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Developing Wheat for Improved Yield and Adaptation Under a Changing Climate: Optimization of a Few Key Genes

M.A.N. Nazim Ud Dowla [a], Ian Edwards [a,b], Graham O'Hara [a], Shahidul Islam [a], Wujun Ma [a,*]

[a] School of Veterinary and Life Sciences, Murdoch University, Perth, WA 6150, Australia
[b] Edstar Genetics Pty. Ltd., Perth, WA 6150, Australia

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ABSTRACT

Wheat grown under rain-fed conditions is often affected by drought worldwide. Future projections from a climate simulation model predict that the combined effects of increasing temperature and changing rainfall patterns will aggravate this drought scenario and may significantly reduce wheat yields unless appropriate varieties are adopted. Wheat is adapted to a wide range of environments due to the diversity in its phenology genes. Wheat phenology offers the opportunity to fight against drought by modifying crop developmental phases according to water availability in target environments. This review summarizes recent advances in wheat phenology research, including vernalization (*Vrn*), photoperiod (*Ppd*), and also dwarfing (*Rht*) genes. The alleles, haplotypes, and copy number variation identified for *Vrn* and *Ppd* genes respond differently in different climatic conditions, and thus could alter not only the development phases but also the yield. Compared with the model plant *Arabidopsis*, more phenology genes have not yet been identified in wheat; quantifying their effects in target environments would benefit the breeding of wheat for improved drought tolerance. Hence, there is scope to maximize yields in water-limited environments by deploying appropriate phenology gene combinations along with *Rht* genes and other important physiological traits that are associated with drought resistance.

1. Introduction

Cereals constitute a prime global human food source. Among them, wheat (*Triticum aestivum* L.) ranks as the second most important food after rice, and is the most widely cultivated cereal in the world. It is one of the central pillars of food security, supplying 20% of total calories and a similar portion of total protein to the world's population [1]. The average global wheat yield is 3.3 $t \cdot hm^{-2}$; however, it varies widely, with regional averages ranging from 1.7 $t \cdot hm^{-2}$ in Australia to a potential of up to 9 $t \cdot hm^{-2}$ in other parts of the world (data from FAOSTAT database 2015 [2]). The yield penalty is usually due to different environmental stresses that reduce yield potential by 69.1% [3]. In most developed countries, wheat is mainly grown in rain-fed marginal land, where inadequate and erratic rainfall limits the yield (Table 1) [4]. Drought is a key stress that constrains wheat production on about 6.5×10^7 hm^2 of land worldwide [5] and reduces yield by up to 50% [6]. Modeling exercises have revealed that water stress in marginal wheat-growing environments reduces 50%–90% of their yield potential under irrigated conditions [7]. In 2012, the overall global wheat production decreased by 1.4%, mainly due to severe drought in the United States, Europe, and central Asia (data from FAOSTAT database 2013 [2]). The Australian wheat yield dropped by 46% in 2006 compared with the yield trend of the previous 50 years, resulting in billion dollar losses for the wheat industry (data from FAOSTAT database 2012 [2]).

The impact of future drought episodes on wheat production is expected to increase due to the effects of climate change on temperature and precipitation. It is estimated that the 1 °C increase of temperature that has occurred during the last 29 years has resulted in a 6% reduction of wheat yield compared with the expected yield without global warming effects [8]. According to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), the global mean temperature will increase by 3.7 °C by the end of this century, with incidents of hottest days and coolest nights occurring 50% more frequently than at present [9]. Changes in the precipitation pattern coupled with increasing temperature would affect the major crop production of the world, and

* Corresponding author.
E-mail address: w.ma@murdoch.edu.au (W. Ma).

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Table 1
Major wheat producers of the world: five year (2008–2012) averages of production, area harvested, and area irrigated for wheat [4].

Country/Region	Production (t)	Area harvested (10^7 m^2)	Area irrigated (10^7 m^2)
Australia	24.51	13650	–
Canada	26.22	9200	–
China (mainland)	116.15	24110	–
France	38.37	5540	30.24
India	84.36	28640	–
Pakistan	23.40	8860	7335.00
Russian	52.19	24090	–
Turkey	19.99	7980	–
Ukraine	20.34	6480	46.90
USA	60.91	20060	1662.00
World	678.02	220400	13241.50

wheat production could decline by 23.2%–27.2% by 2050, unless protective measures for limiting global warming or appropriate cultivars and crop management practices are adopted [10]. Wheat production in low-latitude sites would be more vulnerable with the rise of a 3–5 °C temperature scenario, compared with production in high latitude regions, and yields could decline by up to 40% with an increase of 2 °C in temperature [11]. In Australia, wheat belts are typical of those in a Mediterranean climate: most precipitation occurs in winter, followed by less-frequent rain in spring and hot dry summer. Thus, water stress in spring is the major factor limiting yield improvement in these regions and often coincides with stem elongation, flowering, and grain filling [12]. In these environments, terminal heat often combines with drought during the grain-filling period and further limits grain yield [13]. In their Fifth Assessment Report, the IPCC predicted that an increase in mean annual temperature by 2.2–5 °C with +5% to −30% change in precipitation patterns will result in the expansion of drought-affected areas by 5.4%, 4.6%, and 3.8% by 2030, 2050, and 2070, respectively [9]. In this situation, plant breeders must be well-prepared to embrace the challenges of climate change and to feed the world by developing varieties that are better adapted to water-limited environments. Better utilization of the available genetic resources of wheat is essential in order to maintain and maximize wheat yield potential in water-limited environments, and the optimization of phenology is one of the most effective ways to achieve this goal.

Phenology is the key factor for crop adaptation to a particular environment. A proper understanding of the genetic control of phenological traits will enable breeders to develop crops that are better adapted to a specific environment. It is well documented that yield loss due to drought depends on the growth stage at drought occurrence, as well as the duration and intensity of the stress [14,15]. Spike development, from terminal spikelet initiation to anthesis, is the most important phase in determining grain yield, as it has been observed that a heavier spike at anthesis is positively correlated with grain yield [16] and can be manipulated without affecting other phases [17]. Therefore, adverse effects of drought could be minimized by ensuring that the most sensitive developmental stages do not occur during stress periods [18]. Hence, fine-tuning of flowering and the duration of developmental phases are advocated for better adaptation of wheat in water-limited environments or to escape from these constraints [19–22]. Phenology genes also regulate the physiological development of wheat [23], and some morpho-physiological traits have been identified as effective in breeding drought-adaptive varieties [24,25]. Taking account of many important traits and their interactions in stress environments, a sound understanding of the genetic control and physiological basis of drought tolerance would facilitate the improvement of yield in water-limited environments. We acknowledge the importance of good agronomic practices, that is, management, and several other traits involved in physiological mechanisms to reduce adverse effects of drought; however, this review focuses on the phenology genes as one of the most important measures to avoid drought stress (Fig. 1). Therefore, an effort has been made to summarize the progress achieved to date on key phenology genes and the integration of this knowledge in breeding new varieties that are adapted to future climate change. Moreover, an attempt has been taken to compile information on molecular markers for the identified alleles of vernalization (*Vrn*) and photoperiod (*Ppd*) genes that will help in evaluating the cultivars that are adapted to target environments as well as marker-assisted breeding.

2. Phenology genes

Wheat is adapted to a wide range of agricultural environments [26]. The synchrony of flowering to a wider range of climatic conditions is largely controlled by ① *Vrn* genes (exposure to cold temperature requirement), ② *Ppd* genes (photoperiod sensitivity), and ③ autonomous earliness *per se* (*Eps*) genes [27]. Hence, the adaptation of a genotype to a particular environment depends on the interaction of these three groups of genes.

2.1. Vernalization genes

Vernalization promotes the switching of the plant vegetative phase to the reproductive phase by inducing floral primordia from leaf primordia in the shoot apical meristem [28,29]. In wheat, three genes determine the vernalization requirement: *Vrn1*, *Vrn2*, and *Vrn3* [30–32]. The three orthologous *Vrn1* genes—*Vrn-A1*, *Vrn-B1*, and *Vrn-D1*—are located on the long arms of the homoeologous chromosomes 5A, 5B, and 5D, respectively, in common wheat, and mainly control the vernalization requirement [30,31,33,34]. The *Vrn2* gene is also located on the long arm of 5A; and *Vrn3* is

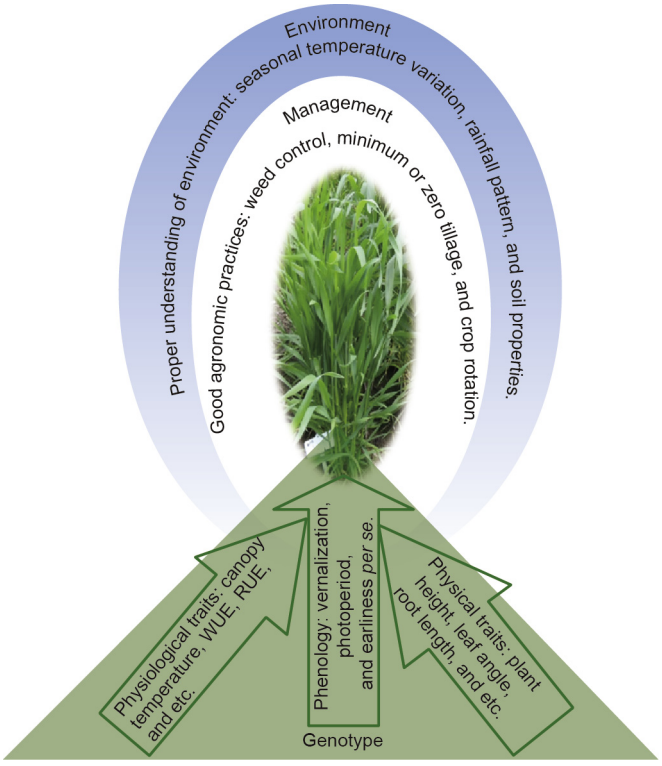

Fig. 1. Drought shield: complementary approaches to sustain wheat yield in water-limited environments. WUE: water-use efficiency; RUE: radiation use efficiency.

located on the short arm of chromosome 7B [32,35–37]. Winter wheat varieties require a certain period of cold to induce flowering, whereas varieties that flower without vernalization are referred to as spring types. The dominant alleles of *Vrn-A1*, *Vrn-B1*, *Vrn-D1*, and *Vrn3* are responsible for the spring growth habit; thus, a dominant allele at any of the three *Vrn1* loci confers a spring type. On the other hand, *Vrn2* is dominant for the winter type and is epistatic to dominant alleles of *Vrn1* [31,37–39]. *Vrn2* is a floral repressor that delays flowering, but vernalization under long days suppresses the expression of *Vrn2* and enhances the expression of *Vrn1* [40]. Multiple alleles of *Vrn1* with different levels of responses to vernalization and effects on flowering have been identified (Table 2) [41–55], and have an adaptive value [56–61]. The extent of flowering depends on the basal level of *Vrn1* expression [62]; some alleles of *Vrn1* are expressed without prior cold treatment, thus allowing flowering without vernalization [36,62,63]. Mutations in the promoter or deletion in the first intron of the *Vrn1* gene cause expression of *Vrn1* without vernalization, and the alleles lacking the larger section are more active during earlier flowering without vernalization [36,44,45,64,65]. On the other hand, varieties of wheat and barley flower early without vernalization when they lack a functional copy of the *Vrn2* gene [31,37]. The *Vrn3* gene also expresses at a high level when *Vrn2* is absent, and active alleles of *Vrn3* accelerate flowering irrespective of day length or vernalization [32]. Thus, five loci of *Vrn* genes influence flowering by controlling the vernalization requirement of wheat cultivars in different parts of the world [30,32,66,67].

2.2. Photoperiod genes

Wheat is a long day plant, requiring exposure to long days (> 14 h light) for flowering, whereas photoperiod-insensitive varieties flower early in short days (10 h or less light) [54,68,69]. This photoperiod sensitivity is controlled by the semi-dominant homoeologous *Ppd1* gene on the short arm of chromosome group 2; as is the case with *Vrn1*, the dominant allele confers photoperiod insensitivity [70–74]. The effects of the photoperiod-insensitive allele *Ppd* were studied thoroughly by Worland [22] over a 14 year period in different wheat-growing regions; their work revealed that insensitive *Ppd1* advances flowering time by 9–15 days, and that this earliness can be utilized to obtain yield advantages in water-limited environments by drought avoidance. The early *Ppd* gene also has some pleiotropic effects including reduced plant height and number of tillers, and fewer spikelets per ear [73]. However, an increase in spikelet fertility can compensate for the yield penalty [74]. It is clear that *Ppd* insensitivity brings forward the time of terminal spikelet formation, thus advancing the flowering time by reducing the number of spikelets in the ear. However, it does not influence the rates of leaf and flower primordial production. There is also variation among the potency of three *Ppd1a* loci, where plants with *Ppd-A1a* and *Ppd-D1a* are earlier in flowering than plants with *Ppd-B1a* [52]. In the same way that a number of *Vrn1* alleles have been identified, a number of alleles and their haplotypes have also been identified recently for all three homoeologous loci of the *Ppd* gene (Table 2) in both bread and durum wheat [49,51,53–55,75]. These findings have a great agronomic importance for deployment in breeding programs.

2.3. Earliness per se genes

The *Eps* genes control flowering time independent of temperature and photoperiod. To date, very few *Eps* genes have been identified in wheat, but several quantitative trait locus (QTL) studies revealed that most of the chromosome groups carry such genes and that they are present as QTL effects rather than as major genes in the *Ppd* and *Vrn* pathways [74,76–81]. The *Eps* genes are involved in the fine-tuning of flowering time [82], and hence can be utilized for adaptation to specific climatic conditions.

Table 2
Current status of the identified alleles for *Vrn1* and *Ppd1* loci.

Gene	Allele	Sequence variation from wild type	Response to light/temperature	Ref.
Vrn-A1	*Vrn-A1a*	231-bp and 140-bp insertions in the promoter region of common wheat	Insensitive	[44]
	Vrn-A1b	20-bp deletion in the promoter region of common wheat	Insensitive	[44]
	Vrn-A1c	7222 bp deletion in intron 1	Insensitive	[45]
	Vrn-A1d	32-bp deletion in the promoter region of tetraploid wheat	Insensitive	[44]
	Vrn-A1e	54-bp deletion in the promoter region of tetraploid wheat	Insensitive	[44]
	vrn-A1	Wild type	Sensitive	[44]
Vrn-B1	*Vrn-B1a*	6850 bp deletion in intron 1	Insensitive	[45]
	Vrn-B1b	6850 bp and 36 bp deletion in intron 1	Insensitive	[46]
	Vrn-B1c	817 bp deletion and 432 bp duplication in intron 1	Insensitive	[47]
	vrn-B1	Wild type	Sensitive	[45]
Vrn-D1	*Vrn-D1a*	4235 bp deletion in intron 1	Insensitive	[45]
	Vrn-D1b	C replaced by A at translation site in CArG-box of wild type	Facultative	[48]
	vrn-D1	Wild type	Sensitive	[45]
Ppd-A1	*Ppd-A1a1*	1085 bp deletion in the promoter region	Insensitive	[49]
	Ppd-A1a2	1027 bp deletion in the promoter region	Insensitive	[20]
	Ppd-A1a3	1117 bp deletion in the promoter region	Insensitive	[50]
	Ppd-A1a4	684 bp deletion in the promoter region	Insensitive	[51]
	ppd-A1b	Wild type	Sensitive	[50]
Ppd-B1	*Ppd-B1a.1*	308 bp insertion in the promoter region	Insensitive	[49]
	Ppd-B1a.2	Four copies of *Ppd-B1*	Insensitive	[52]
	Ppd-B1a.3	Three copies of *Ppd-B1*	Insensitive	[52]
	Ppd-B1a.4	Two copies of *Ppd-B1*	Insensitive	[52]
	Ppd-B1e	—	—	[53]
	ppd-B1b	Wild type	Sensitive	[52]
Ppd-D1	*Ppd-D1a.1*	2089 bp deletion in the promoter region	Insensitive	[54]
	Ppd-D1a.2	5 bp deletion in exon 7	Intermediate	[55]
	ppd-D1b.1	Wild type	Sensitive	[54]
	ppd-D1b.2	Insertion of transposable element in the intron 1	Sensitive	[55]

3. Molecular intervention of phenology genes

In concordance with studies on *Arabidopsis*, important progress has been made at the molecular level to elucidate the flowering pathway in wheat. Molecular and sequence analysis revealed that *Vrn1* encodes a MADS-box transcription factor similar to the *Arabidopsis* meristem identity genes *APETALA1* (*AP1*), *CAULIFLOWER* (*CAL*), and *FRUITFULL* (*FRU*), which regulate the shoot apical meristem to determine the transition from vegetative to reproductive development [36]. Insertions, deletions, and mutations in the promoter region are associated with allelic variation of *Vrn1* [44]. Following this finding, a series of molecular markers have been developed (Table 3) [32,44,45,48,52,54,55,83,84] and successfully utilized to identify allele frequency of the local wheat cultivars as well as these from the International Maize and Wheat Improvement Center (CIMMYT) collection [45,83,85,86]. The *Vrn2* encodes a zinc finger-CCT domain transcription factor and is a floral repressor, down-regulated by both vernalization treatment and short day length [37]. *Vrn2* plays a very similar role to that of *FLOWERING LOCUS C* (*FLC*) in *Arabidopsis* but actually has no orthologs, suggesting an independent evolution of the vernalization pathways [87]. Vernalization gene *Vrn3* is similar to *Arabidopsis FLOWERING LOCUS T* (*FT*), and the dominant allele is associated with a retro element insertion in the *Triticum aestivum* L. (*TaFT*) promoter, results in

Table 3
Polymerase chain reaction (PCR) markers for the different vernalization and photoperiod response alleles.

Allele	Primer	Primer sequence (5′–3′)	Annealing temperature (°C)	Product size	Ref.
Vrn-A1a	VRNA1F	GAAAGGAAAAATTCTGCTCG	50	965 and 876	[44]
Vrn-A1b				714	
Vrn-A1c	VRN1-INT1R	TGCACCTTCCC(C/G)CGCCCCAT		734	
vrn-A1				734	
Vrn-A1	BT706	CATTGTTCCTTCCTGTCCCACCC	63	1431	[84]
	BT750	ATTACTCGTACAGCCATCTCAGCC			
Vrn-A1c (Langdon)	Ex1/C/F	GTTTCTCCACCGAGTCATGGT	55.6	522	[45]
	Intr1/A/R3	AAGTAAGACAACACGAATGTGAGA			
Vrn-A1c (IL 369)	Intr1/A/F2	AGCCTCCACGGTTTGAAAGTAA	58.9	1170	
	Intr1/A/R3	AAGTAAGACAACACGAATGTGAGA			
vrn-A1	Intr1/C/F	GCACTCCTAACCCACTAACC	56	1068	
	Intr1/AB/R	TCATCCATCATCAAGGCAAA			
Vrn-B1a	Intr1/B/F	CAAGTGGAACGGTTAGGACA	58	709	
	Intr1/B/R3	CTCATGCCAAAAATTGAAGATGA			
vrn-B1	Intr1/B/F	CAAGTGGAACGGTTAGGACA	56.4	1149	
	Intr1/B/R4	CAAATGAAAAGGAATGAGAGCA			
Vrn-D1	Intr1/D/F	GTTGTCTGCCTCATCAAATCC	61	1671	
	Intr1/D/R3	GGTCACTGGTGGTCTGTGC			
vrn-D1	Intr1/D/F	GTTGTCTGCCTCATCAAATCC	61	997	
	Intr1/D/R4	AAATGAAAAGGAACGGAGCG			
Vrn-D1a	VRN1DF	CGACCCGGGCGGCACGAGTG	65	612	[48]
	VRN1-SNP161CR	AGGATGGCCAGGCCAAAACG			
Vrn-D1b	VRN1DF	CGACCCGGGCGGCACGAGTG			
	VRN1-SNP161AR	AGGATGGCCAGGCCAAAACT			
Vrn-3	FT-B-INS-F	CATAATGCCAAGCCGGTGAGTAC	63	1200	[32]
	FT-B-INS-R	ATGTCTGCCAATTAGCTAGC			
vrn-3	FT-B-NOINS-F or	ATGCTTTCGCTTGCCATCC or	57	1140 or 691	
	FT-B-NOINS-F2	GCTGTGTGATCTTGCTCTCC			
	FT-B-NOINS-R	CTATCCCTACCGGCCATTAG			
Ppd-D1a	Ppd-D1_F	ACGCCTCCCACTACACTG	54	288	[54]
	Ppd-D1_R2	AND CACTGGTGGTAGCTGAGATT			
ppd-D1b	Ppd-D1_F	ACGCCTCCCACTACACTG	54	414	
	Ppd-D1_R1 and	GTTGGTTCAAACAGAGAGC			
16 bp deletion in exon 8	Ppd-D1exon8_F1	GATGAACATGAAACGGG	52	320 or 326 and 22,	
	Ppd-D1exon8_R1	GTCTAAATAGTAGGTACTAGG		257, 69, and 22	
Ppd-B1	Ppd-B1exon3SNP_F1	AGACGATTCATTCCGCTCC	55	471, 328, and 155	
	Ppd-B1exon3SNP_R1	TCTGAATGATGATACACCATG			
	Ppd-B1_2ndcopy_ F1	TAACTGCTCGTCACAAGTGC	55	425 and 475	
	Ppd-B1_2ndcopy_R1	CCGGAACCTGAGGATCATC			
5 bp deletion in exon 7	D5-1F	GAATGGCTTCTCCTGGTC	50	1032 or 1027	[55]
	D5-1R	GATGGGCGAAACCTTATT			
	D5-2F	GTGTCCTTTGCGAATCCTT	53	184 or 179	
	D5-2R	TTGGAGCCTTGCTTCATCT			
A TE insertion in intron 1	D520F	AGGTCCTTACTCATACTCAATCTCA	50	2612	
	D520R	CTCCCATTGTTGGTGTTGTTA			
	D78F	CCATTCGAGGAGACGATTCAT	55	1005	
	D78R	CTGAGAAAGAACAGAGTCAA			
Truncated *Ppd-B1* gene in the	219H05F2	TAACTGCTCCTCACAAGTGC	56	425	[52]
"Chinese Spring" allele	97J10R2	CCGGAACCTGAGGATCATC			
Intact *Ppd-B1* copies in the	Ppd-B1_F25	AAAACATTATGCATATAGCTTGTGTC	58	994	
"Chinese Spring" allele	Ppd-B1_R70	CAGACATGGACTCGGAACAC			
Intact *Ppd-B1* copies in the	Ppd-B1_F31	CCAGGCGAGTGATTTACACA	58	223	
"Sonora64"/"Timstein" allele	Ppd-B1_R36	GGGCACGTTAACACACCTTT			

Table 3 (*continued*)

Allele	Primer	Primer sequence (5′–3′)	Annealing temperature (°C)	Product size	Ref.
Vrn-A1b	Vrn-P2	CCTGCCGGAATCCTCGTTTT CTACGCCCCTACCCTCCAACA	63	147 or 167	[83]
Vrn-B1b	Vrn-P7	CCAATCTCACATGCCTCCAA ATGCGCCATGAACAACAAAG	59	215 or 252	
Vrn-B3c	Vrn-P14	GCTTTGAACTCCAAGGAGAA ATAATCAGCAGGTGAACCAG	52	1401	
vrn-B3/*Vrn-B3*	Vrn-P15	ACTCATCATCACCACTTCCT TAATGCTTAATTCGTGGCTG	51	1499	
Vrn-B3 promoter	Vrn-P16	GTCCATACAAATCATGCCAC TTCTGACAGTTTTAGTTGCG	51	491	
Vrn-B3 promoter	Vrn-P17	GCTTTCGCTTGCCATCCCAT GCGGGAACGCTAATCTCCTG	62	898	
Vrn-B3 promoter	—	TTTGAGACAGGAGATTAGCG ACCATCATGAGGCACCATTA	53	1131	
		GCTTTGAACTCCAAGGAGAA ATAATCAGCAGGTGAACCAG	52	1425	
		CCGTTCACCATCTATTGCTC CACCCAAATCCTTCATCTCA	55	1259	
Vrn-B3-RT	—	GGAGGTGATGTGCTACGAGA TTGTAGAGCTCGGCGAAGTC	55	147	

early flowering [32]. Recent screening of a set of Chinese wheat cultivars led to the discovery of two more dominant alleles of *Vrn3*, and 80 days variation in heading has been observed due to their action [83]. Allelic variations of these *Vrn1* genes quantify the vernalization effects, and determine flowering time by interacting with photoperiod gene *Ppd1*. The latter is a member of a pseudo response regulator (PRR) gene family in which insensitivity is associated with deletion or transposon insertion within the promoter region, as well as with copy number variation [52,54]. In wheat, *Ppd1* directly regulates the *FLOWERING LOCUS T1* (*FT1*); mutants with promoter deletions result in the overexpression of *FT1*, causing early flowering [51]. Markers have been developed to identify the *Ppd* mutants with different promoter deletions (Table 2) that will facilitate their effects on the flowering time of wheat [49,51,53,54].

The complicated interaction of these phenology genes has resulted in two conflicting models of the flowering regulatory network: The first model, designated as *Vrn2* to *FT* [88], recommends that *Vrn2* represses *FT* expression but that vernalization during winter slightly up-regulates *Vrn1*, causing down-regulation of *Vrn2* and the release of *FT* expression. This *FT* then interacts with *Ppd1* and again up-regulates the *Vrn1* beyond the threshold to initiate flowering under long day length [89]. By contrast, the second model, known as *FT* to *Vrn2*, was proposed by Shimada et al. [90], who suggested that *Vrn1* promotes *FT* transcription, which down-regulates *Vrn2* to initiate flowering based on the fact that the maintained vegetative phase (*mvp*) mutants lacking *Vrn1* fail to up-regulate *FT*. Subsequent detailed experimentation by Distelfeld and Dubcovsky [88] with the *mvp* mutants segregating for *Vrn1* and *Vrn2* deletions resulted in evidence to contradict both of the previously proposed models; we therefore suggest that more investigation should be conducted to elucidate the flowering network of wheat, and that doing so may lead to the identification of more genes that interact in the flowering pathway.

4. Dwarfing genes

The introduction of dwarfing (*Rht*) genes into cereals, including wheat, was a key driver of the green revolution. Since then, *Rht-B1b* and *Rht-D1b* (previously known as *Rht1* and *Rht2,* respectively) are the most commonly adopted *Rht* genes in wheat-breeding programs throughout the world [91]. Together, these two semi-dwarfing genes produce the dwarf phenotype, whereas alone in combination with their counterpart *Rht-B1a* or *Rht-D1a*, they produce semi-dwarf plants in nature. The plants with these genes are less prone to lodging and are more effective in partitioning assimilates to the grain. Some researchers have suggested that the improved yield potential of such varieties is only limited to a favorable growth environment [92,93]. However, these specific *Rht* genes are insensitive to endogenous gibberellins, and produce shorter plants with smaller cells [94]. These smaller size cells are consequently responsible for the shorter coleoptile length, less early vigor, smaller leaf area, lower water-use efficiencies, and poor seedling establishment, especially in water-limited environments [95–99]. The insensitivity to gibberellins of both the *Rht-B1b* and *Rht-D1b* alleles is due to single nucleotide substitutions that create a translational stop codon, TGA, reducing the plant's ability to respond to gibberellins [100].

Most of the world's wheat is grown without irrigation; because of the dependence on seasonal rainfall, the potential yield is often hampered by water scarcity. About 50% of rainwater can be lost directly through soil evaporation, whereas early vigor can increase water-use efficiency by 25% and thus improve yield [101–104]. Again, deep sowing of longer season varieties is often recommended to obtain yield benefits in dry areas, such as those occurring in southern Australia, but seedling establishment is impaired when dwarf/semi-dwarf varieties are sown more than 5 cm deep [96]. Consequently, farmers wait until the first rains before sowing, resulting in between 140 and 330 kg yield loss per week per hectare being reported in Australian wheat crops [105,106]. Wheat varieties with longer coleoptiles are able to emerge sooner when sown deep, and have greater early vigor [107,108]. Moreover, early vigor and longer coleoptiles help plants to avoid the phytotoxic effects of residual herbicides, compete against weeds, and reduce evaporative water loss by shading. Hence, breeding for vigorous seedling growth and breeding for longer coleoptiles are the prime objectives for the better adaptation of wheat in water-limited environments [109–111]. A project with these objectives is currently underway at the CIMMYT in Mexico[†].

[†] Edwards IB–personal communication.

On the other hand, a number of *Rht* genes such as *Rht 7*, *Rht 8*, *Rht 9*, *Rht 13*, and *Rht 14* have been reported, which have potential in reducing plant height without affecting seedling vigor and tissue response to gibberellins [112–114]. Under stress conditions, taller varieties store assimilates in the stem and do not depend entirely on current assimilation for grain filling [115]. Several studies across many favorable and unfavorable environments demonstrated that plants with heights of 70–100 cm are better yielders than those that are taller or shorter than this range [97,116]. Therefore, the accumulation of minor *Rht* genes or combination with one of the gibberellins insensitive genes for shorter plant height are desirable [116,117], as shown by different studies that used *Rht*8 and/or *Rht*13 alleles with *Rht1* and/or *Rht2* to maximize yields compared with other dwarf/semi-dwarf varieties [91]. Markers linked to these *Rht* alleles make it easier to select both alleles simultaneously across a large population [118,119].

5. Physiological aspects of phenology and dwarfing genes

Grain yield is strongly influenced by the timing of developmental stages in a particular environment, making crop phenology a critical component for yield physiology [120]. Moisture stress at the reproductive stage, especially that period from a few weeks before anthesis to a few days after anthesis, has the most critical effect on crop yields in water-limited environments [25,121]. Passioura [122] emphasized the importance of water use, water-use efficiency, and harvest index (HI) for crop yields in dry areas. In dry environments, an important portion of soil moisture that could be available for transpiration is evaporated from a barren soil surface, thus indirectly affecting dry matter accumulation by limiting water availability to roots, and modifying canopy temperature [123]. In this situation, faster early seedling growth is beneficial to prevent evaporation by shading. Moreover, late-flowering cultivars continue to produce tillers until they receive the signal for reproductive development, and many of them cannot produce fertile spikes, but put pressure on the available soil moisture through normal transpiration. In this regard, heading date and effective tiller number should be additional considerations for improving water-use efficiency in varieties being developed for drought environments. Moreover, water requirement varies throughout the growth period and is higher during seed setting and development stages. Hence, there is an opportunity to improve yield through changes in crop development. The synchronization of crop developmental stages by phenological adjustment with seasonal moisture availability should be the most important target for new wheat varieties being developed for water-limited environments such as those that occur in Mediterranean climate regions.

HI and ultimately final grain yield largely depend on pre- and post-anthesis biomass production, mobilization of assimilates to florets, and the pattern of water supply during the life cycle [111,124]. One strategy for raising the HI may be increasing the assimilate movement to developing florets, which will prevent floret abortion before anthesis. This can be done by increasing the duration of spike growth with a reduction in the earlier period for larger ear development [16]. Moreover, this larger ear will also contribute more photosynthate during grain filling along with the flag leaf, thereby increasing the HI. Studies on two alternative spring alleles of *Vrn-A1* have shown their significant influence on the variation in root and vegetative morphology such as rosette growth habit, plant height, and leaf length [125]. A significant relation has recently been observed between the duration of pre-anthesis growth phases and the tillering and dry matter accumulation [126]. A detailed study of Australian wheat cultivars over several years and a wide range of locations has revealed that cultivars with one spring allele in any of the three *Vrn1* loci are the earliest in heading when compared with cultivars having two spring alleles [127]. Again, spring alleles in all three *Vrn1* loci have very small effects in forwarding the heading date, which suggests the presence of epistatic or overdose effects. This study also showed that *Vrn-B1* has a weaker effect on the reduction of heading time compared with *Vrn-A1* or *Vrn-D1*. Recently, however, it has been shown that *Vrn-B1* has the greatest effect on grain yield [128].

Semi-dwarf varieties with *Rht-D1b* are advantageous over *Rht-B1b* in environments with high maximum temperatures and lower rainfall during the flowering and grain-filling periods, as *Rht-D1b* is associated with less leaf porosity in plants relative to *Rht-B1b*, leading to slow transpiration before heading and leaving more soil moisture for later use [128,129]. Plants reduce their water use during drought stress by means of accelerated leaf desiccation and death, which causes a reduction of current photosynthate [130–133]. As a result, stem reserves become an important source of carbohydrate for grain filling [134–136]. However, *Rht-B1b* and *Rht-D1b* genes reduce stem reserves by 35% and 39%, respectively [137]; hence, taller varieties often perform better in stress environments when there is a shortage of assimilates, compared with the modern dwarf cultivars.

6. Future strategies

Difficulties in the identification and precise measurement of key physiological determinants of yield is the bottleneck in the improvement of drought tolerance in plants, and its complex genetic control makes progress more difficult [138–140]. Hence, the improvement of plant traits at both physiological and molecular levels is vital in order to address this complex issue.

The current use of automated high-throughput plant-phenotyping facilities greatly assists researchers in phenotyping plants more precisely and accurately. An in-depth understanding of plant physiology will help dissecting the genetic components of drought tolerance, while molecular and genomic tools will help to identify candidate genes and QTLs for drought-tolerance traits. The integration of physiology with molecular tools will provide new insights into gene function. To optimize output in drought research, a detailed knowledge of the growing environment and of genotype-environment interactions is essential. Fine-tuning a genotype to a specific environment is possible by combining the best-suited alleles of phenology genes to adapt better in the existing environment.

Recent studies have revealed that copy number variation of phenology genes also plays a vital role in crop adaptation. An increased copy number of *Ppd-B1* confers earlier flowering, and an increased copy number of *Vrn-A1* requires a longer vernalization period and is thus associated with late flowering [52]. A similar investigation for the copy number variation of *Ppd-B1* in Australian wheat cultivars resulted in the identification of five alleles with one to four copies as well as a null copy of *Ppd-B*, where plants with an allele with a lower copy number were the latest in heading relative to plants with an allele having more copies [53]. In addition, the haplotypes variation identified in other studies for these genes was found to affect several yield-contributing parameters, and thus adaptation to different environments [51,55]. As a result, several attempts have been made to determine the value of the alleles of *Vrn1* and *Ppd1* genes over the past few years in the local environments of different countries [52,55,68,73,83,84,86,127,128,141]. In most cases, the plant material did not cover all the available alleles present in nature, or even the same allele in different genetic backgrounds. Thus, obtaining the true effect of an allele in breeding a variety will warrant the development of appropriate near-isogenic line (NIL) populations of the locally adapted cultivars with different alleles, which will require significant effort. An earlier example of a successful attempt is Triple Dirk, which was developed by Pugsley [30] to

study the alleles of the *Vrn1* gene; at present, the John Innes Center in the UK is performing substantial research in developing this type of population for different *Ppd1* alleles. Such efforts will certainly advance research into phenology genes in optimizing plant development and productivity in local water-limited environments. Therefore, intensive and thorough research to optimize the effect of each allele/haplotype of the phenology genes would enable plant breeders to determine the basic genetic architecture of wheat in each key growing environment, for better yields under stress conditions. Thus, once molecular and physiological tools are used to identify and prove the efficiency of different traits and their regulating genes for drought tolerance, these various useful traits could be aggregated in the base population through a marker-assisted gene pyramiding scheme, as demonstrated by Servin et al. [142]. In summary, success against the adverse effects of climate change relies on the consequences of proper characterization of target environments (i.e., soil properties, precipitation pattern, drought severity, and etc.); and then on designing an appropriate crop ideotype that combines useful phenology with other drought-tolerance-attributing genes, along with good management practices.

7. Conclusion

Drought is a major threat to world agriculture, and is predicted to worsen in the near future due to climate change. Wheat is the most widely grown cereal crop in the world and is vital for global food security. Altering the developmental stages and maturity of wheat is one of the best ways to combat drought without compromising yield. However, current knowledge about the number of genes that control flowering and maturity in wheat is limited. Based on knowledge obtained from the model plant species *Arabidopsis*, in which more than 80 genes have been reported to control flowering, it is logical to conclude that many new genes and genetic pathways for wheat flowering and maturity are yet to be discovered. However, the fact is that different genetic pathways finally converge, interact, and ultimately lead to the activation of floral identity genes in the floral primordia [143], and these interacting networks that promote flowering are yet to be unveiled. As significant research efforts are currently underway, knowledge on wheat-flowering genes and pathways will increase over time and will require advances in computational biology in order to integrate and interpret this information. In addition, future international collaboration will help to combine the cumulative efforts of the research underway in different research groups and disciplines; the challenge for the breeders will be to integrate this work into new genetic combinations.

Compliance with ethics guidelines

M.A.N. Nazim Ud Dowla, Ian Edwards, Graham O'Hara, Shahidul Islam, and Wujun Ma declare that they have no conflict of interest or financial conflicts to disclose.

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