerts A, Tisserant E, Veneault-Fourrey C, Joly DL, Hacquard S, Amselem J, Cantarel BL, Chiu R (2011) Obligate biotrophy features unraveled by the genomic analysis of rust fungi. *Proc Natl Acad Sci U S A* 108(22):9166–9171
- FAO (2010) The second report on the state of the world’s plant genetic resources for food and agriculture. FAO, Rome
- Fetch TG Jr, Steffenson BJ, Nevo E (2003) Diversity and sources of multiple disease resistance in *Hordeum spontaneum*. *Plant Dis* 87(12):1439–1448

- Fetch T Jr, Johnston PA, Pickering R (2009) Chromosomal location and inheritance of stem rust resistance transferred from *Hordeum bulbosum* into cultivated barley (*H. vulgare*). *Phytopathology* 99(4):339–343
- Friedt W, Horsley RD, Harvey BL et al (2011) Barley breeding history, progress, objectives, and technology. In: *Barley*. Wiley-Blackwell, pp 160–220
- Fu Y-B, Horbach C (2012) Genetic diversity in a core subset of wild barley germplasm. *Diversity* 4(2):239–257
- Ganal MW, Plieske J, Hohmeyer A, Polley A, Röder MS (2018) High throughput genotyping for cereal research and breeding. In: Miedaner T, Korzun V (eds) *Applications of genetic and genomic research in cereals*. Woodhead Publishing, Sawston
- Gangwar OP, Bhardwaj SC, Singh GP, Prasad P, Kumar S (2018) Barley disease and their management: an Indian perspective. *Wheat Barley Res* 10(3):138–150
- Gosain, K (1996) Long-term effects of barley bread products on metabolic control of non-insulin-dependent diabetes mellitus. Master's thesis, University of Alberta, Edmonton, AB
- Han Y, Broughton S, Liu L, Zhang X-Q, Zeng J, He X, Li C (2021) Highly efficient and genotype independent barley gene editing based on anther culture. *Plant Comm* 2(2):100082
- Harwood WA (2019) An introduction to barley: the crop and the model. In: *Barley*. Humana Press, New York, pp 1–5
- Hautsalo J, Novakazi F, Jalli M, Göransson M, Manninen O, Isoahti M, Reitan L, Bergersen S, Krusell L, Damsgård Robertsen C, Orabi J, Due Jensen J, Jahoor A, Bengtsson T, PPP Barley Consortium (2021) Pyramiding of scald resistance genes in four spring barley MAGIC populations. *Theor Appl Genet* 134(12):3829–3843
- Hickey LT, Germán SE, Pereyra SA, Diaz JE, Ziems LA, Fowler RA, Platz GJ, Franckowiak JD, Dieters MJ (2017) Speed breeding for multiple disease resistance in barley. *Euphytica* 213(3):64
- Hoseinzadeh P, Zhou R, Mascher M, Himmelbach A, Niks RE, Schweizer P, Stein N (2019) High resolution genetic and physical mapping of a major powdery mildew resistance locus in barley. *Front Plant Sci* 10:146
- Hu H, Choudhury S, Shabala S, Gupta S, Zhou M (2019) Genomic regions on chromosome 5H containing a novel QTL conferring barley yellow dwarf virus-PAV (BYDV-PAV) tolerance in barley. *Sci Rep* 9(1):1
- Inostroza L, delPozo A, Matus I et al (2008) Association mapping of plant height, yield, and yield stability in recombinant chromosome substitution lines (RCSLs) using *Hordeum vulgare* subsp. *spontaneum* as a source of donor alleles in a *Hordeum vulgare* subsp. *vulgare* background. *Mol Breed* 23:365–376. <https://doi.org/10.1007/s11032-008-9239-6>
- Jayakodi M, Padmarasu S, Haberer G, Bonthala VS, Gundlach H, Monat C, Lux T, Kamal N, Lang D, Himmelbach A, Ens J (2020) The barley pan-genome reveals the hidden legacy of mutation breeding. *Nature* 588(7837):284–289
- Jin Y, Steffenson BJ (1999) *Puccinia coronata* var. *hordei* var nov.: morphology and pathogenicity. *Mycologia* 91:877–884
- Jin Y, Steffenson BJ, Miller JD (1994) Inheritance of resistance to pathotypes QCC and MCC of *Puccinia graminis* f. sp. *tritici* in barley line Q21861 and temperature effects on the expression of resistance. *Pathology* 84:452–455
- Joshi I, Kumar A, Kohli D, Singh AK, Sirohi A, Subramanian K, Chaudhury A, Jain PK (2020) Conferring root-knot nematode resistance via host-delivered RNAi-mediated silencing of four Mi-*msp* genes in Arabidopsis. *Plant Sci* 298:110592
- Kis A, Tholt G, Ivanics M, Várallyay É, Jenes B, Havelda Z (2016) Polycistronic artificial miRNA-mediated resistance to wheat dwarf virus in barley is highly efficient at low temperature. *Mol Plant Pathol* 17(3):427–437
- Knüpfper H, van Hintum TJJ (2003) Summarised diversity—the barley core collection. In: von Bothmer R, van Hintum TJJ, Knüpfper H, Sato K (eds) *Diversity in barley (Hordeum vulgare)*. Elsevier Science B.V., Amsterdam, pp 259–267
- Koch A, Biedenkopf D, Furch A, Weber L, Rossbach O, Abdellatif E et al (2016) An RNAi-based control of *Fusarium graminearum* infections through spraying of long dsRNAs involves a plant

- passage and is controlled by the fungal silencing machinery. *PLoS Pathog* 12(10):e1005901. <https://doi.org/10.1371/journal.ppat.1005901>
- Leng Y, Zhao M, Wang R, Steffenson BJ, Brueggeman RS, Zhong S (2018) The gene conferring susceptibility to spot blotch caused by *Cochliobolus sativus* is located at the Mla locus in barley cultivar Bowman. *Theor Appl Genet* 131(7):1531–1539. <https://doi.org/10.1007/s00122-018-3095-5>
- Leng Y, Zhao M, Fiedler J, Dreiseitl A, Chao S, Li X, Zhong S (2020) Molecular mapping of loci conferring susceptibility to spot blotch and resistance to powdery mildew in barley using the sequencing-based genotyping approach. *Phytopathology* 110:140–146
- Low YC, Lawton MA, Di R (2020) Validation of barley 2OGO gene as a functional orthologue of Arabidopsis DMR6 gene in Fusarium head blight susceptibility. *Sci Rep* 10(1):1–3
- Marshall D, Sutton RL (1995) Epidemiology of stripe rust, virulence of *Puccinia striiformis* f. sp. hordei, and yield loss in barley. *Plant Dis* 79:732–737
- Martinez VM, Newman K, Newman CW (1991) Barley diets with different fat sources have hypocholesterolemic effects in chickens. *J Nutr* 122:1070–1076
- Mastebroek HD, Balkema-Bomstra AG, Gaj M (1995) Genetic analysis of powdery mildew (*Erysiphe graminis* f. sp. hordei) resistance derived from wild barley (*Hordeum vulgare* ssp. *Spontaneum*). *Plant Breed* 114:121–125
- Mathre DE (1997) Compendium of barley diseases. American Phytopathological Society, St. Paul, MN
- Matus I, Corey A, Filichkin T, Hayes PM, Vales MI, Kling J, Riera-Lizarazu O, Sato K, Powell W, Waugh R (2003) Development and characterization of recombinant chromosome substitution lines (RCSLs) using *Hordeum vulgare* subsp. *spontaneum* as a source of donor alleles in a *Hordeum vulgare* subsp. *vulgare* background. *Genome* 46:1010–1023. <https://doi.org/10.1139/g03-080>
- Mayer KF, Waugh R, Langridge P, Close TJ, Wise RP, Graner A, Matsumoto T, Sato K, Schulman A, Muehlbauer GJ, Stein N (2012) A physical, genetic and functional sequence assembly of the barley genome. *Nature* 491(7426):711–716
- Murray GM, Brennan JP (2010) Estimating disease losses to the Australian barley industry. *Australas Plant Pathol* 39:85–96
- Neupane A, Tamang P, Brueggeman RS, Friesen TL (2015) Evaluation of a barley core collection for spot form net blotch reaction reveals distinct genotype-specific pathogen virulence and host susceptibility. *Phytopathology* 105(4):509–517
- Newton AC, Flavell AJ, George TS, Leat P, Mullholland B, Ramsay L, Revoredo-Giha C, Russell J, Steffenson BJ, Swanston JS, Thomas WT (2011) Crops that feed the world. Barley: a resilient crop? Strengths and weaknesses in the context of food security. *Food Sec* 3:141–178
- Nice LM, Steffenson BJ, Brown-Guedira GL, Akhunov ED, Liu C, Kono TJ, Morrell PL, Blake TK, Horsley RD, Smith KP, Muehlbauer GJ (2016) Development and genetic characterization of an advanced backcross-nested association mapping (AB-NAM) population of wild cultivated barley. *Genetics* 203:1453–1467. <https://doi.org/10.1534/genetics.116.190736>
- Ogrodowicz P, Kuczyńska A, Mikołajczak K, Adamski T, Surma M, Krajewski P, Cwiek-Kupczyńska H, Kempa M, Rokicki M, Jasińska D (2020) Mapping of quantitative trait loci for traits linked to fusarium head blight in barley. *PLoS One* 15(2):e0222375
- Oğuz AÇ (2019) Resistance of wild barley (*Hordeum spontaneum*) and barley landraces to leaf stripe (*Drechslera graminea*). *Phytopathol Mediterr* 58(3):485–495. <https://doi.org/10.14601/Phyto-10885>
- Oscarsson M, Andersson R, Salomonsson AC, Åman P (1996) Chemical composition of barley samples focusing on dietary fibre components. *J Cereal Sci* 24:161–170
- Perovic D, Kopahnke D, Habekuss A, Ordon F, Serfling A (2018) Marker-based harnessing of genetic diversity to improve resistance of barley to fungal and viral diseases. In: Miedaner T, Korzun V (eds) *Applications of genetic and genomic research in cereals*. Elsevier, Amsterdam, pp 137–164
- Pessaraki M (2016) *Handbook of plant and crop stress*. CRC Press, Boca Raton

- Pickering R, Ruge-Wehling B, Johnston P, Schweizer G, Ackermann P, Wehling P (2006) The transfer of a gene conferring resistance to scald (*Rhynchosporium secalis*) from *Hordeum bulbosum* into *H. vulgare* chromosome 4HS. *Plant Breed* 125:576–579
- Pillen K, Zacharias A, Léon J (2003) Advanced backcross QTL analysis in barley (*Hordeum vulgare* L.). *Theor Appl Genet* 107:340–352. <https://doi.org/10.1007/s00122-003-1253-9>
- Poehlman JM (1994) Breeding barley and oats. In: Poehlman JM (ed) *Breeding field crops*. Iowa State University Press, Ames, IA, pp 378–420
- Pogoda M, Liu F, Douchkov D, Djamei A, Reif JC, Schweizer P, Schulthess AW (2020) Identification of novel genetic factors underlying the host-pathogen interaction between barley (*Hordeum vulgare* L.) and powdery mildew (*Blumeria graminis* f. sp. *hordei*). *PLoS One* 15(7):e0235565
- Prakash V, Verma RPS (2009) Inheritance of yellow rust resistance in barley (*Hordeum vulgare* L.). *Indian J Genet Plant Breed* 69(2):99–101
- Reddy M, Reddy P, Prasad BN, Munilakshmi U (2014) Grain and milling quality of barley and their suitability for preparation of traditional south Indian products. *Int Organ Sci Res J Pharm* 4:23–27
- Risk JM, Selter LL, Chauhan H, Krattinger SG, Kumléhn J, Hensel G, Viccars LA, Richardson TM, Buesing G, Troller A, Lagudah ES (2013) The wheat Lr34 gene provides resistance against multiple fungal pathogens in barley. *Plant Biotechnol J* 11(7):847–854
- Sato K, Shin-I T, Seki M, Shinozaki K, Yoshida H, Takeda K, Yamazaki Y, Conte M, Kohara Y (2009) Development of 5006 full-length cDNAs in barley: a tool for accessing cereal genomics resources. *DNA Res* 16(2):81–89
- Sannemann W, Huang BE, Mathew B, Léon J (2015) Multi-parent advanced generation inter-cross in barley: high-resolution quantitative trait locus mapping for flowering time as a proof of concept. *Mol Breed* 35:1–16
- Savary S, Ficke A, Aubertot J-N, Hollier C (2012) Crop losses due to diseases and their implications for global food production losses and food security. *Food Security* 4(2):519–537
- Sayed H, Baum M (2018) Marker-assisted selection for scald (*Rhynchosporium commune* L.) resistance gene (s) in barley breeding for dry areas. *J Plant Protect Res* 58:335–344
- Schmalenbach I, Körber N, Pillen K (2008) Selecting a set of wild barley introgression lines and verification of QTL effects for resistance to powdery mildew and leaf rust. *Theor Appl Genet* 117:1093–1106. <https://doi.org/10.1007/s00122-008-0847-7>
- Schnaithmann F, Kopahnke D, Pillen K (2014) A first step toward the development of a barley NAM population and its utilization to detect QTLs conferring leaf rust seedling resistance. *Theor Appl Genet* 127:1513–1525. <https://doi.org/10.1007/s00122-014-2315-x>
- Schreiber M, Mascher M, Wright J, Padmarasu S, Himmelbach A, Heavens D, Milne L, Clavijo BJ, Stein N, Waugh R (2020) A genome assembly of the barley ‘transformation reference’ cultivar Golden Promise. *G3-Genes Genom Genet* 10(6):1823–1827
- Singh S, Singh H, Sharma A, Meeta M, Singh B, Joshi N, Grover P, Al-Yassin A, Kumar S (2014a) Inheritance of spot blotch resistance in barley (*Hordeum vulgare* L.). *Can J Plant Sci* 94:1203–1209
- Singh T, Mishra VK, Prasad LC, Chand R (2014b) Genetic evaluation of barley (*Hordeum vulgare* L.) germplasm for resistance components of spot blotch disease. *Electr J Plant Breed* 5(2):158–164
- Singh J, Lal C, Kumar D, Khippal A, Kumar L, Kumar V, Malik R, Kumar S, Kharub AS, Verma RPS, Sharma I (2016) Widening the genetic base of Indian barley through the use of exotics. *Int J Trop Agric* 34(1):1–10
- Steffenson BJ, Olivera P, Roy JK, Jin Y, Smith KP, Muehlbauer GJ (2007) A walk on the wild side: mining wild wheat and barley collections for rust resistance genes. *Aust J Agric Res* 58:532–544
- Stein N, Graner A (2005) Map-based gene isolation in cereal genomes. In: Gupta PK, Varshney RK (eds) *Cereal genomics*. Springer, Dordrecht, pp 331–360

- Stein N, Prasad M, Scholz U, Thiel T, Zhang H, Wolf M, Kota R, Varshney RK, Perovic D, Grosse I, Graner A (2007) A 1,000-loci transcript map of the barley genome: new anchoring points for integrative grass genomics. *Theor Appl Genet* 114(5):823–839
- Therése B, Åhman I, Manninen O, Reitan L, Christerson T, Jensen JD, Krusell L, Jahoor A, Orabi J (2017) A novel QTL for powdery mildew resistance in nordic spring barley (*Hordeum vulgare* L. ssp. *vulgare*) revealed by genome-wide association study. *Front Plant Sci* 8:1954. <https://doi.org/10.3389/fpls.2017.01954>
- Tiwari IM, Jesuraj A, Kamboj R, Devanna BN, Botella JR, Sharma TR (2017) Host delivered RNAi, an efficient approach to increase rice resistance to sheath blight pathogen (*Rhizoctonia solani*). *Sci Rep* 7(1):1–4
- Vatter T, Maurer A, Perovic D, Kopahnke D, Pillen K, Ordon F (2018) Identification of QTL conferring resistance to stripe rust (*Puccinia striiformis* f. sp. *hordei*) and leaf rust (*Puccinia hordei*) in barley using nested association mapping (NAM). *PLoS One* 13(1):e0191666
- Verma RPS, Kumar V, Sarkar B, Kharub AS, Kumar D, Selvakumar R, Malik R, Sharma I (2012) Barley cultivars releases in India: names, parentages, origins and adaptations. *Research bulletin no 29, DWR, Karnal, India*, p 26
- Visioni A, Rehman S, Viash SS, Singh SP, Vishwakarma R, Gyawali S, Al-Abdallat AM, Verma RPS (2020) Genome wide association mapping of spot blotch resistance at seedling and adult plant stages in barley. *Front Plant Sci* 11:642
- Werner BT, Gaffar FY, Schuemann J, Biedenkopf D, Koch AM (2020) RNA-spray-mediated silencing of *Fusarium graminearum* *AGO* and *DCL* genes improve barley disease resistance. *Front Plant Sci* 11:476. <https://doi.org/10.3389/fpls.2020.00476>
- Xiaohui Y, Kong HY, Meiyalaghan V, Casonato S, Chng S, Jones EE, Butler RC, Pickering R, Johnston PA (2018) Genetic mapping of a barley leaf rust resistance gene *Rph26* introgressed from *Hordeum bulbosum*. *Theor Appl Genet* 131:2567–2580
- Zang W, Eckstein PE, Colin M, Voth D, Himmelbach A, Beier S, Stein N, Scoles GJ, Beattie AD (2015) Fine mapping and identification of a candidate gene for the barley Un8 true loose smut resistance gene. *Theor Appl Genet* 128(7):1343–1357
- Zhang H, Sreenivasulu N, Weschke W, Stein N, Rudd S, Radchuk V, Potokina E, Scholz U, Schweizer P, Zierold U, Langridge P (2004) Large scale analysis of the barley transcriptome based on expressed sequence tags. *Plant J* 40(2):276–290
- Zohary D, Hopf M (2000) *Domestication of plants in the old world: the origin and spread of cultivated plants in West Asia, Europe, and the Nile Valley*, 3rd edn. Oxford University Press, pp 59–69