Review

Unlocking the Yield Potential of Wheat: Influence of Major Growth Habit and Adaptation Genes

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ABSTRACT

Improvement of grain yield has been the primary goal of many wheat (*Triticum aestivum* L.) breeding programs. Yield, nevertheless, has a complex genetic architecture which imposes constraints for breeding and selection. Among the main genetic factors affecting grain yield in wheat are the major growth habit and adaptation genes which include the vernalization, photoperiod, and reduced height genes. Optimizing flowering time and plant stature through selecting favorable alleles that control these traits could improve adaptation, which consequently could raise grain yield potential in target environments. Recently, genomewide association mapping and genomic selection approaches have revealed the complex genetic architecture of heading date and plant height in wheat. Non-invasive, fast, and accurate high-throughput phenotyping platforms have also been implemented to facilitate phenotypic field evaluation for flowering time and plant height. Crop simulation studies for future climate change scenarios favor the early flowering wheat ideotypes for improved yield and yield potential. Fine-tuning the adaptability and growth habit genes in modern cultivars remains crucial in raising the yield potential of wheat amidst changing climate and environmental conditions.

KEYWORDS: genomewide association study; growth habit; high-throughput phenotyping; grain yield; plant ideotypes; photoperiod; reduced height; vernalization; wheat; yield potential

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ABBREVIATIONS

ABLUP, Best linear unbiased prediction with pedigree information only; BRR, Bayesian Ridge Regression; EN, Elastic Net; GBLUP, Genomic best linear unbiased prediction; GA, gibberellic acid; GBS, genotyping-by-

sequencing; GW; grain weight; GWAS, Genomewide association study; GS, Genomic selection; HBLUP, Best linear unbiased prediction with both genomic and pedigree information; HD, heading date; HTP, high-throughput phenotyping; KN, kernel number; LASSO, Least absolute shrinkage and selection operator; *Ppd*, photoperiod genes; RKHS, Reproducing Kernel Hilbert Space; *Rht*, reduced height genes; RRBLUP, Ridge regression best linear unbiased prediction; SNP, single nucleotide polymorphism; *Vrn*, vernalization genes; W-BLUP, Weighted best linear unbiased prediction

INTRODUCTION

Wheat (*Triticum aestivum*) has remained one of the primary sources of calories worldwide. Its cultivation in many parts of the world is a result of its wide adaptation brought about by the major growth habit and adaptability genes such as the those involved in controlling vernalization, photoperiod response, and plant height. While an increased in wheat production has been observed in the past decades, the threats of changes in global temperatures and weather patterns continue to impede production. Climate change alters relationships among crops, pests, pathogens, and weeds, and reduces the number of pollinating insects, increases water scarcity and increases concentration of found-level ozone [1]. Without changes in agronomic management practices and the use of different wheat cultivars, the projected global wheat production will decrease by 2.3 to 7% and by 2.4 to 10.5% under an increase of 1.5 °C and 2.0 °C in temperature [2]. In a previous simulation study by Asseng et al. [3], a 6% reduction in wheat production globally has been estimated for each ^{0}C of increase in temperature. Using simulations for 32 major wheat producing areas in Mexico, Guarin et al. [4] recently projected a 12% reduction in wheat production because of climate change.

Temperature-related climate extremes were also observed to have stronger associations with yield anomalies (i.e., the fluctuation of yields from overall trends) for maize (*Zea mays*), soybeans (*Glycine max*), rice (*Oryza sativa*), and wheat; temperature-related predictors were also more strongly correlated with crop yield deviations than precipitation-related climate factors, such as drought or extreme rainfall [5]. These observations, together with results from other recent studies [6–9] showed the negative effects of global temperature changes on wheat production. One of the best strategies to maintain and maximize the yield potential of wheat amidst global climate changes is the optimization of its phenology which is a major factor for adaptation to a specific environment [10]. Together with the major phenology genes, reduced height genes play a crucial role in developing wheat lines with reduced lodging, and greater harvest index, and hence increased yield potential. To improve yield potential in wheat, the impact of these major adaptation and height genes should be considered in modern wheat breeding programs.

In this review, we focused on the influence of genes involved in controlling response to vernalization, photoperiod, and plant stature on yield potential in wheat. We reviewed genetic mapping, genomic selection, and high-throughput phenotyping approaches that have been implemented to understand the genetic architecture of heading date and plant height, and how information derived from these approaches could facilitate breeding for improved yield potential in wheat. Finally, strategies for increasing yield potential through breeding and selection for growth habit and adaptation genes were discussed.

MAJOR GROWTH HABIT AND ADAPTATION GENES IN WHEAT

Vernalization, photoperiod, and reduced height genes are the three genetic systems that control growth habit and adaptation in wheat [11]. Temperature cues for vernalization, together with photoperiod are the main environmental cues that plants monitor to determine the appropriate time to flower [12,13], whereas reduced height genes are associated with increased resistance to lodging, improved partitioning of assimilates, and increased grain number [14,15]. The ability of wheat to synchronize its flowering during favorable conditions is central to its global adaptability, and hence to its success [16–18]. A deeper understanding of the effects of these genes is thus crucial to unlocking the potential for breeding of wheat cultivars that are higher yielding and better adapted to target environments.

Vernalization Genes

In wheat and other cereals, vernalization is the requirement for a long exposure to low temperature to induce and accelerate flowering [19,20]. Vernalization helps prevent flowering during the winter which can consequently damage the cold-sensitive meristem of the plant and permits flowering under favorable conditions in the spring [21]. As such, it is an important adaptation in response to cold environments for the transition of the plant from the vegetative to the reproductive phase [18]. Flower development will only start once the risk of damage because cold is minimal, i.e., flowering is delayed until winter and the danger of vegetative frost damage has passed [22].

Allelic variation in genes controlling vernalization response (*Vrn*) divides wheat cultivars into the “non-vernalization requiring” spring, facultative, and the “cold-requiring” winter habits [23–25]. Differences in the effects conferred by these genes exists from complete insensitivity to partial or weak sensitivity, depending on the type of *Vrn* alleles present [18,26]. The main gene controlling vernalization requirement is the *VRN1*, with three homoeologous copies designated as *Vrn-A1*, *Vrn-B1*, and *Vrn-D1* on chromosomes 5A, 5B, and 5D, respectively [17,27]. In terms of potency, it has been observed that *Vrn-A1* has the strongest effect on inhibiting vernalization requirement, followed by *Vrn-D1*, and *Vrn-B1* [28]; thus, plants with dominant *Vrn-A1* will head first while those having *Vrn-B1* will

head last, provided that other genetic factors remain constant [29]. Copy number variation (CNV) for *Vrn-A1* was also been found to result in an increased vernalization requirement for cultivated bread wheat, indicating the potential role of CNV in wheat adaptation [26]. It has also been shown that wheat responds linearly to vernalization duration, suggesting the quantitative nature of vernalization response [30]. The other major vernalization response genes, *VRN2* and *VRN3*, have been mapped to chromosomes 4A [31] and 7B [32], respectively. One or more dominant alleles for *VRN1* and *VRN3* results in a facultative or spring growth habit, whereas dominant allele(s) for *VRN2* results to a winter wheat type [29].

Molecular characterization of the vernalization response genes rendered further insights to their structure and biological functions. Using a positional cloning approach, Yan et al. [19] mapped and cloned the *Vrn-A1* gene in the wild relative *T. monococcum* and found that it is perfectly linked to the MADS-box genes *AP1* (*APETALA1*) and *AGLG1* (agamous-like gene from grasses). Analyses of gene expression profiles led to identifying the former as the better candidate for the *VRN1* gene and that a deletion in its promoter was associated with spring growth habit. An examination of the allelic variation in the promoter region of *VRN1* further revealed duplication in the promoter region of the *Vrn-A1a* allele [19]. Moreover, it was found that *Vrn-A1b* allele has two mutations in the host direct duplication region and a 20-bp deletion in the 5'-UTR (untranslated region) [19]. Ultimately, it was proposed that *VRN1* genes are likely to have extra sites of regulation localized outside the promoter region. *VRN2* was identified as a dominant repressor of flowering that is down regulated by vernalization through a positional cloning approach [33], whereas *VRN3* was later identified as an orthologue of the flowering time (*FT*) gene in *Arabidopsis* [32].

Photoperiod Genes

Photoperiodism is the phenomenon where plants respond to variable day and/or night length by receiving signals in the form of cryptochrome or phytochrome to initiate flowering [34]. In wheat, photoperiod sensitive cultivars require long days for induction of flowering, whereas photoperiod insensitive genotypes flower independently of day length [11]. Photoperiod insensitive cultivars of wheat immediately shift to reproductive growth with a rise in temperature in the spring, whereas photoperiod sensitive cultivars continue in the vegetative phase until the day length sufficiently increases to satisfy the photoperiod requirement [35]. Next to vernalization requirement, photoperiod response is regarded as the second most important genetic system determining flowering time, and hence adaptation of wheat to different agro-climatic conditions [29]. Photoperiod response is mainly controlled by the photoperiod (*Ppd*) loci, with three homoeologous copies of the gene designated as *Ppd-A1, Ppd-B1,* and *Ppd-D1*, located on the short arms of chromosomes 2A, 2B, and 2D of

wheat, respectively [35–37]. The *Ppd-D1* allele is regarded as the most potent in conferring insensitivity to photoperiod, followed by *Ppd-B1* and *Ppd-A1* [21,38].

Molecular mapping and characterization of the photoperiod response genes revealed the occurrence of genetic sequence divergence between related genes from different species, variation in the number of gene copies, and the existence of epigenetic fingerprints, i.e., not related to changes in the DNA sequences. Beales et al. [39], for instance, identified a "misexpressed" pseudo-response regulator in the photoperiod insensitive *Ppd-D1a* mutant of wheat and demonstrated the gene to be collinear with the *Ppd-H1* gene of barley (*Hordeum vulgare*). A 2-kb deletion upstream of the coding region of the *Ppd-D1a* gene was further identified. Sun et al. [40] reported two different methylation patterns or haplotypes in the regulatory region of *Ppd-B1* alleles that are associated with both CNV and photoperiod insensitivity. In another study, Hanocq et al. [41] detected four different photoperiod sensitivity QTL from chromosomes 2B, 2D, 5A, and 7D using an F_7 recombinant inbred line (RIL) population derived from a cross between cultivars "Renan" and "Recital". Prior to this, Shindo et al. [42] identified markers linked to photoperiod sensitivity on chromosomes 2B, 4B, 5A, 5B, and 7A when they examined an F_8 RIL population derived from a cross between *T. aestivum* (cv. "Chinese Spring") and *T. spelta* (var. *"dumalemiamum"*).

Currently, at least five different alleles for *Ppd-A1* have been identified, four of which confer insensitivity to photoperiod and are characterized by the presence of a deletion in the promoter region [38,43–45]. Likewise, six different alleles for *Ppd-B1* have been identified and were related to CNV and insertions in the promoter region [26,44,46]. The *Ppd-D1* gene has been shown to possess at least four different alleles, characterized by deletions in the promoter and coding region, as well as insertions of transposable elements in a non-coding sequence [21,39,47].

Reduced Height Genes

Remarkable improvement in yield and productivity of wheat cultivars during the "Green Revolution" have been primarily attributed to the introduction of reduced height (*Rht*) genes which rendered resistance to lodging and higher harvest index (HI) [48–50]. A higher HI signifies that a greater proportion of the products of photosynthesis accumulates in the grains rather than in the leaves [49,51] and is a consequence of reduced internal competition for assimilate supply between the developing ear and the stem during elongation before flowering [52].

Reduced height genes are classified to be either gibberellin (GA)-sensitive or GA-insensitive, based on whether applied GA does or does not result in increased stem elongation [48]. The *Rht-B1b* and *Rht-D1b* reduced height genes have been classified as GA-insensitive, whereas *Rht4*, *Rht5*, *Rht12*, and *Rht13* were regarded as the GA-sensitive alleles [53]. *Rht-B1* and *Rht-D1* encode DELLA proteins, characterized by the presence of aspartate

(D), glutamate, (E), leucine (L), leucine (L), and alanine (A) or DELLA motifs in the N-terminal region, which act to repress GA-responsive growth; a limited response to GA for GA-insensitive alleles results in improved resistance to stem lodging and yield benefits through an increase in grain number [50]. It was demonstrated that severe dwarfism caused by *Rht-B1c* is caused by an intragenic insertion whereas extreme dwarfism due to *Rht-D1c* is attributed to the overexpression of the *Rht-D1b* allele. Peng et al. [54] demonstrated that *Rht-B1* and *Rht-D1* encode mutant gibberellin response modulators that are orthologues of the *Arabidopsis* gibberellic acid insensitive (GAI) gene.

PCR-based markers for *Rht-B1b* and *Rht-D1b* detect point mutations which define these alleles in wheat. They are "perfect markers" since they are specific for the base pair changes responsible for the semi-dwarf phenotype [55]. *Rht-B1b* and *Rht-D1b* alleles were introduced into commercial wheat cultivars from the Japanese variety "Norin 10" in the 1960s as part of wheat improvement programs in the USA and Mexico [55]. In another study, Ellis et al. [56] were able to identify the chromosomal locations of several *Rht* genes by screening populations of recombinant inbred and double haploid lines of bread wheat. Linked markers were found for *Rht5* on chromosome 3BS, *Rht12* on 5AL, and *Rht13* on 7BS, which accounted for most of the phenotypic variation in these populations. The height-reducing effect of these genes across target environments was also observed. More recently, *Rht24* has been mapped on chromosome 6A using a RIL population derived from a "Jingdong 8" × "Aikang 58" cross [57]. This QTL designated as *QPH.caas-6A* was mapped to a 1.85 cM interval between markers *TaAP2* and *TaFAR* and was observed to reduce height by 8.0%–10.4% (average of 6.0–8.0 cm across environments). Furthermore, the gene was associated with an increased thousand grain weight, indicating a potential effect of *Rht24* on yield potential.

BREEDING FOR IMPROVED YIELD POTENTIAL OF WHEAT: FINE-TUNING FLOWERING TIME AND PLANT STATURE THROUGH THE MAJOR GROWTH HABIT AND ADAPTATION GENES

Improvement in grain yield is a primary objective of wheat breeding programs [58]. As the timely occurrence of flowering is a major determinant of grain yield in wheat [59], one strategy implemented has been the modification of its developmental pattern that best suit specific growing conditions to ensure that appropriate flowering time and life cycle duration are met [29]. Altering the developmental pattern of modern wheat cultivars entails selection for the appropriate adaptation and height genes and their combinations for optimal yield in target environments.

Vernalization response genes are known to contribute indirectly to yield potential by influencing flowering time [60], as well as tiller and spikelet number in sensitive genotypes [61]. Genotypes having dominant alleles in combination at two *Vrn* loci tend to be early maturing and high yielding. This suggests that combining specific alleles in spring wheat may

improve yield potential [18,62]. Moreover, Iqbal et al. [63] suggested that early maturing spring cultivars with desirable grain yield potential may be developed by combining dominant *Vrn* alleles. After examining a collection of Canadian spring wheat germplasm, Kamran et al. [18] reported that 74% of soft white lines possessing a less potent vernalization gene, *Vrn-B1* either alone or in combination with other *Vrn* genes are higher yielding. The results of another study by Kamran et al. [25] suggested the possible role of *Vrn-D1* in producing higher grain yield on a set of Canadian spring wheat lines. Zhang et al. [64] identified combinations of vernalization response genes that resulted to high yield in drought and well-watered conditions for a double haploid population of wheat segregating for *Vrn-A1*, *Vrn-B1*, and *Vrn-D1*. The genotype *vrn-A1/vrn-B1/vrn-D1* showed high kernel number (KN) and grain weight (GW) in well-watered environments. Conversely, the genotype *Vrn-A1a/vrn-B1/Vrn-D1a* gave high GW and KN in drought conditions. Stelmakh [62] observed that *Vrn1*, *Vrn2*, and *Vrn3* genes have different effect values in relation to heading date, plant height, and yield components. Decreasing the amount of time required for vernalization for winter wheat could also be an approach to improve yield potential, especially under stressed conditions. Recently, shortening of vernalization requirement has been induced using the plant hormones gibberellins, kinetins, and 6-benzy adenine for winter wheat evaluated under arid and semi-arid environments in Iran [65]. Planting winter wheat as a spring wheat (with no vernalization treatment) resulted in optimum yields through priming and spraying of plant growth regulators. In another study, the higher grain yield of winter type near-isogenic lines (NIL) containing *Vrn-D1b* compared with the spring wheat line “Asakazekomugi” under early sown conditions was attributed to high dry matter production resulting from greater stem elongation conferred by the *b* allele of the *Vrn-D1* gene [66].

Photoperiod genes play an important role in accelerating or delaying flowering time in spring after the vernalization requirement has been satisfied [35]. An examination of the effect of the insensitive allele *Ppd-A1a* on the heading date of Japanese wheat revealed that cultivars from the Kanto region possessing the allele headed ~7–10 days earlier, whereas varieties from Hokkaido headed 2.5 days earlier, than the sensitive genotypes [67]. Foulkes et al. [68] observed an average advanced flowering by 9–12 days of wheat NIL coming from the UK and Kamran et al. [18] noted reduction for time of flowering for wheat genotypes from Canada. Using introgression lines developed from the spring wheat variety “Paragon”, Shaw et al. [69] observed that wheat lines lacking *Ppd-B1* flowered 10–15 days later than controls under long day conditions, whereas candidate loss-of-function for *Ppd-A1* delayed flowering by 1–5 days, confirming the effects of loss-of-function mutations to flowering under long days. Similarly, Kiss et al. [70] observed that lines possessing photoperiod-insensitive alleles for *Ppd-D1* and *Ppd-B1* headed the earliest among a worldwide collection of 683 wheat genotypes. In another study,

Guedira et al. [71] identified QTL related to photoperiod response and vernalization sensitivity on chromosomes 2B and 5B, respectively. These QTL associated with the environmentally sensitive photoperiod and vernalization genes were shown to be the major determinants of heading dates in eastern US soft wheat winter germplasm. Worland et al. [72] previously demonstrated that early flowering *Ppd-1* wheat genotypes produce larger grains and greater yields in the Southern European growing regions. Kamran et al. [18] noted that yield advantages with photoperiod insensitive cultivars were possibly due to escapes from hot summers by maturing earlier as hot, dry conditions are associated with decreased tiller number and decreased grain weight.

Gene interactions among the major groth habit loci can result in improve yield potential and adaptation in wheat. Under early spring sowing conditions, Kolev et al. [73] observed that the allele combinations *Ppd-D1a/Vrn-A1a* and *Ppd-D1b/Vrn-A1a* were higher yielding than other combinations in a set of Bulgarian varieties. In another study, Addison et al. [74] identified the *Vrn-B1* locus, with the short vernalization allele from the winter wheat cultivar “AGS2000” favorable for yield. Furthermore, it was observed that *vrn-B1* acted additively with a region on chromosome 2B near the *Ppd-B1* locus, demonstrating that a shorter vernalization requirement combined with photoperiod sensitivity may play an important role for adaptation and improved yield potential of soft red winter wheat cultivars to southern US growing conditions. Recently, genotypic variation and additive interaction among *Vrn* and *Ppd* genes resulted in significant differences for grain filling duration, plant height, biomass at anthesis, and harvest index in durum wheat landraces and modern cultivars [75]. In another study, Dowla et al. [76] observed that the interaction of *Rht-D1b* with *Ppd-D1a* and at least two spring-type alleles of *Vrn1* resulted in the highest grain yield across different environments possibly due to the earlier flowering and avoidance of terminal drought. In the molecular level, the initiation of heading and flowering through the vernalization regulatory network is controlled by *Vrn1*, *Vrn2*, and *Vrn3* through a positive feedback mechanism mediated by RNA binding and MADS-box proteins such as *TaGRP2* and *TaVRT2*; this pathway subsequently interacts with the photoperiod regulatory network via *Ppd1*, phytochromes (*TaPHYC*), and *Hd1*-like proteins (e.g., *TaHD1*) to regulate heading date and time of flowering in wheat [77].

Environmental conditions can also influence the major growth habit genes and hence yield. The ambient temperature can affect heading date after the vegetative phase of wheat consquently influencing grain yield potential. High ambient temperatures have been linked to rapid transitions to the reproductive stage in long days, whereas reproductive development has been inhibited in short days [78]. Furthermore, gene mediated-interactions between temperature and day-length through floral promoters such as *FPF1-like3* or *VER2-like* might speed-up reproductive development under high temperatures in long days [78].

The increased yields of wheat varieties during the “Green Revolution” was attributed primarily to the presence of *Rht* genes in wheat [50]. Slafer and Araus [79] observed that reducing height to a certain level has no effect on the crop’s ability to capture resources while markedly improving the efficiency with which these resources are used to produce yield. Yield advantages of shorter wheat plants over tall controls were earlier observed by Flintham et al. [52] when they conducted yield trials in eastern England and Central Germany. In another study, Addisu et al. [80] observed that *Rht-D1b* was associated with reduced height, increased harvest index, and grain yield when they examined wheat NIL under two contrasting production systems. The semi-dwarfing *Rht-B1b* and *Rht-D1b* genes, located at chromosomes 4B and 4D of wheat, respectively are usually associated with increased wheat yields [81], but their effects vary with environment [53]. Reduction in height was observed to be correlated with reduced lodging score and increased grain number in a set of four inbred wheat populations segregating for one or more gibberellin-responsive dwarfing genes and in a set of NIL and recombinant inbred lines derived from the cross between “Magnif M1” and “Chuan-mai 18” containing *Rht13* [81]. It was further observed that semi-dwarf wheat lines containing *Rht13* had high yield, biomass, harvest index, and spike number indicating the potential use of this gene for improving performance. Another reduced height gene in chromosome 5A, *Rht12*, was previously observed to have an additive effect with *Ppd-D1a* and this interaction resulted in advanced flowering time and improved yields of Chinese winter wheat cultivars [82]. Overall, yield penalties for wheat lines containing *Rht-B1b* and *Rht-D1b* have been observed in dry environments, which indicates that drought among others factors, could be a limitation for the dwarf and semi-dwarf lines containing these major height genes [83]. This could favor the use of taller, faster-growing wheat lines in arid and semi-arid conditions. In future climatic conditions, when more frequent drought is expected, taller wheat plants might be better suited to many growing regions; whereas in irrigated environments, semi-dwarf and dwarf plants would be more adapted [83]. Ultimately, using the GA-sensitive *Rht* genes in breeding programs should be explored further for improving yield potential of wheat in well-watered conditions.

ALLELE DIVERSITY OF THE MAJOR GROWTH HABIT AND ADAPTATION GENES IN WHEAT

Selection for increased adaptation of wheat in various growing regions can be demonstrated by the allelic variation of growth habit and adaptation genes present across different breeding populations (**Table 1**). The frequency of alleles controlling response to vernalization is mainly dependent on whether spring or winter wheat types are required for specific regions or environments. *Vrn-A1a* and *Vrn-B1a*, for example, were predominant in a population of 245 spring bread wheat lines from Europe [84], whereas a worldwide collection of wheat lines across five different

mega-environments had < 5% of these *Vrn* spring alleles present [70]. The semi-dwarfing *Rht-D1b* was observed to be the main allele controlling shorter stature in southern US winter wheat lines [85,86], whereas *Rht-D1a* had higher frequency in wheat breeding lines from Canada [87] and Korea [88]. In a worldwide collection of both winter and spring types of wheat, *Ppd-D1a*, which controls insensitivity to day length, was found to be present in 58% of the lines evaluated [70]. The higher frequency of this *Ppd* insensitivity allele for wheat lines from Australia [89], China [21], Korea [88], and southern US [86] further demonstrates the positive selection for early flowering types of wheat. Early flowering wheat ideotypes were related with improved grain yield potential based on crop modeling studies for future climate change scenarios. An ideotype with earlier flowering time, longer grain filling, larger maximum grain size, and larger radiation use efficiency among others was predicted to be "ideal" for a "wet" South Eastern Australian environment based on recent simulations done using Global Climate models [90]. Accelerating the rate of crop development through early flowering and maturity by adjusting daylength response was also found to be optimal for improved yield potential under drought stress for a 2050 simulated climate change scenario at multiple sites in Europe [91].

Table 1. A survey of the distribution of major growth habit and adaptation genes across different populations of wheat from diverse geographic regions.

Reference	No. of lines	Type	Geographic origin of lines	Gene (Phenotype)	Frequency (%)
Kiss et al. [70]	683	Winter, Spring	Worldwide collection from five continents	*Ppd-B1a* (insensitive)	17
				Ppd-D1a (insensitive)	58
				Vrn-A1a (spring)	2
				Vrn-B1a (spring)	3
				Vrn-D1a (spring)	3
Shcherban et al. [84]	245	Spring	Europe	*Ppd-D1a* (insensitive)	9
				Vrn-A1a (spring)	62
				Vrn-B1a (spring)	68
				Vrn-D1a (spring)	5
Chen et al. [21]	173	Winter, Spring	Yellow and Huai Valley, China	*Ppd-D1a* (insensitive)	93
				Vrn-A1a (spring)	5
				Vrn-B1a (spring)	7
Lozada et al. [85]	239	Winter	Southern US	*Vrn-D1a* (spring)	14
				Rht-D1b (dwarfing)	64
				Ppd-B1a (insensitive)	15
				Ppd-D1a (insensitive)	55A

Table 1. *Cont.*

Reference	No. of lines	Type	Geographic origin of lines	Gene (Phenotype)	Frequency [%]
Chen et al. [87]	82	Spring	Canada	*Ppd-D1a* (insensitive)	32
				Ppd-D1b (sensitive)	68
				Vrn-A1a (spring)	94
				Vrn-D1a (spring)	2
				Rht-B1b (dwarfing)	10
				Rht-D1b (dwarfing)	16
Grogan et al. [92]	299	Winter	US Great Plains	*Ppd-A1a* (insensitive)	98
				Ppd-D1b (sensitive)	71
				Ppd-D1a (insensitive)	29
Cho et al. [88]	410	Winter, Spring	Korea	*Rht-B1a* (tall)	78
				Rht-D1a (tall)	79
				Ppd-B1a (insensitive)	6
				Ppd-B1b (sensitive)	94
				Ppd-D1a (insensitive)	75
				Ppd-D1b (sensitive)	25
				Vrn-D1a (spring)	34
Harris et al. [89]	47	Winter, Spring	Australia	*Ppd-B1b* (sensitive)	57
				Rht-B1b (dwarfing)	72
				Rht-B1a (tall)	27
				Rht-D1a (tall)	95
				Ppd-B1b (sensitive)	57
				Ppd-D1a (insensitive)	100
				Vrn-A1a (spring)	49
				Vrn-B1a (spring)	60

GENOMICS-ASSSISTED BREEDING TO DISSECT THE GENETIC BASIS OF THE MAJOR GROWTH HABIT AND ADAPTATION GENES IN WHEAT

The abundance of available DNA sequence information in recent years is valuable in dissecting the genetic basis of genes related to growth habit and adaptation in wheat. In particular, the development of next-generation sequencing technologies such as genotyping-by-sequencing (GBS) [93–95] and single nucleotide polymorphism (SNP) chips such as the Illumina 9K [96] and 90K [97] platforms enabled marker discovery and genotyping for the identification of loci underpinning growth habit and adaptation related traits. Among the strategies that have been implemented to study the genetic architecture of major growth habit and adaptation traits are genomewide association studies (GWAS) and genomic selection. Combining these genomics approaches with high-througput phenotyping strategies to understand the genetic architecture of adaptation and growth habit is a key to unlocking yield potential in wheat (**Figure 1**).

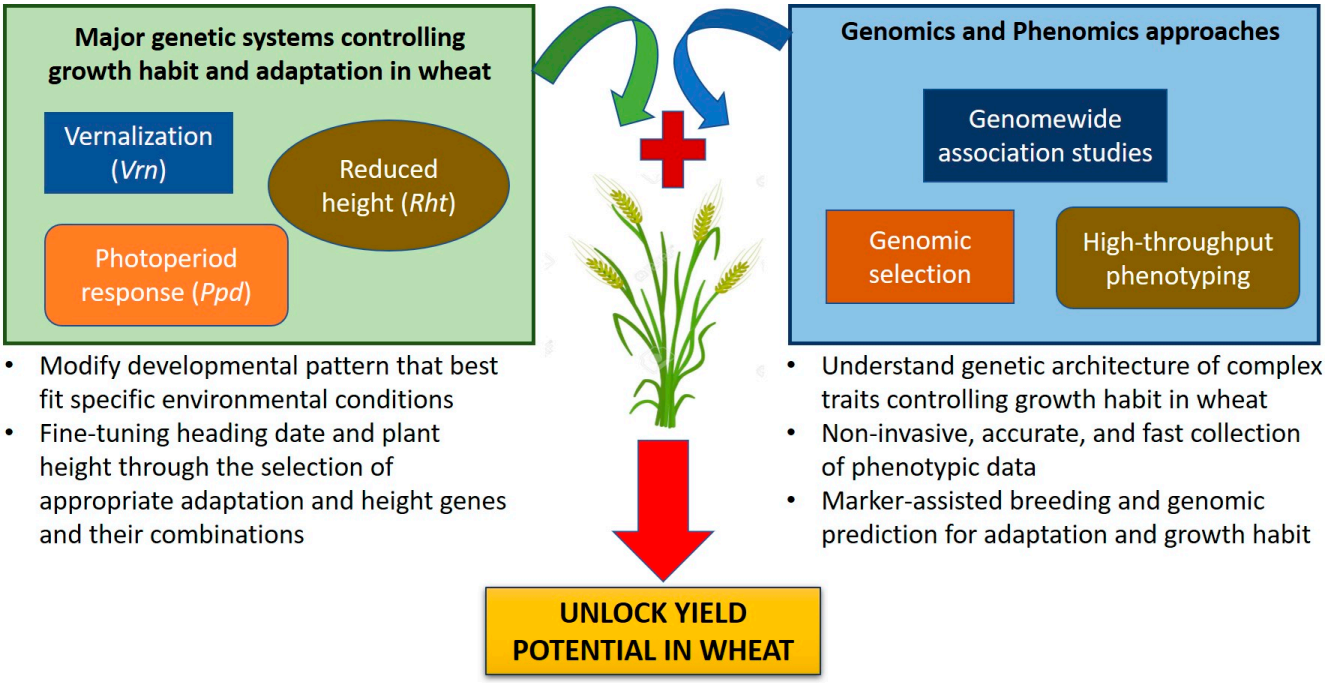

Figure 1. A key to unlocking yield potential in wheat is through understanding the genetic architecture of growth habit and adaptation traits using genomics and phenomics approaches. Selecting the appropriate alleles and their combinations that suit specific growing conditions (e.g., well-watered or drought-stressed environments) would facilitate improvement of yield and yield potential.

GWAS relies on linkage disequilibrium, the non-random association of alleles at multiple loci, to identify significant marker-trait associations [98]. The high rate of recombination events of diverse (or natural) populations used in association analyses allows a better mapping resolution compared to traditional linkage or QTL mapping approaches [99]. Information from GWAS could be used for marker-assisted breeding, for introgression of important genes across populations, gene cloning, assessment of genetic diversity, and identification of causative loci, functional markers, and alleles [100–103]. Previous studies have used a GWAS approach to identify key regions in the genome controlling plant height and heading date in wheat using different marker platforms such as DArT, Illumina SNP chips, and GBS-derived SNP markers (**Table 2**). Genetic mapping for plant height revealed the influence of the major *Rht* genes in controlling the trait across different wheat breeding populations. In addition, genetic loci independent of the major *Rht* genes previously mapped on 4B and 4D have been identified in other chromosomes such as 1A, 1D, 2B, 3B, 5B, 6A, 6B, and 7D [104–106], indicating the complex genetic architecture for plant stature in wheat. Likewise, for heading date, the major genes involved in response to photoperiod and vernalization have been identified through previous association mapping studies [107–109]. Marker-trait associations for heading date were mapped to different chromosomal regions not associated with the *Ppd* and *Vrn* genes, also demonstrating the genetic complexity of the trait.

Table 2. Summary of genomewide association studies conducted for heading date (HD) and plant height (PH) in wheat.

Trait	Chr.	No. of markers	Platform	No. of lines	No. of marker-trait associations identified	GWAS model [1]	Origin of lines	Reference
HD	1A, 1B, 2A, 2B, 3A, 3D, 5A, 5B, 7B	7934	Illumina 90K	358	438	K	Europe	Zanke et al. [108]
HD	1B, 2A, 2B, 2D, 3A, 3B, 5A, 5B, 5D, 6B, 6D, 7A, 7B, 7D	2975	GBS	96	35	K-Q	Japan	Kobayashi et al. [109]
HD	All chromosomes except 4D, 5D, and 6D	~2000–2100	DArT	376	134	K, K-PC, K-Q	Europe	Bordes et al. [107]
HD	1A, 1B, 2B, 3B, 4B, 5D, 6A, 6B	835	DArT	96	16	K-Q	Australia, Argentina, Asia, Europe, Mexico, USA	Gerard et al. [110]
HD	2A, 2D, 5B, 5D, 6D	20890	Illumina 90K	163	10	K	China	Zhang et al. [111]
HD	1A, 2A, 2B, 2D, 3A, 3B, 4A, 4B, 5A, 5B, 6A, 6B, 6D, 7A	6492	Illumina 90K	402	27	K-Q, Kc-Q	USA	Gizaw et al. [112]
PH	1D, 2B, 4A, 4D, 5A, 5B, 6B	19192	Illumina 90K	237	7	K-PC, K-Q	USA	Godoy et al. [105]
PH	4A, 4D, 6A	24038	Illumina 90K	568	4	K-PC	Australia	Garcia et al. [106]
PH	5B, 5D, 6B, 7B	15430	Illumina 90K	105	7	K-PC, K-Q	China	Wang et al. [113]
PH	1A, 1B, 2A, 2B, 2D, 3B, 4A, 4B, 5B, 6B, 7D	3245	Ilumina 90K	194	13	K-Q	Europe, Mexico	Turuspekov et al. [104]
PH	4B, 5B, 7A	19933	Illumina 90K SNPs	81	3	K-PC	Canada	Chen et al. [114]

[1] K- kinship; K-PC- kinship + principal components; K-Q - kinship + population structure; Kc-Q - compressed kinship matrix + population structure model.

The limitation of association genetics, however, lies on the fact that complex traits are controlled by multiple loci with minor effects which cannot always be identified by a standard GWAS approach. In addition, unexpected LD, low allele frequency, small effects size, and genetic heterogeneity remain an issue for the implementation of GWAS [115]. A complementary method, genomic selection (GS) [116] has thus been proposed, with pioneering works in livestock species and later implemented to plant systems. In GS, a selection model is trained using a training set [a population with phenotype and genotype data] and the performance (i.e., breeding values) of lines belonging to the validation or test set [unphenotyped population with genotypic information] is predicted [117]. GS therefore estimates the "genetic worth" of an individual through the calculation of genomic estimated breeding values, which could be a selection criterion in identifying potential parents or superior lines to advance in the breeding program [118]. Previous GS studies demonstrated moderate to high prediction ability for both heading date and plant height, where heritability was related to improved predictions (**Table 3**). Overall, heading date was observed to have lower predictability compared to plant height, which suggests that it has a more complex genetic architecture than the latter. It should be emphasized, however, that the accuracy of predictions in GS is not only affected by heritability but also by other factors such as training population size, relatedness between training and test populations, type of prediction model used, validation type implemented, and number of markers [119–123]. GS complements observations from GWAS regarding the genetic complexity of heading date and plant height in wheat.

Table 3. Summary of various genomic selection studies conducted for heading date (HD) and plant height (PH) in wheat.

Trait	Validation scheme	Heritability	Prediction model [1]	Accuracy	Reference
HD	Multi population cross-validation	0.88	LASSO	0.31	Charmet et al. [124]
HD	Cross-validation	0.85	RRBLUP, BayesC, W-BLUP	0.404–0.576	Zhao et al. [125]
HD	Five-fold cross-validation	0.84–0.90	RRBLUP	0.04–0.20	Herter et al. [126]
HD	Cross-validation	0.54	RRBLUP	0.53–0.66	Sarinelli et al [86]
HD	Ten-fold cross-validation	0.95	RRBLUP, EN, RKHS, BRR	0.55–0.60	Huang et al. [127]

Table 3. *Cont.*

Trait	Validation scheme	Heritability	Prediction model [1]	Accuracy	Reference
HD	Five-fold cross validation	0.87	GBLUP, ABLUP, HBLUP	0.33–0.54	Ashraf et al. [128]
PH	Five-fold cross validation	0.74	GBLUP	0.28–0.96	Norman et al. [129]
PH	Cross-validation	0.82	RRBLUP, BayesC, W-BLUP	0.395–0.502	Zhao et al. [125]
PH	Cross-validation	0.66–0.95	GBLUP	0.662–0.750	Sukumaran et al. [130]
PH	Cross-validation; independent validation	0.96–0.98	RRBLUP	0.55–0.70	Herter et al. [126]
PH	Cross-validation	0.57	RRBLUP	0.57–0.62	Sarinelli et al. [86]
PH	Cross-validation	0.95	RRBLUP, EN, RKHS, BRR	0.45–0.54	Huang et al. [127]
PH	Five-fold cross validation	0.46	GBLUP, ABLUP, HBLUP	0.38–0.57	Ashraf et al. [128]

[1] ABLUP- Best linear unbiased prediction with pedigree information only; BRR- Bayesian Ridge Regression; EN- Elastic Net; GBLUP- Genomic best linear unbiased prediction; HBLUP- Best linear unbiased prediction with both genomic and pedigree information; LASSO- Least absolute shrinkage and selection operator; RKHS- Reproducing Kernel Hilbert Space; RRBLUP- Ridge regression best linear unbiased prediction; W-BLUP- Weighted best linear unbiased prediction.

HIGH-THROUGHPUT PHENOTYPING FOR GROWTH HABIT IN WHEAT

In breeding populations, efficient selection is related to efficient phenotyping [131]. Phenotyping is a bottleneck for genetic mapping and selection studies due to the need for many lines to be assessed across multiple locations [132]. Emerging tools such as high-throughput (HTP) field phenotyping have circumvented this issue by providing faster and more efficient collection of phenotype data in a non-destructive manner [133,134]. Types of HTP platforms include satellite imaging, unmanned aerial vehicles (UAVs), and proximal phenotyping such as ground-based vehicles or sensors [135–137]. Satellite imaging provides a high multispectral spatial resolution; nonetheless, major restrictions include variable weather conditions, limited frequency of imaging, cost, and time to access the images collected [137]. UAVs, on the other hand, offer a customizable, accurate, cost-effective, and innovative remote sensing platform for data collection in the field [138]. Ground-based platforms are advantageous in that they operate directly in the field, could be used in multiple sites, and have the potential for increased spatial resolution [139].

Traditional phenotyping for plant height in wheat involves measuring the height of plants on the middle of each plot using a ruler or measuring stick. Wheat plant height is usually recorded as the measurement from the

ground to the tip of the head or spike, excluding the awn when present. This method is laborious, time-consuming, and introduces considerable error or variation in the measurements. Due to its association with traits such as yield, biomass, lodging resistance, and water stress, plant height remains an attractive trait to study using HTP approaches [140,141]. In wheat, plant height data has been collected through different HTP platforms. Previously, strong positive correlations (R^2 = 0.86; RMSE = 78.93 cm) were observed between canopy height of wheat measured through Light Detection and Range (LiDAR) sensors and height measured manually with a ruler [142]. In another study, similar accuracies between plant height of wheat derived from LiDAR and with height data collected from UAV was observed; nonetheless, the flexibility, affordability, and advances in cameras of UAV platforms, makes UAV a more appropriate choice to conduct large scale phenotyping for plant height [143]. A time-series evaluation of double haploid wheat lines was also conducted using a UAV-based platform and a high correlation (R^2 = 0.80–0.85) between UAV estimates and ground-based height data at booting and mid-grain filling stages was observed [141]. Furthermore, using the UAV data in the same study, novel QTL associated with accelerated growth was identified in chromosome 6D. Prediction accuracies using UAV and ground-based height data was also found to be significantly high (0.47–0.55). Overall, previous studies indicated the feasibility of HTP platforms to facilitate the genomic analyses for plant height in bread wheat.

Information on growth stages allows proper field management and operations and provides an early predictor for yield [143]. Collection of developmental stage data, however, can be labor intensive, as frequent visit to the field is required, in addition to the substantial number of lines that need to be evaluated. Recently, machine learning and computer vision approaches have been implemented for data collected using HTP platforms for the accurate assessment of developmental stages in wheat. For example, a fully automated, fixed-site phenotyping system carrying multiple sensors called Field Scanalyzer® [139] was previously used to examine heading and flowering time in UK wheat through the application of computer vision on digital images [144]. Results evaluated under a support vector machine to determine pre-define classes (e.g., ear emergence, time of flowering) in the final step yielded at least 95% accuracy across different heading stages, and 85% accuracy for flowering time. This method was further capable of distinguishing critical stages of growth from the Red-Green-Blue (RGB) images collected from the field, and were not affected by environmental conditions or differences in illumination. A “course-to-fine wheat ear detection mechanism” method that allows an automatic observation of heading in wheat has also been proposed [145]. This approach involves a “two-course detection” step to determine the candidate ear (head) region, and a fine-detection step, in which non-ear areas are subsequently removed from the analyses. This

method was observed to be acceptable, and significantly outperformed existing methods for high-throughput evaluation of crop development.

PROSPECTS IN BREEDING FOR PHENOLOGY IN WHEAT

Genomics and phenomics strategies could facilitate breeding and selection for favorable growth habit and developmental genes to fine-tune heading date and plant height that suit specific growing conditions. There are still some knowledge gaps on the current understanding of these genetic systems that needs to be filled, and hence other strategies should be implemented to dissect the the genetic architecture of growth habit in wheat. Integrating trancriptomics with genomics through using function associated specific trait (FAST) markers [146], for example, can be explored across different genomic selection models to enhance trait prediction for plant height and flowering time. Data from proteomics, metabolomics, and multi-omics profiling can give insights on how different gene and gene products interact to form a certain growth habit in wheat across different environmental conditions [77,147]. Exploring the epigenome can also give information on how certain growth habit and adaptation genes are expressed beyond their DNA sequence makeup. A holistic view of the major growth habit and adaptation genes through the different “omics” approaches can help breeders unlock yield and yield potential in wheat in the context of a changing climate.

CONCLUSIONS

Major genes controlling adaptation and growth habit have impact on the yield potential of wheat in diverse environments. Vernalization and photoperiod genes are important to fine-tune heading and flowering time, which consequently affects yield. Optimal plant height is necessary to avoid yield losses resulting from lodging and to optimize harvest index. Genetic mapping, genomic selection, and high-throughput phenotyping approaches could be used to select for wheat breeding lines with improved adaptation. Breeding efforts to select for the best combinations of growth habit and adaptation genes for target environments using genomics and phenomics approaches should be continued to facilitate increased yield potential in wheat breeding programs. As crop production is continuously being affected by global climate change, breeding for the optimal flowering time and plant height through the major phenology genes remains relevant to improve the yield potential of wheat.

AUTHOR CONTRIBUTIONS

DNL wrote and prepared the original draft; AHC and REM reviewed and edited the manuscript.

CONFLICTS OF INTEREST

The authors declare that they have no conflict of interest.

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