Chapter 5

Impact of Growth Habit and Architecture Genes on Adaptation and Performance of Bread Wheat

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Abstract

In bread wheat (*Triticum aestivum* L.), flowering time and plant stature are important phenological and agronomic traits for adaptation, yield potential, and yield stability. Timely flowering is critical for production, and the flowering window has to be late enough to avoid early season frosts but early enough to avoid late season stresses such as heat and terminal drought. Flowering time is controlled mainly by vernalization, photoperiod response, and earliness *per se* genes, which can be exploited to fine-tune growth and tailor flowering time for the production of desirable wheat cultivars. Tailoring flowering time could help reduce preharvest sprouting problems by escaping high temperatures and late season rainfall, which promote preharvest sprouting, hence yield loss. Concisely summarizing available information on flowering time and identifying research gaps could provide direction for future research. This chapter, therefore, discusses: (i) the progress made in discovering genes involved and the impact of their extensive allelic variation on flowering time, (ii) the potential benefits of tailoring wheat's flowering time to improve yield, and (iii) the benefits of introgressing genes for other complimentary traits, such as semidwarf and preharvest sprouting resistance on advanced lines to achieve higher yield, thus, sustainable food security.

Keywords: earliness *per se*, flowering time, photoperiod response, preharvest sprouting, semidwarf, vernalization, yield

1. Introduction

The performance of a wheat cultivar, which is normally measured by its adaptability and yield potential under target environments, is dependent on genetic and environmental factors as well as the interaction between these factors. Timely flowering, that is the switch

from the vegetative phase to the reproductive phase, and the duration of the life cycle fine-tune a cultivar to the targeted environment [1, 2]. Flowering is essential for reproductive success and occurs when conditions are favorable to maximize pollination, seed development, seed dispersal, and subsequent germination [1]. Flowering success is demonstrated by the ability of the plant to efficiently use a range of available resources including water, nutrients, temperature, day length, radiant energy, and relevant endogenous signals to maximize its potential yield and to escape stressful conditions during growth and development [1, 3]. Consequently, there is a need to better understand the genetic control of flowering time in wheat. Understanding the genetic control of the components of the life cycle, although complex, will enable plant breeders to exploit associated genes, thus fine-tune the growth and development of the crop to fulfill the demands of a specific environment and to increase yield [1, 4]. Discovering genes that control flowering time in wheat have been one of the key research goals for decades [1] and is increasingly gaining importance due to the impact of projected climate change [5]. As a result, many loci influencing flowering time has been successfully mapped and their effects determined [1, 4].

The duration of the life cycle of bread wheat is controlled by numerous genes, including those associated with seed germination, vegetative growth, flowering time, seed maturation, and seed dispersal [6]. These processes form the foundation of the reproductive strategy of flowering plants. The interaction between these genes and the environment defines the ultimate phenotype [7, 8]. Flowering time is an important component of the life cycle with a very wide and complex genetic control. Three groups of genes with major influence on flowering time of wheat include vernalization response genes, photoperiod response genes, and genes controlling the developmental rate (earliness *per se* (*eps*)) when vernalization and photoperiod response requirements have been met [1, 9, 10]. With the exception of *eps* genes, the environment plays a role in the expression of vernalization and photoperiod response genes and thus, to their contribution towards flowering time and growth of wheat [1, 11, 12]. Reviewing currently available genetic and genomic resources for flowering time and the progress made so far toward introgressing known genes in elite germplasm is vital to guide future research. This chapter, therefore, discusses the progress made in discovering genes involved and the impact of their extensive allelic variation on flowering time. Additionally, the potential benefits of tailoring the flowering time of wheat to improve yield in the wheat production industry are also discussed. Furthermore, the chapter discusses the benefits of introgressing genes for other complimentary traits such as semidwarf and preharvest sprouting resistance on promising or advanced wheat breeding lines.

2. The process of flowering in bread wheat

The process of flowering involves multiple interactions between major genes (vernalization, photoperiod response, and *eps* genes) and endogenous factors such as the developmental stage and floral gene activities acting together to promote flower initiation [13]. Crucial to the process of floral initiation is the establishment and maintenance of meristems. A specified

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class of vernalization response genes called *Vrn-1* series (*Vrn-A1*, *Vrn-B1*, and *Vrn-D1*) is responsible for this task in wheat [14–16]. The process consists of pools of undifferentiated cells that could either give rise to lateral organs such as leaves, auxiliary shoots (including flowers), and internode tissue, or that could serve as a continuing supply of new meristem cells. As a result, the type of cells produced and their ultimate developmental fate as part of vegetative or reproductive structures determine whether flowering occurs [13]. To initiate flowering, the flowering response or signal must be transferred through florigen to apices and induces meristem identity genes involved in the initiation of flowering following the accumulation of a light signal (photoperiod response) on the leaves [17–19]. This process is mediated by both vernalization and photoperiod response genes [18, 20]. Future research should identify the meristem identity genes controlling floral transition and inflorescence development in wheat and other cereal crops [21].

3. The influence of vernalization genes on the flowering time of bread wheat

Bread wheat is generally classified as spring or winter types according to its response to low temperatures during the vegetative phase [22–24]. Exposure to low temperatures (0–10°C) for several weeks (usually 6–8 weeks) is necessary for the development of tillers and the induction of flowering in winter wheat, whereas tillering and flowering of spring wheat occur regardless of temperature [22, 25]. The flowering models of the temperate cereals indicate that before vernalization, *Vrn-3* series is repressed by *Vrn-2* and long exposure to low temperatures is necessary for the upregulation of *Vrn-1* series and downregulation of *Vrn-2* in the leaves. Failure of these processes will delay the flowering process [26–28]. As spring approaches, the *Vrn-3* levels are upregulated (a process mediated by photoperiod genes) and signals are sent from the leaves to shoot apices to increase the *Vrn-1* transcription above threshold levels for the induction of flowering [10, 28]. Winter wheat types are considered to be ancestral to spring wheat types [29] and the winter alleles of *Vrn-A1* genes are considered to be ancestral to the spring alleles. The insensitivity of spring wheat to vernalization is due to mutational loss of the repressor binding site in the regulatory region of one or more *Vrn-1* genes [30] and is responsible for the early flowering ability of spring wheat [31]. Spring wheat varieties have been bred to adapt to diverse agroclimatic conditions attributing to their much shorter flowering time as compared to winter wheat [4, 32].

Substitution line analyses have identified four major series of genes controlling the length of the vernalization period in bread wheat (**Table 1**). According to Yan et al [17], the *Vrn-B3* gene (7BS) was identified as a flowering time (FT)-like gene, as have its homologous *Vrn-A3* and *Vrn-D3* on 7AS and 7DS, respectively [19]. Among the identified major genes controlling vernalization response, the *Vrn-1* series (*Vrn-A1*, *Vrn-B1*, *Vrn-D1*) is the predominant one in reducing vernalization requirement [31, 33]. However, even with fulfilled vernalization requirement, photoperiod sensitive bread wheat cannot flower until a critical day length has been reached [5].

Major gene series	Gene(s) comprised	Gene location	Reference
Vrn-1	*Vrn-A1, Vrn-B1* and *Vrn-D1*	Long arms of chromosomes 5A, 5B and 5D, respectively	[31, 34]
Vrn-2	Not specified	chromosomes 4B, 4D and 5A	[35]
Vrn-3	*Vrn-A3, Vrn-B3* and *Vrn-D3*	Short arms of chromosomes 7A, 7B and 7D, respectively	[36]
Vrn-4	*Vrn-D4*	Chromosome 5D	[37]

Table 1. Vernalization genes/class of genes identified in bread wheat to date.

4. The influence of photoperiod response genes on the flowering time of bread wheat

Photoperiod is the day length and number of long days that a wheat cultivar must reach (a threshold) for floral initiation [38]. The duration of exposure to light can be categorized into three groups namely, short-day (SD, 11-14 h), long-day (LD, 18 h), and day-neutral (DN) or facultative [39]. The winter wheat and spring wheat varieties can be photoperiod-sensitive or photoperiod-insensitive. Photoperiod-insensitive varieties are early flowering both under SD and LD conditions, in contrast to the photoperiod-sensitive varieties that require exposure to LD for weeks before they can initiate flowering [38, 40]. Several genes controlling photoperiod response have been successfully identified in wheat (**Table 2**). The *Ppd-1* genes (*Ppd-A1*, *Ppd-B1*, and *Ppd-D1*) induce flowering time irrespective of the day length in contrast to the *Ppd-B2* gene reported on the short arm of chromosome 7B, which accelerates flowering time only under LD conditions [41, 42, 43]. The potency of the insensitivity of the photoperiod response genes has been ranked in the order:

Ppd-D1 > *Ppd-B1* > *Ppd-A1* [38, 44].

Gene	Gene location	Reference
Ppd-D1 (formerly *Ppd1*)	Chromosome 2D	[27, 38, 40, 44, 45, 49]
Ppd-B1 (formerly *Ppd2*)	Chromosome 2B	[27, 38, 40, 44, 45, 49]
Ppd-A1 (formerly *Ppd3*)	Chromosome 2A	[27, 38, 40, 44, 45, 49]
Ppd-B2	Short arm of chromosome 7B	[50]

Table 2. Photoperiod response genes identified in bread wheat to date.

Photoperiod insensitivity is beneficial for crops grown in short-growing seasons with high summer temperatures in order to avoid heat stress during grain-filling stages [44, 45, 46]. Earlier flowering conferred by the *Ppd-D1a* insensitive allele has broadened the adaptation of cultivars over a range of environments and increased yield potential in improved cultivars, in southern Europe, Asian, Mediterranean, and North African regions [11, 47, 48]. However, the desirability of this allele depends on the target environment. For example, in the northern parts of Europe, which do not experience late season stress, the *Ppd-D1a* allele is not selected

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for due to the shortened vegetative phase associated with this allele, which results in considerably lower yield potential in these environments [5].

5. The interaction of *Vrn* and *Ppd* alleles and its impact on flowering time of bread wheat

Various studies have been conducted to study the interaction between *Vrn-1* and *Ppd-1* active alleles and the impact of their different combinations on the flowering time of bread wheat. Cultivars containing different combinations of *Vrn-1* and *Ppd-1* alleles will respond differently under different environmental conditions and thus, display different heading dates or flowering times [3, 9, 23, 51, 52]. It was discovered that *Vrn-A1* genotypes (either single or in combination with other *Vrn* alleles) are the earliest in flowering followed by *Vrn-B1* and then *Vrn-D1* genotypes [53]. In fully vernalized winter wheat, *Ppd-D1a* allele advanced flowering time by up to 24 days [54, 55]. However, in the presence of an active allele of *Vrn-1*, the flowering time of wheat was reduced by at least 30 days [54, 56]. It was reported that wheat genotypes with all three dominant alleles of *Vrn-1* genes (*Vrn-A1*, *Vrn-B1*, and *Vrn-D1*) head quite early compared to mono- or di-dominant gene combinations [28]. Similar information was also reported by various authors [5, 9, 57–59]. From the results of the above-mentioned studies, it was shown which combinations of alleles perform better than others. In agreement with Zhang et al. [53], it was demonstrated in the other studies mentioned above that *Vrn-B1* and/or *Vrn-D1* alleles are less effective in advancing flowering time as compared to the *Vrn-A1* allele. The *Vrn-1* genotypes are reported to be marginally early in flowering time in the following order:

Vrn-A1 Vrn-B1 Vrn-D1 > *Vrn-A1 Vrn-B1*, *Vrn-A1 VrnD1* or *Vrn-A1* > *Vrn-B1* or *Vrn-D1*.

An epistatic interaction between the *Vrn-A1* and *Vrn-D1* active alleles was demonstrated in a study [9]. The same study confirmed an additive/complementary interaction for flowering time between the photoperiod-insensitive *Ppd-D1a* allele and the *Vrn-1* active alleles [57, 60]. Moreover, it was noted that although genotypes carrying *Vrn-1* and *Ppd-D1a* alleles are early flowering under both SD and LD conditions, the flowering time is delayed by low temperatures under SD conditions. Overall, it is concluded that *Ppd-1* and *Vrn-1* genes participate in a similar pathway to control flowering time [10]. This implies that even though vernalization and photoperiod responses are independent processes, fulfillment of both requirements is necessary for early flowering of bread wheat. Flowering will be delayed if these processes did not occur [28] and the extent of this delay will depend on the *Ppd* gene present in the variety, as well as the environmental conditions [43].

6. The influence of earliness *per se* (*eps*) genes on the flowering time of bread wheat

A third class of genes controlling flowering time of wheat is the earliness *per se* (*eps*) genes. *Eps* genes affect phenological development of wheat when all photoperiod and vernaliza-

tion requirements have been satisfied [1, 11]. However, genes of all three classes (*Vrn*, *Ppd*, and *eps*) exert pleiotropic effects on other aspects of plant growth and development [1]. Whereas the major *Vrn* and *Ppd* genes govern the gross adaptation to environments, the *eps* genes have been shown to largely fine-tune the flowering time of wheat varieties for their regional adaptations [1, 61–63]. Sufficient information is now available on the effect of *eps* genes in determining flowering time of wheat. Genetic analyses show that these loci have been mapped only as QTL effects rather than major genes because of their relatively small effect [1, 6]. This makes it difficult to undertake a comparative analysis of *eps* effects with confidence. Nevertheless, comparative genetic studies indicate that most wheat chromosomes harbor *eps* genes [1, 11, 64]. Worland [11] reported the likelihood of the existence of these genes on chromosome groups 2, 3, 4, 6, and 7. It was suggested in the same study that these genes fine-tune flowering time probably by determining the amount and rate at which vegetative and floral primordia are produced. A detailed mapping in bread wheat has detected *eps* loci on chromosomes of homologous group 2 and on the short arm of chromosome 3A [65, 66]. A locus on chromosome 2B is orthologous with the *eps2* gene in barley (*Hordeum vulgare*) [6, 11, 64], whereas the one on chromosome 3A is orthologous with the *Eps-3Am* gene in einkorn wheat (*Triticum monococcum*) [67]. The locus on chromosome 3A has been reported to also have significant effects on plant height, thousand kernel weight, and number of grains per plant [66]. However, no *eps* genes have been cloned as yet in bread wheat [12, 68] as compared to barley [6, 61, 69] and einkorn wheat [67]. More than 90 QTL for heading date, with most of them believed to play a role in fine-tuning flowering time, have been reported to be spread over almost the entire wheat genome [62, 70]. Recently, Zikhali et al. [12] validated the presence of an *eps* effect on 1DL in hexaploid wheat. Some qualities of *eps* genes, such as high heritability and their independency on the environment, display a platform for this class of genes to be efficiently used in breeding programs to modify the flowering time of wheat by advancing/shortening its life cycle [61]. With further studies, it will be possible to fine-tune flowering time to regional climatic variations using these loci (including those of *Vrn* and *Ppd*) once their primary and pleiotropic effects have been identified.

7. The influence of height-reducing genes on the flowering time of bread wheat

Among the most important growth habit parameters influencing adaptation and yield potential of bread wheat to various environments is plant height. The most common genes for reduced height (*Rht*, also called semidwarf) in wheat have been mapped on *Rht-B1* and *Rht-D1* loci on chromosomes 4B and 4D, respectively [71]. Another potentially valuable height reducing gene, designated *Rht*8, has been mapped on chromosome 2D of bread wheat [72, 73]. The alleles of the two genes, *Rht-B1b* and *Rht-D1b*, inhibit cell elongation due to insensitivity to the growth hormone gibberellic acid in contrast to the *Rht*8 gene. The primary mechanism of height reduction caused by these alleles (*Rht-B1b* and *Rht-D1b*) is a reduction in the rate of stem development and dry matter accumulation in vegetative tissue, leading to increased

partitioning of water and nutrients to the spike [74]. Consequently, more fertile florets and more seeds per spike are produced.

*Rht*8 genotypes were reported to compare very well with *Rht-B1b* and *Rht-D1b* genotypes in hot and dry environments (i.e. short growing season) [73]. This was evident in a study conducted by Lanning et al. [71] under terminal drought stress in Montana and Washington. In the study, the *Rht*8 semidwarf lines appeared to have superior seed characteristics (significantly higher kernel weight and grain protein content) relative to the *Rht-B1b* and *Rht-D1b* lines which even had reduced grain protein content relative to the wild-type. However, other studies reported higher yield potential associated with *Rht-B1b* and *Rht-D1b* genotypes under high input growing conditions (i.e., irrigated) as compared to *Rht*8 and standard height genotypes [75, 76]. The performance of semidwarf wheat lines was evaluated relative to standard height lines using a recombinant inbred line (RIL) population grown in both rain-fed and irrigated conditions in Montana [77]. Semidwarf lines containing *Rht-D1b* were discovered to have superior yield as compared to standard height lines. Moreover, McNeal et al. [78] observed that semidwarf wheat lines containing either *Rht-B1b* or *Rht-D1b* outyielded tall lines in Montana, except in very low yield potential environments where tall lines were superior. From these results, it can be concluded that when opting for high yield potential under normal or high input growing conditions, *Rht-B1b* and *Rht-D1b* genotypes are the best, but when planting in hot and dry (low yielding) environments, *Rht*8 genotypes should be selected for. The success of the *Rht* genes has resulted in their wide deployment in wheat breeding programs globally [79].

A moderate but significant correlation between flowering time and plant height has been reported in bread wheat [5, 80–82]. Shorter genotypes tend to flower earlier than the taller ones [5]. This effect was proposed to be mainly due to the *Rht-B1b* allele, suggesting a possible effect of the *Rht-B1* gene on heading date in wheat. Similar results were also reported by Wilhelm et al. [80], confirming the significant effect of *Rht-B1* on flowering time and suggested a possibility of genes controlling plant height to also affect flowering time. However, other studies report that earliness is often associated with reduced height and potentially reduced resource capture, therefore, reduced yield [42, 83]. This suggested negative correlation between earliness and yield remains a challenge in wheat breeding programs, posing a need to modify flowering time to suit local climatic conditions while maintaining or even increasing yield potential. The biggest challenge is to incorporate all or as many of the favorable and/or agricultural important traits as possible in one cultivar [84, 85].

8. The potential benefits of tailoring flowering time of wheat in the wheat production industry

Flowering time is a complex trait that is responsible for wide adaptation of wheat (and other cereal crops) to different environments [4, 21, 86]. This trait could be modified or tailored to local climatic conditions to achieve desired characteristics such as improved yield [87, 88].

Similar studies have been conducted successfully whereby high temperatures and drought stress during anthesis and grain filling were avoided through tailoring flowering time of wheat to local climatic conditions [42, 89].

The potential advantage of tailoring flowering time can be used to escape environmental conditions that lead to yield loss, such as high temperatures or conditions that lead to poor wheat quality, such as rain during harvest time. This could contribute to reducing the worldwide physiological phenomenon of preharvest sprouting (PHS). Preharvest sprouting, which is the germination of seed grains in the mother ear before harvest due to humid conditions, is prevalent in wheat-growing regions experiencing high rainfall during the period of grain maturity and ripening [90]. This results in significant losses in the wheat production industry such as the downgrading of premium milling quality wheat to feed quality [91]. Resistance to PHS is a highly desirable trait sought by plant breeders globally [92, 93]. In addition to breeding for resistance of this trait, tailoring flowering time for the production of early flowering cultivars, which will escape conditions favorable to PHS, could help reduce the problem.

9. The role of diagnostic molecular markers in the detection of allelic variation among the major growth habit genes influencing the flowering time of bread wheat

The fact that current wheat germplasm has not been characterized fully in terms of important agronomic traits limits the use of wheat germplasm to a certain extent. Identifying the alleles of these genes and estimating the effects of their combination on growth, heading date, and ultimately grain yield will enhance the selection of cultivars with wide adaptability to a set of environments [57]. This knowledge can help accelerate the introgression of adaptability and yield-contributing genes by predicting the best combinations for enhanced yield potential and adaptation [28]. Moreover, the identification of alleles of growth habit genes subsequently leads to the development of a series of molecular markers (allele-specific DNA markers) for improved identification of these alleles in future [46, 86, 94].

The development of allele-specific DNA markers has allowed for efficient detection of extensive allelic variation existing among genes controlling flowering time in bread wheat [35, 46, 95]. Through these markers, it has been revealed that the allelic variation at the *Vrn-A1* locus (*Vrn-A1a*, *Vrn-A1b*, and *Vrn-A1c*) results from mutations within the promoter sequence [26] and/or deletions within the first intron of this gene [26, 95]. For the *Vrn-B1* and *Vrn-D1* loci, their allelic variation is determined only by deletions within the first intron sequence of the gene [95]. Diagnostic markers are available to differentiate among these forms and consequently, significant progress in understanding the molecular basis of vernalization has been made in wheat and barley species [15, 16, 94, 96].

For photoperiod response genes, photoperiod insensitivity is induced by indels in the 5′ upstream region of pseudoresponse regulator (PPR) genes, which do not exist in photoperiod-sensitive varieties [41, 46, 49]. For instance, a 2 kb deletion in the *Ppd-D1* promoter region of chromosome

2D results in a semi-dominant, photoperiod-insensitive allele (*Ppd-D1a*). The semidominant *Ppd-D1a* mutation has been identified as the major source of earliness in wheat varieties globally. This most potent allele upregulates the expression of the *Vrn-3* gene, which is a homologue of the *flowering locus T* (*FT*) of *A. thaliana* [9], under both SD and LD conditions, therefore confers early flowering in wheat [13, 43].

The *Ppd-D1* gene is said to exist in several forms. Six haplotypes (alleles) of this gene have been identified [40], four of which were common in bread wheat. The same study provided molecular markers to distinguish among these alleles and elucidated that they have different levels of expression. Haplotype I, which is equivalent to *Ppd-D1a* in Beales et al [46] and Eagles et al [57], had the highest level of expression, and it was suggested that Haplotype II is a progenitor of the others and probably photoperiod-sensitive. To further their work, Guo et al. [40] developed a method which identified allelic variation within a locus that Eagles et al. [57] and Fischer [97] labeled as *Ppd-D1b*, eventually dividing that single classification into three alleles.

The alleles of *Ppd-D1* were also identified by Cane et al. [98] using allele-specific molecular markers. Lines carrying *Ppd-D1a* were identified with a large deletion in the promoter region by the method described in references [46] and [60]. Lines with a deletion in exon 7 were classified as *Ppd-D1d* carriers. Lines harboring *Ppd-D1c* alleles manifested a *mariner*-like transposable element in intron 1 and lines not characterized as either *Ppd-D1a*, *Ppd-D1c*, or *Ppd-D1d* were designated as *Ppd-D1b*. Frequent alleles of *Ppd-D1*, *Vrn-A1*, *Vrn-B1*, and *Vrn-D1* genes can be accurately identified using current molecular techniques. Inaccurate classification of alleles could reduce the accuracy of estimation of their effects on flowering time [57, 98].

Besides the *Ppd-D1* gene, two more loci namely, *Ppd-A1* and *Ppd-B1*, have been identified and shown to have effects as strong as that of *Ppd-D1* in accelerating flowering time in bread wheat [20, 41, 42, 99]. In a study to investigate the effect of *Ppd-B1a* allele on flowering time in wheat, it was shown that *Ppd-B1* displays copy number variation (CNV) [20]. Wheat genotypes with only one copy allele are photoperiod-sensitive whereas an increased copy number (2–4 copies) results in a day-neutral, early flowering phenotype. A complementary study [100] confirmed that wheat genotypes with the three-copy allele (termed *Ppd-B1a*) and the four-copy allele (termed *Ppd-B1c*) exhibit reduced days to heading as compared to the one-copy allele (termed *Ppd-B1b*) whereas the two-copy allele (termed *Ppd-B1d*) displays increased days to heading (late flowering). These results indicate that the CNV at the *Ppd-B1* locus contributes in fine-tuning the adaptation of wheat to local climatic conditions, in addition to the major effect of *Ppd-D1*.

10. Concluding remarks and future breeding perspectives

The three classes of genes (*Vrn*, *Ppd*, and *eps*) play a vital role in the adaptation and protective mechanisms to ensure successful reproduction of wheat in diverse environments around the world. It has been revealed that a combination of *Vrn*-1 (especially *Vrn-A*1) and *Ppd-D1a*

results in genotypes that are early flowering under both SD and LD conditions, but flowering time is delayed under SD conditions. Moreover, a significant correlation between flowering time and plant height has been reported suggesting the possibility of genes regulating flowering time to also regulate height [5, 80]. Therefore, semidwarf genotypes are said to flower earlier (and may give higher yield) as compared to taller or normal ones depending on the environment and the genotype by environment interactions.

In the view of the current and projected climate change, which will include extreme hot and dry conditions, selecting for *Rht*8 genotypes could be beneficial relative to the *Rht-B1b* and *Rht-D1b* genotypes, which only perform well under high input conditions. In contrast, *Rht*8 genotypes have been shown to perform well and give higher yields under hot and dry environments. Climate change necessitates that the genetic structure of current breeding programs be shaped accordingly. Therefore, breeding for wheat cultivars with flexible response in different environments and that exhibit superior performance under extreme conditions, such as hot and dry environments, should become a priority. Photoperiod insensitivity is usually an advantage in most regions [100]. Therefore, selecting for the trait and incorporating genes for other complementary traits, such as preharvest sprouting resistance into the advanced lines, could be an added advantage in addition to significant yield improvement. Selecting for favorable alleles in targeted environments will contribute to yield improvement in the wheat production industry. This will help to meet the ever-increasing demand, which will mean sustainable food security.

Selection of favorable alleles could increase the level of variation and/or introduce novel sources of resistance to diseases and unfavorable weather conditions into breeding populations [9, 26, 95, 101]. This allows the transfer of genotypes between regions with different climatic conditions but still maintains their level of agronomic performance [5]. The *Ppd-D1a* allele has been selected for by plant breeders in different countries for several decades to enhance yield in certain climatic conditions [10, 46, 100]. Selecting for favorable alleles also allows the development of allele-specific DNA markers for efficient detection of extensive allelic variation among genes controlling traits of agronomic importance [35, 46, 95]. As a result, the genetic components of flowering time and other traits of agronomic importance are now better understood and some of the associated genes are isolated and cloned in wheat and closely related species [15–17, 46, 101]. The information provided in this chapter will therefore be helpful in the current and future breeding programs when breeding for adaptation and improved yield in wheat.

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