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Review Article

Pre-harvest sprouting in wheat: current status and future prospects

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Abstract

Pre- harvest sprouting (PHS) having adverse effects on both crop yields and quality, is one of the major constraints of wheat production in areas with high rainfall. In the north-eastern parts of India and also many areas of the world receiving rainfall during the late maturity stages of the crop affects both grain yields and quality. PHS trait is polygenic trait and affected by number of environmental factors. The available diversity in germplasm for the trait is very limited and for improving tolerance to PHS newer sources needs to be identified. The primary cause of pre-harvest sprouting is the breakdown or lacking of seed dormancy under humid and wet conditions along with the degradation of starch in the germinated seeds due to enhanced alpha amylase activity. This review describes the factors affecting the pre-harvest sprouting tolerance, genes associated with it, physiological, biochemical and molecular mechanism involved, screening technique and breeding approaches to develop PHS s tolerant wheat genotypes.

Keywords: abscisic acid; dormancy; genes, QTLs; gibberellic acid; pre-harvest sprouting (PHS); wheat

1. Introduction

Wheat (*Triticum aestivum* L.), the widely cultivated prime cereal crop under different agro-climatic conditions throughout the world, provides about 20% of protein and 20% calories to the mankind. The 4th advance estimate of crop season 2020-21, projects 109.52 million tonnes production of wheat in India from an area of 34.24 million hectares (Anonymous, 2021). The advent of climate change and increasing human population pressure over the globe are the most critical challenges for the global food production. This has necessitated the breeders to breed high yielding as well as abiotic and biotic stress tolerant crop varieties for erratic climatic fluctuations to meet the future wheat demand of 140 million tonnes by 2050. In recent years, major wheat growing regions throughout the globe experienced extreme and unpredictable weather conditions due to climate change. One of the major abiotic factors that limit wheat productivity is the pre-harvest sprouting (PHS); a phenomenon in which seeds germinate while intact on spike or on the mother plant before harvest (Wang *et al.,* 2019) due to rainfall and high humidity (Andreoli *et al.* 2006) at physiological maturity with breakage of dormancy (Patwa and Penning, 2020). PHS sometimes also characterized as *vivipary* (Fang and Chu, 2008), which occurs in a wide range of cereal crops including wheat. The major factors affecting the pre-harvest sprouting are environmental conditions, seed dormancy, seed coat permeability and color, α-amylase activity, endogenous hormones levels, functional proteins, genes, and quantitative trait loci and others (Gao *et al.,* 2013). Pre-harvest sprouting observed across all the major

wheat growing regions in the world (Cabral *et al.,* 2014), especially in the locations witnessing frequent rainfall and high humidity during late season or prior to harvest (Zhang *et al.,* 2017a). The PHS causes reduction in both wheat grain yield as well as end-use quality (Lin *et al.,* 2018). Pre-harvest sprouting have been reported in most of the cereals crop *viz*., maize, wheat, rice, barley and sorghum (http://www.fao.org/faostat/en/#compare, 2019) from most of the regions of the world including Japan, China, India, the United States, Canada, Australia, North Africa, and throughout Europe (Biddulph *et al.,* 2007; Nakamura, 2018). It is reported as a world-wide problem, occurring once in 10 years in major wheat-producing areas throughout the globe (Olaerts *et al.,* 2018). In India, Eastern and far-eastern states namely Bihar, West Bengal, Jharkhand, Assam are more prone to erratic rainfall patterns frequently and aggravated the situation of PHS in wheat.

Wheat is used for the production of various food products *viz.,* breads, cookies, pasta, biscuits, cakes, noodles, and breakfast cereals (Olaerts *et al.,* 2018). However, sprouting of grains reduces the market value and the level of sprouting decides the suitability of the grain for food or feed industry (Cunha *et al.,* 2004). The price of sprouted wheat could be reduced by 20-50% (Simsek *et al.,* 2014; Sorrells and Sherman, 2007), and if having more than 4% sprouted grains treated as unacceptable for producers and consumers (Moot and Every, 1990; Sorenson and Wiersma, 2004). The average annual losses due to pre-harvest sprouting are approximately $100 million in Canada, while about 24.91 million ha area of wheat is affected in China (Xiao *et al.,* 2002). Annual losses in yield and quality of wheat due to pre-harvest sprouting are around $1 billion globally (Wahl and Rourke, 1994, Bewley *et al.,* 2006, Biddulph *et al.,* 2008, DePauw *et al.,* 2012, Nakamura, 2018; Shao *et al.,* 2018, Vetch *et al.,* 2019; Liton *et al.*, 2021). The main cause of pre-harvest sprouting is the breakdown or lacking seed dormancy under humid and wet conditions which leads to huge economic losses due to the reduction in grain weight and end-use quality (Zhang and Liu, 1989; Kulwal *et al.,* 2012, Kocheshkova *et al.,* 2017; Shao *et al.,* 2018). The pre-harvest sprouting severely downgrades grain quality due to alpha amylase activity which is mainly degrading starch in wheat grain. Therefore, pre-harvest sprouting is directly associated with reductions in both grain yield as well as quality (Lang *et al.,* 2021). Pre-harvest sprouting causes the reduction in quality of grains due to the degradation of starch and protein in germinated kernels (Flintham, 2000; Shorinola *et al.,* 2016). The increase in amylase activity results in the breakdown of grain carbohydrate reserves due to which bread quality of wheat is affected causing sticky crumb and collapsed loaves (Imtiaz *et al.,* 2008). Alpha-amylase activity has a direct effect on the quality of bread and pasta and adversely impacts the malting process (Perten, 1964). Enhanced production of alpha-amylase in wheat grain, due to the pre-harvest sprouting, leads to decrease in Hagberg falling number and adverse effects on cooked pasta quality (Singh *et al.* 2014 Further, PHS causes significant yield reduction and decreases milling and baking quality of wheat grains (Groos *et al.,* 2002). The flour from sprouted wheat produces dough that is difficult to handle due to darker crust color, a sticky crumb texture, and poor slice ability (Ibrahim and Appolonia, 1979; Lorenz *et al.,* 1983; Lukow and Bushuk, 1984; Olaerts *et al.,* 2018).

The various products made from sprouted wheat flour are porous, sticky, and off-color and generally of poor bake quality (Sorenson and Wiersma, 2004). Grant *et al.* (1993) reported that sprouting caused higher cooking losses, decreased firmness and lower spaghetti stickiness values. Although, the effects of PHS on final food product depends on the amount of enzymes present and the breakdown of kernel starches, oils, and proteins (Sorenson and Wiersma, 2004), which negatively affect the quality of various products made from wheat flour namely noodles, Arabic flat-breads (Edwards *et al.,* 1989), breads, cookies, pies (Lorenz *et al.,* 1983). Therefore, research needs to be focused on the development of wheat varieties with enhanced degree of dormancy in PHS affected wheat production areas. In this review, the major focus will be on the factors responsible for pre-harvest sprouting, genes associated with PHS tolerance, physiological, biochemical, molecular mechanism and breeding strategies for the improvement of pre-harvest sprouting tolerance in wheat.

2. Factors affecting Pre-harvest sprouting (PHS)

Pre-harvest sprouting is mainly controlled by seed dormancy but also influenced by several other factors such as genetic control, red seed color (Gfeller and Svejda, 1960; Groos *et al.,* 2002), spike morphology

(King and Richard, 1984), physical barriers to water penetration (Gale, 1989) and environmental factors such as temperature and moisture (Argel and Humphreys, 1983; Ceccato *et al.,* 2011). Details of factors responsible for PSH in wheat are discussed below

2.1 Environment

Seed germination is the most vital step in the life cycle of plant and forms the basis of agricultural production. In contrast, seed dormancy is a phenomenon which prevents germination in spite of favourable environment and avoids losses due to untimely sprouting or germination (Nonogaki *et al.,* 2018). Although seed dormancy is regulated by number of genes ,there exist evidences on the other hand that dormancy is also highly influenced by certain environmental factors. The climate change and its effect are evident in the form of extreme weather events. This leads to the occurrence of PHS more frequently which ultimately results in reduction of seed quality and food production shortages in cereals (Maity and Pramanik, 2013). The weather conditions before 14 days to physiological maturity severely affects seed dormancy (Strand, 1989) and continuous rain and high humidity along with higher temperature at maturity can cause PHS (Reddy *et al.,* 1985; Penfield and MacGregor, 2017). Rain enhances moisture on the spike and with an optimum temperature at the time of seed maturity creates suitable conditions for PHS prior to harvesting (Lunn *et al.,* 2002). The temperature and PHS in barley are positively correlated (Gualano and Benech-Arnold, 2009).

Drought like conditions coupled with high temperature enhanced PHS tolerance in white spring wheat variety Cunderdin, a PHS sensitive genotype to the levels similar to (DM2001) a dormant genotype (Biddulph *et al.,* 2005). Dry conditions with high-temperature before grain maturity leads to PHS tolerance and also found inverse relationship of low temperature with high dormancy rate in wheat (Thomason *et al.,* 2009). Certain environmental conditions related with temperature and rainfall at the time of seed maturity leads to the onset of PHS or LMA (late maturity alpha-amylase activity (Patwa and Penning, 2020). Hence, considering current climate change projections of enhanced temperature and untimely precipitation across the globe, risk of PHS is expected to increase and become a greater challenge in wheat producimg areas in near future (Shorinola *et al.,* 2016).

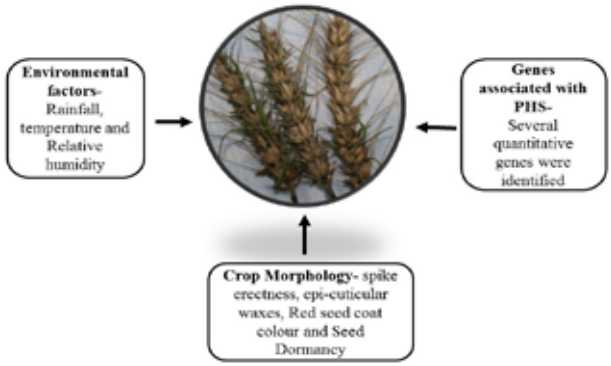

Fig 1. Factors affecting Pre-harvest sprouting in wheat

2.2 Crop morphology

Pre-harvest sprouting (PHS) sensitivity is a complex trait which is controlled by genetic factors along with other factors, such as spike and plant morphology, germination inhibiting compounds in the bracts, stage of maturity of plants and environment. PHS is influenced by water-soluble germination inhibitors in seed coat and morphological structure of spikes *viz*., erectness of spikes and openness of florets (King and Richards, 1984; Gatford *et al.,* 2002; Tan *et al.,* 2006). A number of simple morphological traits of the cereals can create an umbrella effect and so can be used to limit pre-harvest sprouting in cereals. The structure of the wax rather than its amount is considered as an important factor for repelling water entry (King, 1989). The presence of awns leads to uptake of water by the ear-heads and increase in PHS in wheat, but it still remains uncertain if this effect occurs under natural field conditions or the awn or the lemma or glume of awned varieties leads to such correlation (Ji *et al.,* 2018). Presence of epicuticular wax can resist entry of water into ear-head and also provide a physical barrier in reducing PHS but would have little effect on LMA (late maturity alpha-amylase) which is ensued by temperature fluctuations rather than moisture conditions. Barley with smooth and wild-type wax decreases PHS under artificial rainfall conditions as compared to non-glaucous, glossy mutants due to variations in water uptake by the earheads. An extremely glaucous spike phenotype should also be combined with awnless and erect spike phenotype which plays a major role in reducing water uptake (King and Von Wettstein-Knowles, 2000).

2.3 Seed coat colour

Although PHS is highly influenced by the certain environmental factors such as temperature and rain or

humidity at seed maturity, several physical, chemical and genetic factors could also influences the onset and severity of PHS. Physical attributes such as seed testa colour, presence/absence of awns and epicuticular wax are associated with differences in PHS sensitivity (Patwa and Penning, 2020). Several researchers concluded that seed dormancy is closely associated with red grain colour in wheat. Pre-harvest sprouting in wheat is associated with insufficient seed dormancy and it is reported that red seed coat is a traditional marker for resistance to pre harvest sprouting in wheat breeding (Yu-ichi et al. 2016). Many studies during last decade have associated red seed coat with higher level of seed dormancy and PHS tolerance. Catechin and proanthocyanidins (PAs) are synthesized through the flavonoid synthesis pathway are believed to be associated with red seed coat colour in wheat. Early cytogenetics studies suggested that three genes viz., *R-A1*, *R-B1* and *R-D1* on homeologous group- 3 chromosomes control seed coat colour and accumulation of catechin, a precursor of the red pigment that leads to prevention of seed germination having pleiotropic effect (Lin *et al.,* 2016).

On an average, white grained wheat seeds have been reported to be more vulnerable to PHS than red colored wheat seeds, although variation is seen in both groups for resistance (Andreoli *et al.,* 2006). However, PHS occurs occasionally in red seed coat varieties, implicating that the red-grain genotypes alone do not contribute towards resistance against PHS (Flintham, 2000). The varietal differences exists for pre-harvest sprouting (PHS) tolerance and associated grain characteristics *viz*, falling number (FN), -amylase activity, degree of sprouting (DS) under field sprouting (FS) and spike wetting conditions (Ji *et al.,* 2018). Awnless varieties appear to have better sprouting tolerance than awned varieties under intensive sprouting conditions, but found to be comparatively less evident than seed coat colour. The white seeds mutants of 'Chinese Spring' and 'AUS1490' showed increased germination under wet conditions, indicating that R genes is associated with PHS tolerance (Li *et al.,* 2016). However, contribution of R genes to PHS resistance remains unsolved puzzle. Additional genetic effects like -amylase activities, endogenous hormones levels, genes and QTLs, independent of seed coat pigmentation are known to involved in the control seed dormancy in white and red colored seeds as reported by several researchers.

2.4 Seed dormancy

Dormancy is the inhibition of germination of morphologically ripe and healthy seeds even under optimum conditions of temperature, light and moisture (Chouard *et al.*, 1960). Dormancy is a quantitative trait regulated by multiple genes, is strongly influenced by environmental conditions (Nakamura, 2018). There are two main environmental factors *viz.*, temperature and moisture which affects pre-harvest sprouting in wheat especially during the late maturity stage (Hilhorst, 1995; Yanagisawa *et al.,* 2005; Gao *et al.,* 2006), because low temperature and high moisture both are able to break dormancy and promote sprouting of seed (Argel *et al.,* 1983; Ceccato *et al.,* 2011). Therefore, seed dormancy has been considered as major factor that determines pre-harvest sprouting resistance in wheat (Bewley and Black, 1982; Mares and Mrva, 2001; Finch-Savage and Leubner-Metzger, 2006, Lan *et al.,* 2005; Lin *et al.,* 2008; Yang *et al.,* 2011). Dormancy is typically measured by either a germination index (ranging from 0.0 to 1.0) (Reddy *et al.,* 1985) or germination resistance index (ranging from 0 to 50) calculated on hand threshed grains imbibed on filter paper.

Many researchers have reported dormancy as a key genetic constituent of PHS resistance (Sun *et al.*, 2012; Yang *et al.*, 2014). Mechanism of seed dormancy can also be classified as seed-coat imposed dormancy and embryo related dormancy. Former is associated with seed coat inhibitory compounds (Himi *et al.*, 2002) and the later involves the crosstalk of plant hormones *i.e.* ABA (abscisic acid), GA (gibberellin), auxin etc. (Finch Savage *et al.*, 2006; Liu *et al.*, 2013a). Seed coat imposed dormancy is involved particularly in seed survival mechanism. Dormancy is affected by both genetic and environmental factors (Cavangh *et al.*, 2008). Red-grained wheat genotypes exhibit a wide range of seed dormancy and are more resistant to PHS as they contained dominant alleles, whereas white-grained cultivars are susceptible to PHS as they lack seed dormancy at maturity (Freed *et al.*, 1976; Gfeller and Svejda, 1960; Everson *et al.*, 1961; McEwan *et al.*, 1980).

2.5 Genes associated with PHS tolerance

There are several genes which are identified and are found to be associated with PHS tolerance in wheat. Liu *et al.* (2013) observed *TaPHS1,* major gene determining

pre-harvest sprouting resistance and suggested that the pre-harvest sprouting resistance was independent of grain color (qualitative). However, seed color genes may modify the level of pre-harvest sprouting (quantitative) in either pre-harvest sprouting resistant or susceptible genotype groups as determined by *TaPHS1*. Therefore, *TaPHS1* is a highly valuable pre-harvest sprouting resistance gene for breeding white wheat cultivars. Himi and Noda (2005) reported that *R* genes regulate the expressions of the *CHS, CHI*, *F3H* and *DFR* genes that encode enzymes in the early steps of flavonoid synthesis. In fact the *Tamyb10* genes appeared to be located in the same regions as the *R* loci, and *R*, *TaDFR* and *Tamyb10* were proven to be *Myb* type transcription factors (Himi and Noda, 2005; Himi *et al.,* 2011; Bi *et al.,* 2014). It is reported in literature that red-grained wheat is more tolerant to sprouting than white-grained wheat (Probert, 2000; Warner *et al.,* 2000; Groos *et al.,* 2002). In wheat, three *TaSdr* genes *viz*., *TaSdr-A1*, *TaSdr-B1*, and *TaSdr-D1* have been cloned, and are involved in seed dormancy; among which, *TaSdr-B1* on chromosome 2B was observed to play a vital role in regulating seed dormancy (Zhang *et al.,* 2017b; Zhang *et al.,* 2014). Barrero *et al.* (2015) reported another gene *MKK3*-A (mitogen-activated protein kinase 3), also called *TaMKK3-A*, to be located on chromosome 4AL as a candidate gene of *Phs-A1* locus which is associated with duration of seed dormancy (Torada *et al.,* 2016). Another gene, *TaVp1* extensively studied in wheat was linked with seed dormancy and pre-harvest sprouting resistance (Yang *et al.,* 2007a; Chang *et al.,* 2010; Yang *et al.,* 2014; Chang *et al.,* 2011; Hattori *et al.,* 1992; Nakamura and Toyama 2001; Xia *et al.,* 2008; McKibbin *et al.,* 2002) . This gene was mapped about 30 cM from R loci on homologous group 3L chromosomes (Bailey *et al.,* 1999). Further, there are reports that the wheat has several dormancy QTLs, including *QPhs.ocs-3A.1* and *Phs1* (Gong *et al.,* 2014; Mori *et al.,* 2005; Torada *et al.,* 2005; 2008) (Table 1).

3. Physiological, biochemical and molecular mechanism involved in pre-harvest sprouting

PHS tolerance / resistance is associated with a variety of developmental, physiological and morphological characteristics of the spike and seed, including seed coat color and permeability, seed dormancy alpha-amylase activity and plant growth hormone levels (abscisic acid, gibberellin and auxin). Seed dormancy is the most important genetic element influencing PHS resistance; hence researchers have focused on understanding the molecular mechanism of seed dormancy as a way to improve PHS resistance in wheat breeding programmes.

Grain color (GC) is an important genetic factor affecting the brightness of flour and is also associated with seed dormancy and PHS resistance. It is controlled by the *R-1* gene series distally located on long arms of chromosomes 3A, 3B and 3D (Metzger and Silbaugh, 1970). Enzymes like DFR (dihydroflavonol-4-reductase), CHI (chalcone flavanone isomerase), F3H (flavanone 3-hydroxylase), and CHS (chalcone synthase) are expressed only in immature red grains and are nearly repressed in the grains of white wheat (Mir *et al*., 2012; Thomas and Ougham, 2014). *Myb*-type *Tamyb*10-1 transcription factors control anthocyanin production and the red pigment of wheat grain by up-regulating the structural genes encoding DFR, CHI, F3H and CHS in flavonoid biosynthesis pathway (Ali *et al.,* 2019). Groos *et al.* (2002) identified four QTLs for both PHS and GC resistance, three of which were close to R genes and one was mapped on chromosome 5AS using a RIL population. Later on, Zhou *et al.* (2017) detected three main QTLs for PHS resistance, one on chromosome 5D and other two loci co-located with *Tamyb10-1* genes on chromosomes 3A and 3D by Genome wide association mapping studies (GWAS). Recently, Lang *et al.,* (2021) mapped the PHS resistance gene *PHS-3D* from synthetic hexaploid wheat to a 2.4 Mb presence–absence variation (PAV) region and found that its resistance effect was attributed to the pleiotropic *Myb10-D* by integrated omics and functional analyses. Therefore, it is possible to breed PHS-tolerant white wheat by using CRISPR / Cas9 (a gene-editing technology) for altering GC-related genes keeping in view the other dormancy-related QTLs besides those provided by the R-1 genes of the red grained parent used for such editing (Ali *et al*., 2019).

3.1 α- Amylase activity

The α-amylase enzyme widely exists and participates in many physiology processes in plants, which can hydrolyze α-1, 4-glycosidic bond in the saccharides. The expression of α-amylase was involved in plant metabolism and could affect the germination rate, cold tolerance and production of seed (Autio *et al*., 2001) and is strictly controlled by the phytohormones ABA and gibberellin. During grain development ABA inhibits the amylase expression, four

isozymes of α-amylase in wheat have been identified affecting PHS, namely malt-α-amylase (α-amylase-1) located on homologous chromosomes - 6, green-α-amylase (α-amylase-2) located on homologous chromosomes - 7, α-amylase-3 on chromosome -5 and α-amylase-4 has two members on homologous chromosomes -2 and 3 (Gale and Ainsworth, 1984; Zhang *et al.*, 2017c). Among all the three genomes, B genome harbors genes for α-amylase-1 and α-amylase-2. GA3 seemed to be involved in regulation of expression level of α-amylase-1 and α-amylase-2 (Marchylo *et al.*, 1983).

3.2 Plant growth hormones

The growth hormones, such as ABA and GA play important roles in regulation of dormancy and germination in wheat. ABA induces dormancy and GA stimulates seed germination (Kucera *et al.,* 2005; Finkelstein *et al.*, 2008). Several studies have reported the regulatory mechanisms of other hormones like ethylene, jasmonate brassinosteroids, and auxin in controlling seed dormancy, germination and PHS resistance (Liu *et al.*, 2013b; Kim *et al.,* 2019; Ju *et al.,* 2019). Light and temperature, also affect the dormancy and germination by disturbing the balance between ABA and GA levels in cereal crops (Gubler *et al.*, 2008; Lzydorczyk *et al.*, 2017). ABA is an essential hormone that promotes seed dormancy, seed maturation and tolerance to desiccation. During imbibition ABA levels increases upto 2.5-fold in dormant wheat and remains unchanged in non-dormant grains (Ried *et al.*, 1990). ABA level is regulated by its synthesis and catabolism. Zeaxanthin epoxidase (ZEP)/ABA1 and 9-cis-epoxycarotenoid dioxygenase (NCED) are two key enzymes involved in ABA synthesis and PHS regulation. ABA catabolism is mainly the result of hydroxylation by ABA 8′-hydroxylase (ABA8′OH)/cytochrome p450 monooxygenase 707A (CYP707A) (Okamoto *et al.,* 2006). The two genes NCED and CYP707A play important roles in germination and dormancy by controlling the ABA level in seeds. MYB96 and ABI4 can increase ABA levels by affecting the expression of NCED2/6 and CYP707A1/2, respectively (Shu *et al.,* 2013; Lee *et al.,* 2015). Chono *et al.*, (2013) reported the importance of higher embryonic ABA levels in inducing seed dormancy during seed maturation phase in wheat *via* mutational analysis of two homologs of *TaABA8'OH1* i.e. *TaABA8'OH1A* and *TaABA8'OH1D*. The resource of TILLING (Targeting Induced Local Lesions In Genome) mutants, like Kronos and Cadenza, have been developed in wheat. The exome sequences of Kronos and Cadenza mutants have been re-sequenced using Illumina NGS that can be used to screen for mutations in pre-harvest sprouting and dormancy related genes (Nakamura *et al.*, 2011).

GA is another key plant hormone that plays a significant function in seed dormancy and germination control (Finch-Savage *et al.*, 2006). GA breaks seed dormancy and promotes germination mostly by overcoming the mechanical restraint imposed by the aleurone or testa and stimulating the growth of the embryo (Debeaujon and Koornneef, 2000). It also regulates the expression of amylase synthesis genes, which are involved in seed germination and starch hydrolysis in the endosperm. The bioactive GA content in plants is controlled by an equilibrium between its synthesis and inactivation, mediated principally by GA2ox genes (GA2-oxidase encoding), GA3ox (GA3-oxidase encoding), and GA20ox (encoding GA 20-oxidase), respectively (Yamaguchi *et al.*, 2008). In wheat, six GA metabolism genes, *TaKS, TaKO1, TaKAO1, TaGA20ox1, TaGA2ox1*, and *TaGA2ox8*, were detected by GeneChip in dry dormant and after-ripened grains, indicating that they might participate in dormancy regulation (Liu *et al.,* 2013b). In a number of cultivated species, including wheat, rice, and barley many genes were identified which encoded these enzymes and their expression played an important role in dormancy and germination by adjusting seed GA levels (Pearce *et al.*, 2015). The role of GA in regulating seed germination and dormancy was shown by the transcription level of these gene orthologs due to post-ripening as well as in non-dormant and dormant cereal crops. In imbibed post-ripened barley and wheat seeds, for example, the dormancy loss was demonstrated to be related with an enhanced expression of the *TaGA3ox* and *TaGA20ox* genes and to a higher bioactive *GA1* content (Liu *et al.,* 2013c*;* Gubler *et al.*, 2008; Kashiwaruka *et al.*, 2016). GA signals in plants are perceived by the soluble receptor protein gene *GID1* (Gibberellin insensitive dwarf 1), that was first mapped in rice (Ueguchi-Tanaka *et al.,* 2007). Reduced height (Rht)-1 in wheat is an ortholog of GAI (Peng *et al.,* 1999). Notably, Rht-B1b (also known as Rht1) and *Rht-*D1b (also known as Rht2) were used to reduce lodging and to increase grain yield during the Green Revolution (Eshed and Lippman, 2019). Two intragenic *Rht-B1c* suppressor

alleles (*Rht-B1c.23* and *Rht-B1c.26*) reported by Van De Velde *et al.,* (2017) showed improved PHS resistance and have no negative effects on grain yield or quality.

3.3 QTLs Identified for PHS resistance

PHS is a quantitative trait controlled by multiple QTLs or genes that are important for breeding PHS-resistant varieties. Recent advances in the genomics of cereal crops have led to the identification of several genes involved in PHS resistance. PHS resistance QTLs have been reported almost on all wheat chromosomes accounting varying degree of resistance (Tai *et al.,* 2021; Zhou *et al.,* 2017). In wheat, more than 250 QTLs for PHS resistance have been identified in ~40 mapping populations that included hexaploid synthetic wheats, tetraploid durum wheats and diploid einkorn wheats (Gupta *et al.,* 2020). The PHS resistance genes on chromosomes 3A, 3B and 3D regions which encode a Myb transcription factor (*TaMyb10*) are considered to be tightly linked or pleiotropic with red seed coat color determined by dominant R alleles (Himi *et al.,* 2011). A QTL on chromosome 3AS encode for Mother of Flowering Time (*TaMFT*: was cloned which promotes seed dormancy in wheat embryos (Nakamura *et al*., 2011; Lei *et al*., 2013; Liu *et al*., 2013c). A total of 188 QTLs or loci from 40 previous studies associated with resistance to PHS in wheat have been reported (Tai *et al.,* 2021). In a recent study, three *Ae. tauschii*-derived quantitative trait loci (QTLs), *QDor.3D.1, QDor.3D.2*, and *QDor.3D.3*, were detected on chromosome 3DL using four simple sequence repeats (SSR) markers and developed 10 Kompetitive allele-specific PCR (KASP) markers (He *et al.,* 2021). Furthermore, multiple potential genes for PHS resistance have been found using comparative genomics or transcriptome analysis, including *TaSdr-A1* and *TaSdr-B1* on chromosome 2AS and 2BS, *TaPHS1* and *TaMFT* on chromosome 3AS, *TaVp-1* and *Tamyb10* on group- 3 chromosomes, and two tandem genes, *PM19-A1/ A2* encoding ABA-inducible Plasma Membrane 19 proteins and *TaMKK3-A* on 4AL (Ali *et al.,* 2019). Many gene-specific markers, including SSRs (*Xgwm*15, *Xgwm*894 & *Xgwm*937), STMS markers (*Xwmc*104, *Xwmc*397, and *Xwmc*468), and STS markers (*Vp1*-B2 and *Vp1*-B3), were produced for the *Vp1* and can be used to identify PHS resistance in various genotypes. Ogbonnaya *et al.* (2007) discovered that the *Xgwm*894 and *Xgwm*937 markers were significantly linked with PHS resistance and could be exploited to improve PHS resistance in wheat. PHS resistance is governed by both epistatic and additive effects that are influenced by environmental factors. To better understand the complicated genetic structure of QTL, the interaction between QTL epistasis (QXQ) and the environment (Q X E, Q X Q X E) for PHS resistance was explored (Liu *et al*., 2010). Rapid advances in molecular technologies, such as NGS technologies (Brenchley *et al*., 2012), and ongoing chromosomal-based and wheat whole genome sequencing projects (International Wheat Genome Sequencing Consortium, IWGSC) (Clavijo *et al*., 2017; IWGSC 2018), would provide new opportunities for identification and functional analysis of the candidate genes controlling PHS resistance. Liu *et al.* (2010) designed the *TaPHS1*-SNP1 marker, which may be utilized as a diagnostic marker in breeding to identify the *TaPHS1* resistance allele. Rasheed *et al*. (2016) identified five KASP-based functional marker assays for four PHS resistance genes: SDR SNP for *TaSdr*-B1, *TaMFT*-1617R for *TaMFT*-A1, *TaMFT*-721J for *TaMFT*-A1, *Vp1B1*-83 IND for *TaVp*-1B and *Vp1B1*-193 IND for *TaVp*-1B. Furthermore, the CAPS (cleaved amplified polymorphism sequence) marker *Sdr2A*, which is located between the *Xgwm*95 and *Xgwm*372 markers, has been established and can be used for identifying PHS resistant genotypes (Zhang *et al*., 2017).

Genome-wide association (GWA) studies have also facilitated the discovery of variant sites regulating PHS (Table 1). Using GWAS, more than 250 MTA (marker trait associations) for PHS and related traits have been identified. Among known QTLs, 30 QTLs were also shown to be stable over environments; these were considered potentially useful for improvement of PHST in wheat (Gupta *et al.,* 2020). Recently, Tai *et al.* (2021) reported 66 meta-QTLs (MQTLs) distributed on all 21 wheat chromosomes out of 188 valid QTLs for PHS resistance from 40 articles. A major QTL for PHST was introgressed into an elite Indian wheat cv. Lok1 that is PHS susceptible using marker-assisted backcross breeding (Gautam *et al.,* 2021). These PHST (pre-harvest sprouting tolerant) lines were also pyramided with one gene each for high grain protein content (*Gpc-B1*) and leaf rust resistance (*Lr24).* Recently, Wang *et al.* (2021) assessed the distribution of three causal single nucleotide polymorphisms in *TaPHS1* at bases −222, +646, and +666 in 725 Chinese wheat accessions.

Table 1. List of QTL/genes identified for PHS resistance

Trait	Population	QTLs	Chromosome	Nearest Marker	QTL name	Reference
PHS and GC	RILs	5	3AL	*Xffb293*		Groos *et al.* (2002)
			3BL	*Xgwm403*		
			3BL	*Xbcd131*		
			3DL	*Xgwm3*		
			5AS	*Xbcd1871*		
PHS and SD	RILs	3	3A	*Xpsr394-Xgwm5*	*taVp1*	Osa *et al.* (2003)
			3A	*Xcdo345*	*QPhs.ocs-3A.1*	
			3A	*Xpsp3050*	*QPhs.ocs-3A.2*	
PHS	DHLs	4	2B	*Xbarc55-Xwmc474*	*QPhs.cnl-2B.1*	Munkvold *et al.* (2009)
			2D	*Xwmc111-WxPt-999*	*QPhs.cnl-2D.1*	
			3D	*7Xbarc1161*	*QPhs.cnl-3D.1*	
			6D	*Xcfd37-Xbarc196*	*QPhs.cnl-6D.1*	
PHS and GC	RILs	6	3AL	*Xwmc559-1*		Lin *et al.* (2016)
			3AL	*Tamyb10-A1-74*		
			3AL	*Tamyb10-A1-74*		
			3DL	*BS00067163_51*		
			3DL	*Tamyb10-D1-93*		
			1A/1D/3A/5B	*Xbarc148*		
PHS and GC	DHLs	5	3B	*Xbarc77-Xwmc30*	*QGi.crc-3B*	Fofana *et al.* (2009)
			3D	*7Xwmc552-Xwm533*	*QGi.crc-3D*	
			3A	*Xcfa2193-Xwmc594*	*QSi.crc-3A*	
			5D	*Xgwm469-Xcfd10*	*QSi.crc-5D*	
			3D	*Xwmc11-Xcfd223*	*QCli.crc-3D*	
PHS	RILs		2AL	*Xgwm1045-Xgwm296*	*QPhs.ccsu-2A.5*	Mohan *et al.* (2009)
			3AL	*Xgwm153-Xgwm155*	*QPhs.ccsu-3A.1*	
			3BL	*Xgwm1005-Xgwm980*	*QPhs.ccsu-3B.6*	
PHS	DHLs	1	5D	*XCFD40-XBARC1097*	*qPhs5D.1*	Zhu *et al.* (2010)
PHS	RILs	3	1A	*Xwmc611-Xwmc333*	*QPhsd.spa-1A.1*	Knox *et al.* (2012)
			2A	*Xgwm515-Xgwm425*	*QPhsd.spa2A.1*	
			7B	*Xgwm297-Xwmc532*	*QPhsd.spa-7B.1*	
PHS	DHLs	4 + 18 KASP markers developed	3B	*19 SNPs flanking the QTL*	*QSi.crc-3B*	Cabral *et al.* (2014)
			4A	*12 SNPs flanking the QTL*	*QGi.crc-4A*	
			7B	*10 SNPs flanking the QTL*	*QSi.crc-7B*	
			7D	*04 SNPs flanking the QTL*	*QFn.crc-7D*	
PHS	DHLs	5	1A	*wPt-6274*	*QPhs.spa-1A*	Singh *et al.* (2014)
			1B	*Xwmc191*	*QPhs.spa-1B*	
			5B	*wPt-6910-wPt-7400*	*QPhs.spa-5B*	
			7A	*Xcfa2174*	*QPhs.spa-7A*	
			7B	*Xwmc606*	*QPhs.spa-7B*	
PHS and SD	RILs	1	2B	*Xwmc477-Xbarc55*	*Sdr2B*	Zhang *et al.* (2014)
PHS and SD	RILs	1	4A	*wsnp_Ex_ c66324_64493429-CD920298*	*4A-1*	Barrero *et al.* (2015)
PHS and SD	RILs	4	4A	*GBS212432-GBS10994*	*QPhs.pseru-4A.1*	Lin *et al.* (2015)
			4B	*7Xbarc20-Xwmc238*	*QPhs.pseru-4B.1*	
			5A	*TTM_199619-TTM_1259*	*QPhs.pseru-5A.1*	
			5B	*7Xbarc346-2-TTm_62137_50*	*QPhs.pseru-5B.1*	

PHS	RILs	6	3A	*TaMFT*	*QDor-3A*	Cao *et al.* (2016)
			4A	*Cfa2256*	*QDor-4A*	
			1B	*Xbarc181*	*QDor-1B*	
			7B	*UCW99*	*QDor-7B*	
			4A	*Cfa2256*	*QAwn-4A*	
			6B	*Xwmc397*	*QAwn-6B*	
PHS and SD	RILs	1	2A	*Xgwm95-Xgwm372*	*Sdr2A*	Zhang *et al.* (2017a)
PHS and SD	Back cross population	3	2D	*Xwmc503*	*QDor-2D*	Dale *et al.* (2017)
			3D	*Xcfd22*	*QDor-3D*	
			3D	*Vp1-4*	*TaVp1*	
PHS	717 Chinese Wheat landraces	3	3A	*7AX-111578083*	*QTL1*	Zhou *et al.* (2017)
			3D	*3DArT-seq & 5 SNPs*	*QTL2*	
			5D	*AX-109028892*	*QTL3*	
PHS	CM32 and SHW-L1	5 eQTLs	2A	*AX-110609678*	*eQABI4.15DPA.2A.1*	Xiao *et al.* (2021)
			2D	*AX-110515525*	*eQABI4.20DPA.2D.1*	
			2D	*AX-111690676*	*eQABI4.20DPA.2D.2*	
			3B	*AX-95660238*	*eQABI4.20DPA.3B.1*	
			4A	*AX-86175059*	*eQABI4.20DPA.4A.1*	
			4A	*AX-110113739*	*eQABI4.20DPA.4A.2*	
PHS	CSSL	3QTL	3DL	SSR&KASP	QDor.3D.1	He et al. (2021)
			3DL	SSR&KASP	QDor.3D.2,	
			3DL	SSR&KASP	QDor.3D.3	
PHS	SHW-L1			KASP	*QPHS.sicau-3D* (PHS-3D)	Lang *et al.* (2020)
PHS	211 DH + 167 US winter wheat variety	4 + KASP	2AS	KASP-222	*Qphs.hwwg-2A.1*	Shao *et al.* (2018)
			3AS	KASP-314	*Qphs.hwwg-3A.1*	
			3BS	KASP765,471	*Qphs.hwwg-3B.1*	
			5AL	KASP8426	*Qphs.hwwg-5A.1*	
PHS	SHW-L1, Chuanmai 32, AS225, AS60	2	3DL	*AX-94415259*	*qPHS.sicau-3D*	Yang *et al.* (2019)
			1BS	*AX-94924265*	*qPHS.sicau-1B*	
PHS	RILs	5	1D	BS00022188_51 Kukri_c10485_1346	*QPhs.umb-1D*	Liton *et al.* (2021)
			4A.2	BS00068243_51 BS00037019_51	*QPhs.umb-4A*	
			6B.1	RAC875_c63209_154 BobWhite_c1509_622	*QPhs.umb-6B*	
			6D	Jagger_c211_207 IAAV7251	*QPhs.umb-6D*	
			7A	Ku_c8523_166 Kukri_c38390_218	*QPhs.umb-7A*	

4. Breeding approaches for pre-harvest sprouting tolerance in wheat

The development of pre-harvest sprouting resistance lines offers basis for the enrichment of genetic resources in wheat breeding programs; accordingly, introducing genes from wheat-related species could provide an effective way to significantly improve wheat grain quality and its resistance to pre-harvest sprouting (He *et al.,* 2021). Wheat germplasm contains an appreciable amount of variation for pre-harvest sprouting characteristics which could be further exploited to develop pre-harvest sprouting resistance varieties (Wang *et al.,* 2020). The plant breeding strategy for introducing tolerance to pre-harvest sprouting in wheat is to incorporate major genes from different wild relatives or derived lines into modern breeding lines (Andreoli *et al.,* 2006). Details of exotic landraces, varieties and lines exhibiting PHS tolerance are presented below (Table 2).

Table 2. Details of wild relatives / land races/ lines identified having PHS tolerance in wheat

Wild relatives/ land races/ lines identified with PHS tolerance	Country	References
Aegilops tauschii	China	Liu *et al.* (1998)
Triticum turgidum and *Aegilops tauschii* (DD)	China	Liu *et al,* (1998); Yu *et al,* (2014)
Synthetic hexaploid wheat genotypes (SHW-L1)	China	Yang *et al,* (2014)
Chinese landraces viz., Xiaoyuhua, Yongchuanbaike and Baiyuhua	China	Xiao *et al,* (2002)
Hongheshangtou and Wanxianbaimaizi	China	Yang *et al,* (2009); Chang *et al,* (2010)
RL4137	Canada	Bassoi and Flintham, (2005);
BRS177	Brazil	Flintham, (1993)
RL4137	Canada	DePauw *et al,* (2012)
Konde, Kumpa and Swindy cultivars	Australia	Jimenez *et al,* (2017)

The resistance to pre-harvest sprouting in crops is a complex trait which is conditioned by both genetic and environmental factors (Derera *et al.,* 1977, Torada *et al.,* 2008; Barrero *et al.,* 2015). Therefore, the breeding approaches which can be used for the improvement of pre-harvest sprouting improvement in wheat are presented below (Fig. 2).

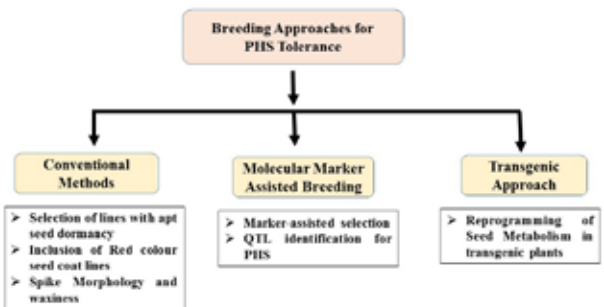

Fig. 2. Breeding approaches for PHS tolerance

Breeding varieties with high pre-harvest sprouting resistance have important implications for reducing yield loss and improving grain quality (Ali *et al.,* 2019). Therefore, breeding for genetically improved wheat with proper seed dormancy is the most effective approach to protect wheat cultivars from pre-harvest sprouting damages (Liu *et al.,* 2008). The wild wheat species (*A. tauschii*) are more dormant (conferring PHS resistance) than domesticated wheat indicating that artificial selection has contributed to the reduction of dormancy in modern wheat (Dong *et al.,* 2015; Volis, 2016). The red grained wheat usually shows more resistance to pre-harvest sprouting as the red colour genes on the long arm of group 3 chromosomes can have pleiotropic effects on pre-harvest sprouting resistance (Groos *et al.,* 2002). Breeding for pre-harvest sprouting resistance in wheat based on phenotypic selection is challenging, because pre-harvest sprouting is expressed as a quantitative character that is influenced by environment and genotype x environment interactions (Anderson *et al.,* 1993). Therefore, selecting for pre-harvest sprouting resistant genotypes on a phenotypic basis at early stages of segregation may not be efficient (Singh *et al.,* 2012).

Several quantitative trait loci or genomic regions affecting pre-harvest sprouting resistance or seed dormancy in wheat have been identified in different gene pools *via* linkage with molecular markers. Therefore, marker-assisted selection was applied in many breeding programs as pre-harvest sprouting resistance genes were cloned on chromosomes 3A (Nakamura *et al.,* 2011; Liu *et al.,* 2013c) and 4A (Torada *et al.,* 2016), and also QTLs for pre-harvest sprouting resistance identified across the genome. The use of molecular markers for marker-assisted selection could be helpful for direct identification of favorable or deleterious alleles in diverse groups of genotypes (Lazo *et al.,* 2004). The first QTL found for grain dormancy in wheat was reported in 1993 (Anderson *et al.,* 1993). Molecular markers have been developed for the causal SNPs in both the promoter and coding region of the TaPHS1 gene (Liu *et al.,* 2015), and the causal SNP for the TaMKK gene (Torada *et al.,* 2016). These markers can be used either to identify germplasm carrying these two genes, or to select resistant lines in breeding materials. The TaPHS1 gene has been successfully transferred through marker assisted selection approach to increase pre-harvest sprouting resistance (Kottearachchi *et al.,* 2006; Gupta *et al.,* 2008). Singh *et al.* (2014) also used simple sequence repeat (SSR) and Diversity Arrays Technology markers (DArT) on Double Haploid (DH) Canadian adapted durum wheat. Kumar *et al.* (2010) developed individual

plant by marker assisted breeding and phenotyped for pre-harvest sprouting tolerance to verify the effect of introgression of pre-harvest sprouting tolerance QTL. However, due to some undesirable traits from the linkage drag, these QTLs have not been widely used in wheat breeding.

Metabolomics is considered as one of the useful approach in understanding the dynamic metabolic changes since metabolomic analysis measures the metabolite composition of cells and its response to external factors. Liu *et al.* (2015) used transgene anti-trx-s byre-programming of 's' metabolism in seeds especially at later seed development (dough development, seed maturing) and post-harvest ripening stages using metabolomes. They concluded that sugars, organic acids, amino acids, choline metabolites and fatty acids of the transgenic and wild-type (control) wheat differed significantly. After 30-days post-harvest ripening, most metabolites in transgenic seeds had higher levels than in controls including amino acids, sugars, organic acids, fatty acids and choline metabolites. These clearly indicated that transgene reduced metabolic activities of mature seeds responsible for pre-harvest sprouting.

Breeding for pre-harvest sprouting resistance for various environments is challenging due to its polygenic nature, poor understanding of the trait, non-standardization of phenotyping techniques and non-availability of suitable donors having seed dormancy. In order to improve pre-harvest sprouting resistance, more information on PHS resistance genetic architecture, PHS resistance pathways and gene regulations, genetic-by-environment interactions, based user-friendly markers and efficient selection method is required.

5. Methods to measure pre-harvest sprouting in wheat

The evaluation of pre-harvest sprouting resistance under field conditions depends on the presence of weather conditions conducive for seed sprouting after physiological maturity; thus, pre-harvest sprouting phenotypic data may not be repeatable in different environments (Graybosch *et al.,* 2013; Kato *et al.,* 2001). Furthermore, environment and genotype × environment interactions influence tolerance to PHS (Kato *et al.,* 2001). Therefore, pre-harvest sprouting damage can be assessed by exposing spikes to artificial rain or through germination tests or by natural/ artificial weathering of the spike (Okuyama *et al.,* 2020) under controlled conditions. Following tests are used to measure Pre-harvest sprouting in wheat.

5.1 Germination test

Germination testing is a useful and easy method for assessing pre-harvest sprouting resistance of different wheat genotypes. Wu and Carver (1999) demonstrated that percentage of germination had good association with field assessment of sprout damage. Percentage of germination was negatively associated with seed dormancy level or sprouting resistance (Biddulph *et al.,* 2008). The genotypes with a higher percentage of sprouted grains resulted in lower falling number values; therefore, these results permitted to suggest that in those cases where the falling number test could not be performed, the germination percentage could be used as a selection tool for pre-harvest sprouting (Okuyama *et al.,* 2020). Further, association between grain germination percentage and falling number allows the wheat breeding programs to have a useful criterion for the selection, early discarding of unsuitable lines and planning a new cycle of hybridization for resistance to pre-harvest sprouting.

5.2. Falling number test

Falling Number test was developed by Hagberg (1960) as a rapid, high throughput method for determining alpha-amylase activity in grain and later adopted by industry as a test for sprout-damaged grain (Best and Muller, 1991). The low falling numbers values result from high levels of the enzyme alpha-amylase (Yu *et al.,* 2015). The falling number test has its limitations in use for breeding owing to the need of an expensive instrument, and the much time-consuming process as compared to spike-wetting tests (Martinez *et al.,* 2018).

6. Screening techniques and approaches for Indian conditions

Although all the methods used for the phenotyping pre-harvest sprouting are time-consuming and labor intensive, under natural condition of field screening is much easier Uunder natural conditions of North East India, where pre monsoon rainfall during normal maturity time of wheat is a normal phenomenon, field screening may be effectively done. Such attempt is known to have done in Shillongani, Assam, India for screening wheat genotypes for PHS tolerance. Moreover, as already discussed, identification

of the molecular markers associated with genes/ QTLs for pre-harvest sprouting may lead to successful breeding of tolerant varieties. Marker-assisted selection is a better way to evaluate pre-harvest sprouting (He *et al.,* 2021). However, the success of marker-assisted selection depends on the identification of molecular markers tightly linked with quantitative trait loci (QTLs) for pre-harvest sprouting resistance (Gao *et al.,* 2013; Kulwal *et al.,* 2012; Mares and Mrva, 2014). Thus, the identification of reliable markers closely linked to pre-harvest sprouting resistance QTLs is crucial for marker-assisted selection method (Kulwal *et al.,* 2012, Gao *et al.,* 2013; Anderson *et al.,* 1993). Kulwal *et al.,* (2005) conducted QTL analysis for pre-harvest sprouting tolerance involving chromosome group-3A using a trait-specific inter-varietal recombinant inbred mapping population derived from a cross SPR8198 (a PHS tolerant genotype) and HD2329 (a PHS susceptible cultivar), and identified a major QTL on 3A- chromosome for pre-harvest sprouting tolerance which explained up to 78.03% of phenotypic variation. Therefore, it could be suggested that the bread wheat genotypes , SPR8198), which carry the desired allele of the major QTL detected might be exploited for developing pre-harvest sprouting tolerant varieties of wheat.

A combination of linkage analysis and association mapping could be the best approach for detecting maximum number of marker-trait associations to be used for molecular breeding (Jaiswal *et al.,* 2012). However, only a few reports on QTL analysis for tolerance to pre-harvest sprouting are available at national level. Department of Genetics and Plant Breeding, Ch. Charan Singh University, Meerut, UP, India has made an excellent progress for identification of QTLs associated with pre-harvest sprouting tolerance in hexaploid wheat, and development pre-harvest sprouting tolerant wheat genotype through marker assisted selection (Kulwal *et al.,* 2005). A major QTL (*QPhs.ccsu-3A.1*) for tolerance to pre-harvest sprouting was mapped on the long arm of wheat chromosome 3A (3AL) using a bi-parental population involving one parental genotype with red grain. This QTL (*QPhs.ccsu-3A.1),* later on *was* successfully transferred into the cultivar, HD2329 using marker-assisted selection (Kumar *et al.,* 2010).

7. Conclusions and future prospects

Breeding varieties for pre-harvest sprouting tolerance is very difficult owing to its genetic complexities, environmental effects and over all poor understanding of the basis and inheritance of the trait. PHS is controlled by polygenes and is difficult to score in the segregating generations. Considering the availability of less variability for the trait, it is important to screen large number of germplasm including wild progenitors to identify new donors for this trait. These identified sources will be used in developing improved tolerant breeding material with added variability for the trait. Few genes/QTLs that have been cloned and linked markers developed could be useful for the transfer of this trait through marker assisted breeding programmes. Back cross breeding could be effectively applied for introgression of major QTLs identified for PHS tolerance With the availability of next generation sequence data, it is now a day's possible to dissect the traits to few Kb regions to enable cloning of the genes concerned. The new Omics technologies would be very useful in the near future to further elucidate the underlying mechanisms contributing to PHS tolerance. Alternatively, variability available in other species/ genera may also be explored which could pave the way for development of transgenic/ cisgenic wheat in near future that are resistant to pre harvest sprouting.

Conflict of Interest

Authors declare that they have no conflict of interest.

Ethical Compliance Statement

NA

Author's Contribution

CS, URK, VG: Collection of literature, Conceptualization, Compilation, Writing original draft, Correspondence; GS, SS, AG, BST, PK: Editing, Data Compilation and analysis; CNM, GK, SKB, AKS, SK, GPS: Final editing, Proof Reading

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