Chapter 11

Barley Phenology: Physiological and Molecular Mechanisms for Heading Date and Modelling of Genotype-Environment-Management Interactions

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Additional information is available at the end of the chapter

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Abstract

Barley heading date is important in adapting barley genotypes to different environments. Important factors affecting heading date in barley are temperatures, photoperiod and sowing date. Sowing date is a management option to influence heading date. It is used to reduce climatic risks such as frosts and water stress at sensitive periods during crop development. Three major genes control heading date in barley. These genes regulate photoperiod (Ppd-H1 and Ppd-H2), vernalization (Vrn- H1, Vrn-H2 and Vrn-H3) and the duration of the vegetative phase (Eps). The Ppd-H1 locus on chromosome 2(2H) regulates flowering time under long days. Ppd-H2 on 2H regulates phenology under short day length. Vernalization is mainly controlled by three loci (VRN-H1, VRN-H2 and VRN-H3), which interact in an epistatic fashion to determine vernalization sensitivity. Appropriate physiological and simulation frameworks such as that of APSIM-Barley are required to complement breeding efforts in order to determine the location of the Eps genes and describe and quantify the effects of environment and management on gene expression and their impact on yields and quality in barley.

Keywords: barley, photoperiod, vernalization, earliness per se, modelling

1. Introduction

World barley production is projected to reach 140 million metric tons (MMT) on 50 m hectares by 2016/2017 [1] with its greatest economic impact being related to its use as feed, food and for

malting. The demand is projected to reach 142 MMT by 2050 [1]. It is therefore one of the major sources of income for the countries where it can be produced. Australia is the fourth largest barley grower in the world, producing about 8.7 MMT of barley in 2015 and contributes up to 30% of the world supply [2,3]. The supplies comprise 2.5 MMT of malting barley and 4.5 MMT of the feed barley [4, 5]. Currently, one-third of the world production is used for malting [6]. The grain is also widely used for human food and livestock feeds, starch production and chemical industries, while the straw is used for roofing huts and animal bedding. Grazing is sometimes performed after harvesting or when the crop is green [4, 7].

There are constraints facing barley-producing nations such as Australia; including transient, unpredictable and varying climatic conditions [8–10]. These environments are characterized by a lack of adequate water in spring and summer periods when evaporation and transpiration are rising rapidly when crops are in the later stages of development, which results in a terminal drought. There is also a problem of frost when the air temperature drops to 2°C or less. Damage to crops from frost may occur at any stage of development but is most damaging at and around flowering. These constraints result in a serious dilemma for growers who must decide whether to delay anthesis to avoid frost damage or flower as early as possible in order to escape the effects of terminal drought [11]. Thus, it is important that barley cultivars demonstrate an adaptation with appropriate rates of development across the heterogeneous environments.

1.1. Barley phenology—its relationship with abiotic stresses, quality and yield

Plant phenology characterises the developmental life cycle events of plants and how these events are influenced by seasonal and inter-annual variations in climate as well as habitat factors [12, 13]. In barley, different development stages, such as spikelet initiation and duration of grain development can seriously influence yield and quality. These stages are regulated by environmental factors such as temperature or growing degree days (GDD), duration and intensity of light, nutrition and husbandry techniques [14]. Heading date is important in adapting barley genotypes to different stresses such as heat stress, waterlogging, salinity and drought. Heat stress can quickly deplete the available moisture through high rates of evapotranspiration and ultimately leading to terminal drought [15]. Both heat and drought at late sowing may interrupt barley developmental processes usually from double ridge (DR) to maturity. The resultant effects of these stresses are reduction in plant height, dry matter accumulation and grain yield [15]. On the other hand, low temperature at early growth stages (Zadoks GS10) may be required for vernalization especially for winter barleys to flower. Apart from the optimum conditions, poor biomass accumulation and significant yield losses are attributed to extreme conditions, high or low temperatures, drought or waterlogged anaerobiosis and other soil-related problems [16]. Advances in crop phenology and modelling have helped with the understanding of how to assess biomass partitioning and effects of abiotic stresses in crops [12]. Modelling has also helped understand the effects of different environments and sowing dates on growth and development of barley plants.

Many scoring systems for plant growth stages have been developed to describe phenology in cereals [14]. The most widely used scales are Feekes scale [14] and Zadoks scale [17]. The majority of the scales described only the morphological traits [12], while very few describe the

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apical developmental processes especially on barley [18]. The vital developmental stages that have significant effects on yield and quality are DR (Zadoks GS30), construction phase which includes stem elongation (31), heading and anthesis (51&61 as in barley) and grain filling stage [19, 20]. DR and terminal spikelet (TS) can only be detected through destructive examination (**Figure 1**). There have been no consistent reports on the use of correlated traits for the determination of the flower/floral initiation stage (GS30), although in some cases surrogate traits such as number of leaves on the main stem have been used to determine this stage [21].

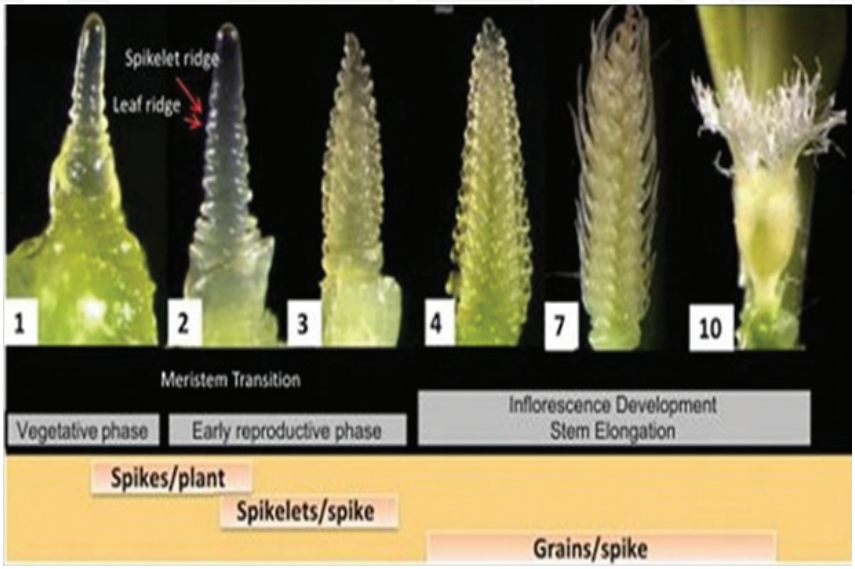

Figure 1. Development stages from double ridge up to terminal spikelet [151].

Developmental stages drive appearance of the main traits in cereals and are sensitive to climate and management [22, 23]. DR stage is an elementary step for predicting flowering date and crop yields and has been an important trait for improving crop productivity and adaptation [24]. Short construction phase (e.g. from Zadoks GS31 to 65) or short grain filling periods often lead to low yields [25]. The increase in the rate of grain filling is a positively correlated with grain weight [26]. A significant increase in grain yield in the high rainfall zones of Australia (usually along the coast with over 550 mm rainfall) was shown to be due to a longer duration between result from an increased time from GS31 to GS65 (i.e. stem elongation to anthesis) in wheat [27].

1.2. Factors affecting phenological development in barley

Barley development has three main stages: germination/emergence to double ridge/stem elongation (GS10 to GS30/31), stem elongation to heading/anthesis (GS30/31 to GS51/61) and heading to physiological maturity (GS51 to GS 94) [15, 28, 29]. The first stage, the basic

vegetative phase, is the stage for the production of phyllochrons, roots and tillers. The agronomic significance of this stage is the generation of enough biomass for livestock feed especially for dual-purpose genotypes [30]. The second stage involves the termination of vegetative growth at GS29. This stage signifies reproductive growth, spikelet initiation and the onset of stem elongation [31] and is required for the production of a higher number of spikelets which directly link to grain yield [32]. The third stage is grain filling, influencing grain size and weight [33]. This stage is essential for yield increase as well as quality. All the three stages are regulated mainly by genetic, environment as well as management.

Important environmental factors affecting barley developmental stages include temperatures and photoperiod [15, 34, 35], both of which vary simultaneously in field conditions. This variability affects developmental events that determine flowering time and consequently yield [35]. Temperature is very important for all plant physiological processes [36], especially for the variation in days to spikelet initiation [37], days to heading and days to flowering (anthesis) in cereals [38, 39]. This observation is supported by Hay et al. [40] and Ellis et al. [41] who reported that the rate of primordia initiation especially spikelet in barley has a linear relationship with average daily temperatures. The rate of initiation of organs in barley also increases linearly with temperature; the optimum temperature for organ development is 25–30°C [37]. However, low temperature is required in some cereals to stimulate flowering (vernalization); this term has **been** used as the basis for classification of barley into winter and spring types. The variation in the development of phyllochrons in different genotypes of barley is more likely due to the variation in the combinations of temperature and photoperiod [12].

Growing degree days (GDD) are often used for measuring developmental events in barley. GDD is the accumulation of the mean daily temperature above a base temperature (0°C in the case of barley) [34, 42]. Below 0°C, the development of the crop will cease while above 0°C the growth will increase linearly with temperature [34, 36, 43]. Using zero as the base temperature (Tb = 0°C) in wheat, Acuna et al. [27] identified an ideotype which may develop sufficient tiller numbers at 650°Cd to harvest about 400–500 heads/m2. The same ideotype had a construction phase duration (CPD) within 800–1200°Cd to be able to escape frost and partitioned more assimilate to developing grain. Miralles et al. [35] reported the GDD that ranges between 950–2000°Cd and 1300–2100°Cd from sowing to flowering in both barley and wheat, respectively [35]. This result reflects the high variability in the GDD for flowering time in barley, indicating that yield might be manipulated using this characteristics.

Photoperiod is also a key environmental factor that affects the development of barley especially in temperate countries. The duration of day-length has a predictable pattern that drives evolutionary plant responses. This forms the basis of classifying barley as a long day, short day and day-neutral (DN) plant [44]. Photoperiod can significantly influence the duration of both vegetative spikelet initiation and stem elongation periods in wheat and barley [45]. The long day-length of higher northern and lower southern latitudes causes both photoperiod-sensitive and photoperiod-insensitive cultivars to flower early. The winter type responds strongly to long days, while spring types vary depending on the selection criterion [46]. For example, in Western Europe and parts of North America, short days increase the duration of vegetative growth of spring-sown barley. This lengthens the time for biomass accumulation and hence

increases yield [46] under temperate growing conditions. Australia has a unique environment that differs from other barley growing regions in higher latitudes [21], where daylength is much shorter in winter, but considerably longer in summer (**Table 1**). However, there is variation in the extent of sensitivity of Australian genotypes to photoperiod. The baseline for the sensitivity ranges from 8 to 10 h of exposure, below which no flowering initiation occurs, while the upper limit ranges from 13 to 18 h [38]. The sensitivity of both vernalization and photoperiod starts immediately after plant emergence [38].

Region	Coordinate	Seasonal sunshine hour duration			
		Winter: June–August	Spring: September–November	Summer: December–February	Autumn: March–May
NT, Darwin					
NT, Katherine	14.465°S, 132.26° E	11–12	12–13	12–13	11–12
Perth	31.95°S, 115.87°E	10–12	11–14	12–14	10–13
Carnarvon	24.88°S, 113.66°E	10–12	11–14	12–14	10–12
Victoria, Mallee	35.11°S, 142.36°E	9–11	11–14	12–14	10–12
Ravensthorpe, WA	33.32°S, 119.82°E	9–11	11–14	12–14	10–12
SA, Wimmera	37.82°S, 140.78°E	9–11	11–15	13–14	10–12
Adelaide	34.93°S, 138.60°E	9–11	11–14	13–15	10–13
Victoria	37.47°S, 144.79°E	9–11	11–15	12–15	9–13
Brisbane, NSW	27.47°S,153.02° E	10–12	11–15	12–14	10–13
Tasmania	42.88°S, 147.32°E	9–10	11–15	13–15	9–13
NSW, Queensland	20.92°S, 142.70° E	9–12	11–14	12–14	12–14
Launceston, Tas	41.44°S, 147.14°E	9–11	11–15	13–15	9–13

Table 1. Sunshine duration across Australian regions and their coordinates [152].

Management is also an important factor that affects phenology in barley; important factors include sowing date, fertilizer application, irrigation and other management practices. Matching the phenology with an appropriate sowing window allows growers to better manage climate risks that are particularly pronounced in Australia, where early sowing may expose the heading of spring barley to frost, while late flowering and terminal drought can curtail grain filling and hence reduce yield [11]. Plant growth and development are affected by high temperatures and water stress in late sowing of spring barley [15, 47], high temperatures at early sowing in Punjab of India [47] and low temperatures with early sowing in Russia [15]. In the same experiment with early sown crops, low tillering capacity as a result of low temperatures caused a significant reduction in grain yield [15]. Similar results were reported by Ram et al. [47], in that very early sowing of spring barley may affect tillering capacity,

although in this case due to high temperatures and reduction in biomass accumulation for late sowing. In addition, sowing date was found to have the most significant effects on the phenological development of cereals, especially during the GS31 (stem elongation phase) in wheat [48].

2. Physiological and molecular mechanisms for heading date and their effects on grain yield and quality

Heading date (spikelet emergence, Zadoks GS51) is a complex trait in barley that has direct impact on grain yield and quality and also forms the basis of evolutional adaptation to the changing climate. The mechanisms of regulating this trait are so complicated that there has been no final conclusion on the specific number of genes that are involved and their interactions [37]. Although the expression of this trait is governed by complex factors such as genetics, physiology and environment [21], neither the plant breeder nor the physiologist can clearly explain their interactions. For example, physiologists have not answered some unresolved developmental issues such as the regulation of the developmental rate within an environment and the cause of the transition between one growth stage to another. Equally, crop breeders need to account for the gene functions, the number of the genes and their interactions that are involved in expression of heading date [37].

2.1. Genetic regulation of heading (flowering) date

Barley improvement dates back to its domestication period. However, significant yield improvements began only in the 1950s as a result of the application of more advanced plant gene technologies [49]. Studies have been conducted on the genetic improvement, which include the determination of genotypic and phenotypic variability in days to flowering and growth phases, as well as comparing different sets of cultivars in barley [29, 50] and wheat [51]. Recent advances in the area of molecular breeding using highly polymorphic molecular makers such as simple sequence repeat (SSR) and single nucleotide polymorphisms (SNPs) have also led to significant progress in the improvement of yield and quality in barley. These markers are being used to tag genes or quantitative trait loci (QTLs) that are of economic importance, offering promises in their use in marker-assisted selection (MAS) [52]. Among all the markers, SNPs and SSRs are unanimously believed to be best suited for the use in marker-assisted breeding [53]. They have been used to assess most of the genes in barley and other cereals through cDNAs, expressed sequence tags (ESTs) and sequenced PCR amplicons that provide use of SNPs in protein encoding transcribed genes.

A genetic study on early versus late heading in barley was first reported in 1907 [54]. Exploration of the effects of environment on heading date was initiated following the reports of Garner et al. [55]. This opinion was supported by other studies that sources of variation in flowering date among different genotypes of barley were due to the effects of seasonal variation, location and sowing date [21]. As a result, genotypic differential response to photoperiod, vernalization and other environmental conditions have been conducted. Three

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groups of genes are responsible for variations in heading date. These include Ppd (photoperiod) [20, 44, 56, 57], Vrn (vernalization) [58, 59] and earliness *per se* (Eps) [60, 61]. Eps determines the time and duration of the reproductive phase. Of the three genes, only Eps gene acts independently of vernalization and photoperiod [19, 20, 62, 63]. All the Vrn genes have been cloned [46, 64–66]. All the three groups of genes have been well researched in wheat, although there is no conclusive evidence that Eps genes have been cloned in all cereals. These genes start to regulate development from emergence GS10 [20]. Hence, there is a lack of information on the genetics, physiological, biochemical functions and location of the Eps gene especially in barley [64, 67, 68]. Unfortunately, the access to the barley genome has not been straightforward because the genome consists of a large number of repetitive sequences [63, 69]. Scientists have explored the opportunities in the colinearity of the genes among the cereals [63, 67, 70, 71] for marker design and elucidation of the effects of the genes on yield and quality and their interaction with the environment in barley [63]. It is, however, important to understand the behaviour and interaction of these Eps genes with different environment and management practices. Particularly in Australia, variable climates make production decisions and genetic improvement for crop adaptation difficult [9]. Evidence of deferential genotype responses to ambient temperature and other climatic parameters is limited in barley [21]; thus, the knowledge of genotype x environment or QTL × environment as well as management (G × E × M) interactions is required to help obtain higher grain yields and quality [72]. The use of crop simulation modelling to predict expression of complex crop traits under diverse environments has provided plant breeders and farm managers with good opportunities to make crucial decisions such as matching the choice of genotypes to an appropriate sowing window or soil type, in different environmental conditions [73]. Therefore, integration of experimentally determined genetic responses to photoperiod, vernalization and Eps will complement plant breeders in their use of genetics and molecular tools in the prediction of flowering time and the understanding of how these genes affect grain yield and quality in different climates and with different management.

2.1.1. Photoperiod genes (Ppd)

The photoperiod pathway is generally classified into two components: the circadian clock and the photoperiod clock regulators [74]. The clock is the receptor of light stimuli perceived by phytochromes (phyA to phyE) and cryptochromes (cry1 and cry2) which are red and far red receptors and blue light receptors, respectively [74]. Temperate cereals, including barley, are quantitative long-day crops [21]; however, some varieties differ in their response to photoperiod [75], as mentioned above. Photoperiod sensitivity can significantly influence the duration of both vegetative and stem elongation periods in wheat and barley [45]. Longer day-length causes both photoperiod-sensitive and photoperiod-insensitive barley cultivars to flower early. There is evidence that specific stages in floral development in wheat and barley may also be sensitive to light intensity [76] and heavy shading during the later stages of ear development may result in the infertility of the spike [76]. As a result, flowering in photosensitive plants like barley may be entirely inhibited if the light intensity is reduced sufficiently during long periods because of the low level of availability of carbohydrates within shaded plants [76]. Therefore,

genotypes vary in the photoperiodic threshold below in which flowering initiation will not take place.

In barley, two photoperiod genes influencing flowering time are *Ppd*-H1 on chromosome 2(2HS), which regulates flowering time under long days [56, 57, 62, 77, 78] and *Ppd*- H2 on chromosome 5(1HL) that regulates flowering time under short days [20, 62, 78]. *Ppd*- H1 is a pseudo-response regulator gene (HvPRR37) [79] and is the major controller of heading date when crops are exposed to long days (LDs). Therefore, the spring varieties of barley consist of this dominant allele. However, the recessive allele ppd-H1 is the major causes of the reduction in photoperiod response in European spring types and hence the reason for late flowering in LDs [46]. Reduced photoperiod responsiveness of the ppd-H1 mutant, which is highly variable in long season conditions, is explained by altered circadian expression of the photoperiod pathway gene CONSTANS and reduced expression of its downstream target, HvFT1, which is controlled by HvCO1, a key regulator of flowering [64, 80]. EARLY FLOWERING3 (ELF3), which is also a member of the circadian clock genes, regulates flowering under the influence of photoperiod [81]. This gene also has a loss-of-function mutant in plants (e.g. barley and some legumes) that causes early flowering in short days (SDs) as well as in LDs. In the same way as the ppd-H1 operates, the recessive mutant *eam8* (mat-a) has a loss of function characteristic [64] that leads to the insensitivity to photoperiod and thus can cause early flowering in both SDs and LDs [64, 81]. However, *eam8* is significantly involved in the expression of *HvFT1* (a flower initiator) which is also an allelic variant at Ppd-*H1* locus [64]. Similarly, the barley *elf3* mutant helps in the expression of the GA20oxidase2 gene, which causes the production of gibberellin (GA) in the apical meristems under SDs. Thus, the production of GA activates the early-flowering *elf3* in SDs in the absence of the *FT1* gene [81]. The second photoperiod gene (*Ppd-H2*) responds to short day-length. *Ppd-H2* acts similarly to *HvFT3* when exposed to SDs. In an experiment conducted using Morex and Steptoe populations, the expression of the HvFT3 was not found in the Steptoe genotype (which has the ppd-H2) but was found in in Morex (which has the Ppd-H2 gene). Therefore, *HvFT3* has been named as the candidate for *Ppd-H2* [82]. In spring barley, the Ppd-H2 allele is the major actor regulating flowering, but is rarely found in commercial winter types [82].

Many other QTLs have been identified from different populations. Ren et al. [57] also detected a major QTL under 18-h photoperiod in glasshouse experiments and mapped the QTL to the Xp12m50B199–Xp13m47B399 interval of flanking markers on chromosome 4H which accounted for 77.48 and 37.81% of phenotypic variation for long photoperiod response in Australia and China, respectively. The gene, *eam7*, showed a stronger effect on flowering time with 55 day and 18 day differences compared to Ppd-H1 (chromosome 2H) and Ppd-H2 (chromosome 1H) [83]. Another *eam7* determining photoperiod insensitivity under short day- length was identified on the short arm of chromosome 6H near the centromere [83]. This gene was 6.7 and 13.0 cM away from two flanking markers Xmwg2264 and Xmwg916, respectively. Environmental factors also had a significant effect on the expression of two different QTLs, for flowering time which were mapped to chromosomes 1HL and 7HS when the population was grown under long photoperiod conditions. However, no QTL was detected in the same lines when they were grown under

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short photoperiod conditions [78]. The QTL for heading date are often linked with yield in barley [19, 84]. These could be the part of the reasons why most of these genes have a highly significant effect on several agronomic traits, such as biomass accumulation including grain yield and grain quality in barley [20, 85]. The photoperiod responsive genes in wheat were found to be in homoeologous series to genes on barley chromosome 1H, 2H [28].

2.1.2. The vernalization genes (VRN)

Vernalization is the requirement for prolonged low temperature to advance flowering in cereals and depends on the growth habit (such as spring or winter types). The winter types of barley require cold exposure before flower initiation, typically below 10°C for a period between 4 and 6 weeks [86], depending on base temperature as defined above. In contrast, the spring types have minimal low temperature dependency and are usually insensitive to vernalization and Short day photoperiod [87]. This behaviour is characteristic of many temperate cereals like barley [87, 88] and associated with the capacity of a genotype to survive the cold winter during vegetative stages [87, 89, 90]. Barley is an excellent model for genetic analysis of low-temperature tolerance in fall-sown cereals [90]. Its responses to vernalization have been observed to vary greatly among genotypes and between growth phases [45, 90].

Vernalization in cultivated barley is mainly controlled by three major Vrn genes [28], Vrn1, Vrn2 and Vrn3 [58], or HvVrn1, HvVrn2, HvVrn3 [88], or Vrn-H1, Vrn-H2 and Vrn-H3 [59]. The Vrn-H1 (also named as Sgh2 or Sh2) is located in the middle of the long arms of 5H [67, 88]. The Vrn-H2 (Sgh or Sh) is found on chromosome 4H [67], while the Vrn-H3 (Sgh3 or Sh3) is on 1H [59]. Vrn-H1 translates the fruit-like MADS-box transcription factor which is an ortholog *APETA-LA1* gene [65]. The allelic difference at this gene locus is essential for flowering in temperate cereals [65, 88, 91] and therefore, it is one of the major determinants of vernalization requirement in barley and wheat [92]. Within the locus, the allele that is responsible for the spring growth habit is Vrn-H1 (the dominant one) [93], while the recessive allele accounts for genetic regulation of the winter habit [65, 67, 88]. A large deletion in the first intron of Vrn-H1 locus in the dominant allele is responsible for the null response to vernalization in spring barley and wheat [93, 94], while no deletion within intron 1 was observed in the winter habit types possessing recessive vrn-H1 allelic loci [67, 88, 93].

The second locus is the Vrn-H2 (Sgh2 or Sh2) which encodes for the zinc finger-CCT (ZCCT-H) transcription factor [93] and is also vernalization dependent. A partial or total deletion of part of this locus has been shown to cause a non-functional mutation of the gene and a recessive form is responsible for the spring growth habit in both barley and wheat [65, 92, 95]. However, it is necessary to understand that the effects of Vrn-H2 under field conditions can only be verified using a variety of sowing dates [59]. The authors further stated that the gene does not affect heading date when crops were autumn sown.

The third is the Vrn-H3 (Sgh3 or *Sh3*) on chromosome 1H [20, 28, 88] and later on 7HS [62, 96]. This gene is an ortholog of the FT gene in *Arabidopsis* [96] and HvFT1 gene [62] which responds to vernalization in both barley and wheat. A study conducted by [96] showed that homologous spring barley with dominant Vrn-H3 allele had an increase in

HvFT transcript rapidly, while the recessive genotype vrn-H3 had low HvFT transcript without vernalization. A strong relationship was found between the Vrn-H3 and Ppd genes as the HvFT was observed to be very low in SD and upregulated in LDs [96]. Finally, for a given winter genotype to respond to vernalization, it must have all three (vrn-H1:Vrn-H2:vrnH3) and all other combinations are reported to be spring types [59, 88, 95]. These three loci (VRN-H1, VRN-H2 and VRN-H3) interact in an epistatic fashion to determine vernalization sensitivity [95].

Since there is a form of homogeneous genetic system for all the cereals with a high degree of synteny (physical co-localization of genetic loci on the same chromosome in an individual or species), the results of one species are frequently applicable to other members of the cereal family [87, 97, 98], including barley. Consequently, the cloning of the candidate genes in diploid wheat (*Triticum monococcum*) of VRN-Am1 and VRN-Am2 [65, 91, 92, 99] and hexaploid wheat (T. *aestivum*) of VRN-1 has considerably increased our understanding of the genetics of vernalization in barley [87].

2.1.3. Basic vegetative phase BVP (Earliness per se, Eps)

Barley has the potential to grow and produce economically viable yields under a wide range of diverse environment-types. Early growth plasticity is determined during the vegetative phase [100], which has extensive genetic diversity. One of these genes is the *Earliness per se*, Eps. This gene regulates the basic vegetative phase (BVP) in barley and influences the time and duration of growth stages from DR (Zadoks GS30) to grain filling stage (Zadoks GS70) [60, 61]. Expression of this gene can only be fully observed when all the other sources of the variations in flowering time have been fixed, i.e. when the environmental stimuli such as exposure to adequate vernalization and photoperiod requirements have been met by the plants [70, 71, 101–103]. In addition, Eps is also actively involved in the fine-tuning of the flowering time in cereals including barley [71, 104]. Various authors have identified the Eps gene in all the chromosomes of common wheat [71] and barley [20, 63, 67]. Recent advances in molecular genetics have shown that the location and physiological effects of the Eps gene on yield and quality in barley are limited [63]. Since most of the cereals share similar genetic synteny [63], it could be assumed that results from studies on reports on wheat could be applied to barley. Efforts to identify the markers linked to the genes and their locations are underway. In wheat, RFLP marker, wg241 was observed to be linked to Eps-Am1 gene on 1H [71]. The gene was found to be 0.7 cM distal to wg241 and 1.4 cM proximal to the barc287 markers [60, 71]. Among the three markers reported in *Brachypodium* and wheat plants, two were identified to be molybdenum transporter 1 (Mot1) (transcriptional regulator) and filamentation temperature-sensitive H4 (FtsH4), respectively [70, 105]. These makers were linked to the Eps gene and were proposed as candidates for Eps-Am1 on chromosome 1H [70, 105]. The predicted MOT1 protein showed differences in the amino acid between the parent lines in which the effects could not be predicted [105]. Thus, any future steps to clone the Eps-Am1 gene should include the generation of mot1 and ftsh4 mutants and the completion of the T. *monococcum* physical map to test for the presence of additional candidate genes.

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2.2. Effects of Eps gene on developmental phases

The genetic and physiological processes that are linked to the adaptation of barley are due to broad differences in the developmental phases. These phases include both the time and duration from spikelet initiation (GS30) and up to grain filling (Zadoks GS70). Most previous research conducted has centred on the effects of Eps gene on the flowering time [61, 65, 67] with fewer focussing on the variations in the duration of each of developmental stages [61, 106, 107]. For example, an study conducted by Lewis et al. [61] using single seed decent and near isogenic lines (NILs) observed a significant interaction between the Eps gene and the timing and duration from vegetative to flowering phase especially from double ridge to terminal spikelet stage in diploid wheat. The interaction showed that the NIL genotypes with the early allele, Eps-e, had the transition to DR stage 35 days earlier (67% less) than the genotypes with the Eps-l alleles. The SSD genotypes had highly significant differences ($P < 0.0001$) in both heading time and number of spikelets per spike between Eps alleles (eps-e and eps-l). The genotypes with the late allele Eps-l flowered 61 days later than those with eps-e alleles (with 76% across temperatures) and produced a mean of 8.7 more spikelets for each spike which was a 56% increase across temperatures [61]. However, results of Valárik et al. [71] and Zikhali et al. [103] showed only a few days of differences (from 1 to 5 days) in flowering time between a pair of near isolines (NILs) and their recombinant inbred lines (RL) in both wheat and rice. In addition, no significant interaction ($P = 0.67$) was observed between Eps genes and the stem elongation stage [61], which is the beginning of construction phase. Also temperature had no significant effects on the gene determining spikelets number per spike [61]. Contrary to this opinion, Slafer et al. [108] observed that lengthening the duration of the stem elongation phase, without modifying total time to anthesis, could increase the number of grains/m2 and consequently the number of grains per unit land area [45]. In general, variations in both flowering time and spikelet number per spike could be due to pleiotropic effects of a single gene or to the effect of tightly linked multiple genes with additive effects [71, 105].

2.3. Effects of temperature on the Eps genes

Temperature is the major environmental factor affecting Eps genes in barley and wheat [61, 101]. Differences exist among genotypes carrying Eps-e for early heading and Eps-l alleles for late heading in wheat [60]. There are significant interactions between the Eps gene and temperature [60, 61]. The genotypes with Eps-l alleles had no interaction with temperatures (21°Cd difference), while lines carrying the Eps-e allele had a shorter thermal time to heading at 16°C than at 23°C (336°Cd difference) [61]. Lewis et al. [61] further showed that the thermal time to flowering for the genotypes with the Eps-e gene was approximately 1557°Cd. These are 1118°Cd less than the thermal time for the late genotypes (2675°Cd) with Eps-l gene. Slafer et al. [106] used four wheat varieties and six differential temperatures (10–25°C) to study the effect of temperature on growth stages. They showed that the developmental phases of individual genotypes were most sensitive to temperature from sowing to anthesis. This variation can be attributed to the allelic diversity at Eps locus in the lines studied. Hence, an in-depth research of genetic variability of the earliness *per se* genes (Eps) is required for a more precise analysis of their effects on developmental stages and temperature sensitivity.

2.4. Effect of sowing date on the Eps genes

In order to maximize yield potential in any environment, cultivars must have an appropriate flowering window and life cycle duration in the target environment [28, 60]. Sowing date is an important factor that governs flowering period, the timing of which needs to escape biotic and abiotic stress. Out of these three major genes, Ppd, Vrn and Eps, Eps genes do not respond to the differential to vernalization or photoperiod and still control timing and duration of flowering independent of these stimuli [28].

2.5. Effect of the Eps gene on grain quality

Yield and quality are important complex traits in any breeding programme. Improvement of these traits is very difficult to achieve due to their genetic, physiological and physical complexity. Grain quality could either be physical, such as size, hardness and lustre, or nutritional such as malting quality. The relationship of Eps gene on heading, spikelets number and number of grains per spike has been shown to be correlated with yield [61]. However, grain quality can also be improved by manipulating the Eps gene loci [109] to improve the physical traits such grain weight or hardness. Experiments conducted by Herndl et al. [110] indicated that with a shorter pre-anthesis period, the relationship between yield and protein is always negative. Crop breeders often focus on increasing yield with little attention on quality traits; thus, there is less information on the effects of the Eps gene on quality traits.

Heading date is a polygenic trait, controlled by Ppd [111, 112], vernalization [37, 38, 41, 111] and Eps genes [111, 113]. These genes interact in an additive nature (cumulative effects of non-allelic genes to a quantitative trait) [111]. The genetic analysis of Eps showed that it can be simply inherited as a Mendelian inheritance, but molecular analysis has not been able to identify an appropriate molecular marker to determine its location [114].

3. Modelling

Crop modelling in agriculture has been used as a physiological framework to undertake simulation of dynamic crop phenology that support crop improvement programmes [115]. Physiologically sound simulation tools will provide quantitative assessments of crop development and yield relative to the genotype, climate, soil and management in sustainable farming systems [116]. These tools should provide ex-ante impact assessments of research outcomes across a wide range of environments [100]. This is particularly true for Australia where a highly variable climate poses challenges for production and crop improvement [9]. With respect to climate change, temperature has increased by 0.9 °C since 1910 per annum and severe heat and drought spells are occurring more frequently in Southern Australia. Total annual rainfall and frost events may also increase in some of the temperate regions such as Tasmania [117]. Other reports indicate a 2–5% reduction in rainfall across most parts of the country [118]. Harrison et al. [119] emphasizes the need for serious attention on the impacts of climate stress on plant phenology. Globally, climate change will further increase temperatures, modify the amount and distribution of rainfall and consequently reduce the probability

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of reliable food and forage production, thereby causing a significant threat to food security and improved livelihood [120]. More than 30% barley yield loss will be attributed to climate change as a result of drought and heat stress by 2050 [121]. Despite this, there has been little research work to determine how the climate change will broadly affect whole farm systems [119, 122], including systems farming barley.

Mathematical functions are being used as tools to simulate crop phenology to predict the effects of climate events and changing environments on yield and quality [24]. These tools help explain the interaction of some of the complex traits related to development and growth and their interaction with the environment. For example, ecophysiological quantitative equations were used by Yin et al. [24] to describe the response of flowering to photoperiod and temperature to predict days to heading and yield in diverse conditions. The equations were used as empirical and mechanistic models to provide important framework for simulating a number of events in crop growth, especially predicting heading date [24, 123]. The empirical models are often based on accumulation of growth degree days adjusted by vernalization and photoperiod [123, 124], while mechanistic models are based on the production of leaves and floral primordia at the apexes [125].

Four important phenology models: 3s-beta-model, 3-plane-linear-model, modified-rice-clock-model (m-RCM) and a logistic model were developed and evaluated in rice [39, 126]. All models were able to predict the flowering time in varying environments although with varying degree of precisions. Model parameter values from reciprocal transfer experiments also resulted in realistic differences in flowering time across all the genotypes in different environments. The models were able to partition variation due to environment and that of the genotypes. Thus, ecophysiological model could be very important for dissecting the relationship between genotype and phenotype [24]. Chapman et al. [73] also developed mechanistic model called QSUN to estimate growth, development and yield of a diverse range of genotypes of sunflower under varied environments. Their model was able to account for leaf area index ($r2 = 0.65$), total biomass ($r2 = 0.96$) and grain yield ($r2 = 0.93$) when tested against actual phenological data. QSUN was also used to analyse the production risk of sunflower grown in highly variable subtropical environments in order to undertake decisions such as the choice of an adapted cultivar and appropriate sowing window in order to obtain higher yields [9]. Another dynamic model was used to investigate the causes and impact of climate change on peanut production in Northern Australia [127]. The model was used in conjunction with the information of district yield to offer an in-depth study of long- term production risk. The study indicated that the stabilization of the above-average yield, which was due to stable summer rainfalls, was responsible for the rapid expansion of peanut industries at that time. Such studies assist in gaining better understanding of complex GxExM and the identification of traits required to manage crops in variable and changing environments [127]. Therefore, choice of an appropriate simulation models for predicting phenology are essential for choosing the best-adapted cultivar for a specific production environment and for helping with timely planning of strategic or tactical management [9, 123].

3.1. The agricultural production systems simulator (APSIM)

The Agricultural Production Systems Simulator (APSIM) is a cropping systems simulation model that combines several decision-support tools. APSIM may be used for accurate predictions of how traits like heading dates impact on grain yield and biomass of different crop genotypes in alternative environment and management conditions and also to consider the long-term consequences of cropping systems on soil conditions [116]. APSIM may also be used to increase the understanding factors influencing heading date of barley when grown under field conditions [12, 115]. The tools within APSIM can also be used to describe genetic parameters regulating phenology with the function of daily temperature and photoperiod to predict flowering time and consequently yield and quality [126]. The major challenges facing barley production are water stress coupled with heat stress during spring and summer and frost events in winter and early spring. District yield records showed about 85% yield loss due to frost events in Australia [128]. A later study with more information was conducted to gauge the impact of frost on grain production in Australia [129]. In the study, APSIM simulated the effects of frost on wheat production areas across Australia. The model predicted increased frequency of frost events in the Australian wheat belt (the main barley production regions in Australia) and also an increase in the mean temperatures with significant yield loss. Zheng et al. [129] concluded that breeding for frost tolerance could give about 20% yield advantage. As for most other modules, the barley module of APSIM (APSIM-Barley) simulates the phenology in a daily time step. The module uses inputs of weather such as radiation and temperature and initial soil nitrogen [130]. The module has 11 growth stages, from sowing to harvest (GS0–GS100) [130]. Manschadi et al. [131] took advantage of APSIM's scientific basis by assessing barley growing patterns under different environment and management. The model was able to account 91% and 82% of the variation for biomass accumulation at maturity and grain yield. Although negative correlation between yield and quality traits [132] and between life cycle and quality traits [133] were reported, maintenance of quality traits is critical in order to alleviate malnutrition [134]. The majority of crop models are constrained in predicting both the physical and cryptic (nutritional) grain quality such as grain size and grain-N content [134], although the model has been used to account for both above and below ground biomass, growth, water, N uptake and leaching [124]. The same model was used to explain some quality parameters such as grain size and grain protein concentration [135]. As a result of the challenges due to frost and drought events faced by barley production, a simulation model, QBAR, was developed to identify appropriate management options such as sowing date in order to increase yield [136]. Thus, QBAR can simulate phenology, soil water, leaf area, biomass accumulation and yield of barley [136]. A more detailed analysis of extreme terminal drought effects and frost risk should be conducted that should include several sowing dates and varieties. QBAR was later modified to (APSIM-Barley) [136], accounted for 91 and 82% variances for biomass accumulation and grain yield, respectively [137]. Further improvement on the QBAR model has been the integration of crop nitrogen balance and grain quality module [136]. It was later used to account for the effects of extreme climatic events, frost and terminal drought on yield and yield components, of which paddock-based crop models could not explain [138]. The authors proposed that QBAR can be used to determine the best man-

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agement decisions such as sowing date to obtain highest grain yield even in the events of frost and water stress.

3.2. Genotype by environment by management (G × E × M)

Information on the target environment for which crop cultivars are to be improved is vital to plant breeders [139]. This is because a higher genetic (G) diversity for flowering time has been reported in diverse environments (E) of barley growing regions where frost and drought events limit crop growth as well as inappropriate agronomic management (M) to improve crop growth and yield [72]. This concept can be extended to include both abiotic factors such as soil, water stress and waterlogging as well as induced stresses due to abiotic (salinity) and biotic factors (pests, weeds and diseases). Environmental factors can be classified into two types: (1) micro-environmental factors such as year-to-year variation in rainfall, drought conditions, pest incidence and (2) macro-environmental factors which include soil type and management practices [140, 141]. The association between the environment and the genotype to produce a specific phenotype is termed as the G × E interaction [141]. Hence, the G × E interaction determines the adaptability and suitability of a specific genotype to a range of environments. Environment could also be a time boundary, such as a year (annuals) [142]. Hence, matching heading date to diverse environment may give a large G × E interaction [142]. Variation in the developmental stages usually from DR to grain filling stages in barley is influenced by G × E [143]. For highly variable environment types like those found in Australia, there is a need for specific adaptation (genotype response and better performance in a specific environment) arising from G × E interaction [144]. Löffler et al. [145] used a crop model index approach to account for the G × E interaction effect in US maize breeding trials. Factorial regression (FR) has been used to describe crop interaction with their environment and help understand G × E [146]. A linear generic model was used to analyze the interaction of 96 genotypes to different environment [126]. The model was able to explain 81% of the total variation in heading date across the environments. The introduction of molecular markers has aided our understanding of the effect of individual gene or QTL effects rather than the cultivar [126]. Yin et al. [126] used a four-parameter ecophysiological model to predict grain yield when QTL-based data inputs were used. The model when used together with the QTL map was able to sufficiently predict days to flowering in barley [126], suggesting that the model could be used to help breeders in Australia to adapt new varieties.

Recent advances in plant breeding combined with dynamic models are now allowing partitioning of the effect of management in the G × E approaches [72]. Higher genetic gain (GA) in yield has been attributed to better understanding of G × M interaction effects in maize crops, where the progressive yield increase in the US has been associated with superior genotypes being grown at higher density [147]. Another example is the choice of a combination of non-tillering genotypes (G) and row spacing (M) in drought prone land can help realize sustainable production and additional value in obtaining moderate yield instead of complete crop failure due to limited availability of water [72, 148]. Another study was conducted to check the performance chickpea genotypes under two different managements, irrigation and rain- fed management systems. The study showed highly significant yield differences among genotypes

and between the two management practices for all the important traits. The study also revealed that both yield and yield components were improved by an average of 48% increase in the number of pods per plant, 36% in total dry weight and 17% in grain yield in the management involving irrigation [149].

It is therefore important to note that the use of models capable of accounting for G × E × M interaction in breeding and agricultural systems can be a powerful tool to better understand environment-specific, complex gene expressions. APSIM-Barley has been used to describe broad adaptation of barley genotypes in anticipation frost or water stress across Australia. In another experiment, leaf area and yield of Baudin, Flagship, Buloke and Capstan, barley cultivars were assessed. The model also reasonably explained the relationship between the leaf area duration and yield as influenced by weather [150]. However, the model has not been used to explore the potential agronomic benefits of exploiting G × M interaction in a specific environment. Matching specific genotypic traits to management option within a target (specific) environment will assist breeders in trait selection and the design of their breeding programs.

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References

[1] IGC, Five-year global supply and demand projections. International Grain Council Report, http://www.igc.int/en/downloads/grainsupdate/IGC_5yearprojections2015.pdf, 2015.

[2] ABC, Barley crop trial for whisky production beats poor season to yield valuable data. Australian Broadcasting Corporation, 2015. http://www.abc.net.au/news/2015-02-05/whisky-barley-trial-crop-beats-poor-season-yields-valuable-data/6072166

[3] Barley Australia. Quality Barley for Australia and the world. 2015 [cited 2015 4 June 2015]; Available from: http://www.barleyaustralia.com.au/industry-information.

[4] CGIAR, Barley, 2015. http://www.cgiar.org/our-strategy/crop-factsheets/barley/

[5] Saisho, D., M. Ishii, K. Hori, and K. Sato, Natural variation of barley vernalization requirements: implication of quantitative variation of winter growth habit as an adaptive trait in East Asia. Plant and Cell Physiology, 2011. 52(5): p. 775–784.

[6] Baik, B.-K. and S.E. Ullrich, Barley for food: characteristics, improvement, and renewed interest. Journal of Cereal Science, 2008. 48(2): p. 233–242.

[7] Akar, T., M. Avci, and F. Dusunceli, Barley: Post harvest operations. The Central Research Institute for Field Crops, Ankara, Turkey, 2004.

[8] Australia, 2015. http://www.barleyaustralia.com.au/industry-information.

[9] Meinke, H., G.L. Hammer, and S.C. Chapman, A sunflower simulation model: II. Simulating production risks in a variable sub-tropical environment. Agronomy Journal, 1993. 85(3): p. 735–742.

[10] Index Mundi, 2015. http://www.indexmundi.com/agriculture/?commodity=barley&graph=yield.

[11] Richards, R.A, Crop improvement for temperate Australia: Future opportunities. Field Crops Research, 1991. 26(2): p. 141–169.

[12] Juskiw, P., Y. Jame, and K. L, Phenological development of spring barley in a short season growing area. Agronomy Journal, 2001. 93: p. 370–379.

[13] Wilczek, A., L. Burghardt, A. Cobb, M. Cooper, S. Welch, and J. Schmitt, Genetic and physiological bases for phenological responses to current and predicted climates. Philosophical Transactions of the Royal Society B: Biological Sciences, 2010. 365(1555): p. 3129–3147.

[14] Landes, A. and J. Porter, Comparison of scales used for categorising the development of wheat, barley, rye and oats. Annals of Applied Biology, 1989. 115(2): p. 343–360.

[15] Hossain, A., J. Teixeira da Silva, M. Lozovskaya, V. Zvolinsky, and V. Mukhortov, High temperature combined with drought affect rainfed spring wheat and barley in south-eastern Russia: yield, relative performance and heat susceptibility index. Journal of Plant Breeding and Crop Science, 2012. 4(11): p. 184–196.

[16] Cattivelli, L., S. Ceccarelli, I. Romagosa, and M. Stanca, Abiotic stresses in barley: problems and solutions. Barley: improvement, production, and uses. Wiley, Harrisonburg, 2010: p. 282–306.

[17] Zadoks, J.C., T.T. Chang, and C.F. Konzak, A decimal code for the growth stages of cereals. Weed Research, 1974. 14(6): p. 415–421.

[18] Banerjee, S. and F. Weinhues, Comparative studies on the development of the spike in wheat, barley and rye. Pflanzenzuchtung, 1965. 54: p. 130–142.

[19] Bezant, J., D. Laurie, N. Pratchett, J. Chojecki, and M. Kearsey, Marker regression mapping of QTL controlling flowering time and plant height in a spring barley (Hordeum vulgare L.) cross. Heredity, 1996. 77(1): p. 64–73.

[20] Laurie, D., N. Pratchett, J. Snape, and J. Bezant, RFLP mapping of five major genes and eight quantitative trait loci controlling flowering time in a winter× spring barley (Hordeum vulgare L.) cross. Genome, 1995. 38(3): p. 575–585.

[21] Boyd, W., C. Li, C. Grime, M. Cakir, S. Potipibool, L. Kaveeta, S. Men, M.J. Kamali, A. Barr, and D. Moody, Conventional and molecular genetic analysis of factors contributing to variation in the timing of heading among spring barley (Hordeum vulgare L.) genotypes grown over a mild winter growing season. Crop and Pasture Science, 2003. 54(12): p. 1277–1301.

[22] Cuesta-Marcos, A., A. Casas, P. Hayes, M. Gracia, J. Lasa, F. Ciudad, P. Codesal, J. Molina-Cano, and E. Igartua, Yield QTL affected by heading date in Mediterranean grown barley. Plant Breeding, 2009. 128(1): p. 46–53.

[23] Cuesta-Marcos, A., E. Igartua, P. Codesal, J.R. Russell, J.L. Molina-Cano, M. Moralejo, P. Szucs, M.P. Gracia, J.M. Lasa, and A.M. Casas, Heading date QTL in a spring× winter barley cross evaluated in Mediterranean environments. Molecular Breeding, 2008. 21(4): p. 455–471.

[24] Yin, X., P.C. Struik, J. Tang, C. Qi, and T. Liu, Model analysis of flowering phenology in recombinant inbred lines of barley. Journal of Experimental Botany, 2005. 56(413): p. 959–965.

[25] Schelling, K., K. Born, C. Weissteiner, and W. Kühbauch, Relationships between yield and quality parameters of malting barley (Hordeum vulgare L.) and phenological and meteorological data. Journal of Agronomy and Crop Science, 2003. 189(2): p. 113–122.

[26] Al-Karaki, G.N., Phenological development-yield relationships in durum wheat cultivars under late-season high-temperature stress in a semiarid environment. ISRN Agronormy, 2012 Article ID 456856.

[27] Acuna, T.B., Can the duration of the spike construction phase increase the yield of wheat? 2015.

[28] Snape, J., K. Butterworth, E. Whitechurch, and A. Worland, Waiting for fine times: genetics of flowering time in wheat. Euphytica, 2001. 119(1–2): p. 185–190.

[29] González, F.G., G.A. Slafer, and D.J. Miralles, Vernalization and photoperiod responses in wheat pre-flowering reproductive phases. Field Crops Research, 2002. 74(2): p. 183–195.

[30] Redmon, L.A., E.G. Kreazer, D.J. Bernardo, and G.W. Horn, Effect of wheat morphological stage at grazing termination on economic return. Agronomy Journal, 1996. 88(1): p. 94–97.

[31] Baker, C. and J. Gallagher, The development of winter wheat in the field. 2. The control of primordium initiation rate by temperature and photoperiod. The Journal of Agricultural Science, 1983. 101(02): p. 337–344.

[32] González, F.G., G.A. Slafer, and D.J. Miralles, Floret development and spike growth as affected by photoperiod during stem elongation in wheat. Field Crops Research, 2003. 81(1): p. 29–38.

[33] Whitechurch, E. and G. Slafer, Contrasting Ppd alleles in wheat: effects on sensitivity to photoperiod in different phases. Field Crops Research, 2002. 73(2): p. 95–105.

[34] McMaster, G. and W. Wilhelm, Phenological responses of wheat and barley to water and temperature: improving simulation models. The Journal of Agricultural Science, 2003. 141(02): p. 129–147.

[35] Miralles, D.J., B.C. Ferro, and G.A. Slafer, Developmental responses to sowing date in wheat, barley and rapeseed. Field Crops Research, 2001. 71(3): p. 211–223.

[36] Went, F., The effect of temperature on plant growth. Annual Review of Plant Physiology, 1953. 4(1): p. 347–362.

[37] Hay, R. and R. Ellis, The control of flowering in wheat and barley: what recent advances in molecular genetics can reveal. Annals of Botany, 1998. 82(5): p. 541–554.

[38] Roberts, E., R. Summerfield, J. Cooper, and R. Ellis, Environmental control of flowering in barley (Hordeum vulgare L.). I. Photoperiod limits to long-day responses, photoperiod-insensitive phases and effects of low-temperature and short-day vernalization. Annals of Botany, 1988. 62(2): p. 127–144.

[39] Yin, X., M.J. Kropff, T. Horie, H. Nakagawa, H.G. Centeno, D. Zhu, and J. Goudriaan, A model for photothermal responses of flowering in rice I. Model description and parameterization. Field Crops Research, 1997. 51(3): p. 189–200.

[40] Hay, R. and E. Kirby, Convergence and synchrony—a review of the coordination of development in wheat. Crop and Pasture Science, 1991. 42(5): p. 661–700.

[41] Ellis, R., E. Roberts, R. Summerfield, and J. Cooper, Environmental control of flowering in barley (Hordeum vulgare L). II. Rate of development as a function of temperature and photoperiod and its modification by low-temperature vernalization. Annals of Botany, 1988: p. 145–158.

[42] Bauer, A., AL. Black, AB. Frank, and E. Vasey, Agronomic Characteristics of Spring Barley in the Northern Great Plains. North Dakota State University Agricultural Experiment Station Bulletin, 1992. 523: p. 47. https://ndawn.ndsu.nodak.edu/help-barley-growing-degree-days.html

[43] McMaster, G.S. and W. Wilhelm, Growing degree-days: one equation, two interpretations. Agricultural and Forest Meteorology, 1997. 87(4): p. 291–300.

[44] Kikuchi, R. and H. Handa, Photoperiodic control of flowering in barley. Breeding Science, 2009. 59(5): p. 546–552.

[45] Miralles and R. Richards, Responses of leaf and tiller emergence and primordium initiation in wheat and barley to interchanged photoperiod. Annals of Botany, 2000. 85(5): p. 655–663.

[46] Turner, A., J. Beales, S. Faure, R. Dunford, and D. Laurie, The pseudo-response regulator Ppd-H1 provides adaptation to photoperiod in barley. Science 2005. 310: p. 1031–1034.

[47] Ram, H., B. Singh, and A. Sharma, Effect of time of sowing on the field performance of barley (Hordeum vulgare L.) in Punjab. Journal of Research, 2010. 47(3 and 4): p. 132–135.

[48] Kiss, I., K. Balla, J. Banyai, O. Veisz, and I. Karsai, Effect of different sowing times on the plant developmental parameters of wheat. Cereal Research Communications, 2015. 42(2): p. 239–251.

[49] Thomas, W., Prospects for molecular breeding of barley. Annals of Applied Biology, 2003. 142(1): p. 1–12.

[50] Borràs, G., I. Romagosa, F. van Eeuwijk, and G.A. Slafer, Genetic variability in duration of pre-heading phases and relationships with leaf appearance and tillering dynamics in a barley population. Field Crops Research, 2009. 113(2): p. 95–104.

[51] Whitechurch, E., G. Slafer, and D. Miralles, Variability in the duration of stem elongation in wheat and barley genotypes. Journal of Agronomy and Crop Science, 2007. 193(2): p. 138–145.

[52] Jahoor, A., L. Eriksen, and G. Backes, QTLs and genes for disease resistance in barley and wheat, in Cereal genomics. 2005, Springer, Kluwer Academic Publishers Dordrecht, The Netherlands. p. 199–251.

[53] Gupta, P.K. and R. Varshney, The development and use of microsatellite markers for genetic analysis and plant breeding with emphasis on bread wheat. Euphytica, 2000. 113(3): p. 163–185.

[54] Smith, L., Cytology and genetics of barley. The Botanical Review, 1951. 17(1): p. 1–51.

[55] Garner, W.W. and H.A. Allard, Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. 1920. Journal of Agricultural Research Volume 18 Number 11, p. 553–606

[56] Wang, J., J. Yang, Q. Jia, J. Zhu, Y. Shang, W. Hua, and M. Zhou, A new QTL for plant height in barley (Hordeum vulgare L.) showing no negative effects on grain yield. PLoS One, 2014. 9(2): p. e90144.

[57] Ren, X., C. Li, M. Cakir, W. Zhang, C. Grime, X.-Q. Zhang, S. Broughton, D. Sun, and R. Lance, A quantitative trait locus for long photoperiod response

mapped on chromosome 4H in barley. Molecular Breeding, 2012. 30(2): p. 1121–1130.

[58] Distelfeld, A., C. Li, and J. Dubcovsky, Regulation of flowering in temperate cereals. Current Opinion in Plant Biology, 2009. 12(2): p. 178–184.

[59] Karsai, I., P. Szucs, K. Mészáros, T. Filichkina, P. Hayes, J. Skinner, L. Láng, and Z. Bedo, The Vrn-H2 locus is a major determinant of flowering time in a facultative× winter growth habit barley (Hordeum vulgare L.) mapping population. Theoretical and Applied Genetics, 2005. 110(8): p. 1458–1466.

[60] Bullrich, L., M. Appendino, G. Tranquilli, S. Lewis, and J. Dubcovsky, Mapping of a thermo-sensitive earliness per se gene on Triticum monococcum chromosome 1Am. Theoretical and Applied Genetics, 2002. 105(4): p. 585–593.

[61] Lewis, S., M.E. Faricelli, M.L. Appendino, M. Valárik, and J. Dubcovsky, The chromosome region including the earliness per se locus Eps-Am1 affects the duration of early developmental phases and spikelet number in diploid wheat. Journal of Experimental Botany, 2008. 59(13): p. 3595–3607.

[62] Wang, G., I. Schmalenbach, M. von Korff, J. Léon, B. Kilian, J. Rode, and K. Pillen, Association of barley photoperiod and vernalization genes with QTLs for flowering time and agronomic traits in a BC2DH population and a set of wild barley introgression lines. Theoretical and Applied Genetics, 2010. 120(8): p. 1559–1574.

[63] LÜ, R.-h., Y.-h. XU, R. Boyd, X.-q. ZHANG, S. Broughton, M. Jones, C.-d. LI, and Y.-f. CHEN, Barley and Wheat Share the Same Gene Controlling the Short Basic Vegetative Period. Journal of Integrative Agriculture, 2013. 12(10): p. 1703–1711.

[64] Faure, S., A.S. Turner, D. Gruszka, V. Christodoulou, S.J. Davis, M. von Korff, and D.A. Laurie, Mutation at the circadian clock gene EARLY MATURITY 8 adapts domesticated barley (Hordeum vulgare) to short growing seasons. Proceedings of the National Academy of Sciences, 2012. 109(21): p. 8328–8333.

[65] Yan, L., A. Loukoianov, G. Tranquilli, M. Helguera, T. Fahima, and J. Dubcovsky, Positional cloning of the wheat vernalization gene VRN1. Proceedings of the National Academy of Sciences, 2003. 100(10): p. 6263–6268.

[66] Yasuda, S., J. Hayashi, and I. Moriya, Genetic constitution for spring growth habit and some other characters in barley cultivars in the Mediterranean coastal regions. Euphytica, 1993. 70(1–2): p. 77–83.

[67] Cockram, J., H. Jones, F.J. Leigh, D. O'Sullivan, W. Powell, D.A. Laurie, and A.J. Greenland, Control of flowering time in temperate cereals: genes, domestication, and sustainable productivity. Journal of Experimental Botany, 2007. 58(6): p. 1231–1244.

[68] Boudiar, R., A. Casas, C. CP, P. Gracia, and E. Igartua, Identification of QTL for agronomic traits contributed by a barley mediterranean landrace. Crop and Pasture

Science, 2016. 67(1): p. 37–46 http://digital.csic.es/bitstream/10261/127755/1/CasasAM_CroPastSci_2016.pdf.

[69] Appels, R., M. Francki, and R. Chibbar, Advances in cereal functional genomics. Functional and Integrative Genomics, 2003. 3(1): p. 1–24.

[70] Faricelli, M.E., M. Valárik, and J. Dubcovsky, Control of flowering time and spike development in cereals: the earliness per se Eps-1 region in wheat, rice, and Brachypodium. Functional and Integrative Genomics, 2010. 10(2): p. 293–306.

[71] Valárik, M., A. Linkiewicz, and J. Dubcovsky, A microcolinearity study at the earliness per se gene Eps-A m 1 region reveals an ancient duplication that preceded the wheat–rice divergence. Theoretical and Applied Genetics, 2006. 112(5): p. 945–957.

[72] Hammer, G.L., G. McLean, S. Chapman, B. Zheng, A. Doherty, M.T. Harrison, E. van Oosterom, and D. Jordan, Crop design for specific adaptation in variable dryland production environments. Crop and Pasture Science, 2014. 65(7): p. 614–626.

[73] Chapman, S.C., G.L. Hammer, and H. Meinke, A sunflower simulation model: I. Model development. Agronomy Journal, 1993. 85(3): p. 725–735.

[74] Imaizumi, T. and S.A. Kay, Photoperiodic control of flowering: not only by coincidence. Trends in Plant Science, 2006. 11(11): p. 550–558.

[75] Dofing, S., Phenological development-yield relationships in spring barley in a subarctic environment. Canadian Journal of Plant Science, 1995. 75(1): p. 93–97.

[76] Aspinall, D. and L. Paleg, Effects of Day-length and Light Intensity on Growth of Barley I. Growth and Development of Apex with a Fluorescent Light Source, 1963, Botanical Gazette Vol. 124, No. 6, p. 429–437.

[77] Laurie, D.A., N. Pratchett, J.H. Bezant, and J.W. Snape, Genetic analysis of a photoperiod response gene on the short arm of chromosome 2 (2H) of Hordeum vulgare (barley). Heredity-LONDON, 1994. 72: p. 619–627.

[78] Börner, A., G. Buck-Sorlin, P. Hayes, S. Malyshev, and V. Korzun, Molecular mapping of major genes and quantitative trait loci determining flowering time in response to photoperiod in barley. Plant Breeding, 2002. 121(2): p. 129–132.

[79] Alqudah, A.M., R. Sharma, R.K. Pasam, A. Graner, B. Kilian, and T. Schnurbusch, Genetic dissection of photoperiod response based on gwas of pre-anthesis phase duration in spring barley. PLoS One, 2014. 9(11): p. e113120.

[80] Laurie, D.A., Comparative genetics of flowering time. Plant Molecular Biology, 1997. 35(1–2): p. 167–177.

[81] Boden, S.A., D. Weiss, J.J. Ross, N.W. Davies, B. Trevaskis, P.M. Chandler, and S.M. Swain, EARLY FLOWERING3 regulates flowering in spring barley by mediating gibberellin production and FLOWERING LOCUS T expression. The Plant Cell, 2014. 26(4): p. 1557–1569.

[82] Casao, M.C., I. Karsai, E. Igartua, M.P. Gracia, O. Veisz, and A.M. Casas, Adaptation of barley to mild winters: a role for PPDH2. BMC Plant Biology, 2011. 11(1): p. 164.

[83] Stracke, S. and A. Börner, Molecular mapping of the photoperiod response gene ea7 in barley. Theoretical and Applied Genetics, 1998. 97(5–6): p. 797–800.

[84] Jarod, A., B. Rollins, M.A. Drosse, S. Mulki, M. Grando, M. Baum, S. Singh, M. Ceccarelli, and v. Korff, Variation at the vernalisation genes Vrn-H1 and Vrn-H2 determines growth and yield stability in barley (Hordeum vulgare) grown under dryland conditions in Syria. Theoretical and Applied Genetics, 2013. 126: p. 2803–2824.

[85] Karsai, I., K. Mészáros, P. Szücs, P. M. Hayes, L. Láng, and Z. Bedö, Effects of loci determining photoperiod sensitivity (Phd-H1) and vernalization response (Sh2) on agronomic traits in the Dicktoo•Morex barley mapping population. Plant Breeding 1999. 118: p. 399—403.

[86] MASWHEAT, Abiotic stress and agronomic traits: vernalization requirement, 2015. http://maswheat.ucdavis.edu/protocols/Vrn/.

[87] von Zitzewitz, J., P. Szucs, J. Dubcovsky, L. Yan, E. Francia, N. Pecchioni, A. Casas, T.H. Chen, P.M. Hayes, and J.S. Skinner, Molecular and structural characterization of barley vernalization genes. Plant Molecular Biology, 2005. 59(3): p. 449–467.

[88] Sasani, S., M.N. Hemming, S.N. Oliver, A. Greenup, R. Tavakkol-Afshari, S. Mahfoozi, K. Poustini, H.-R. Sharifi, E.S. Dennis, and W.J. Peacock, The influence of vernalization and daylength on expression of flowering-time genes in the shoot apex and leaves of barley (Hordeum vulgare). Journal of Experimental Botany, 2009. 60(7): p. 2169–2178.

[89] Hayes, P., F.Q. Chen, A. Corey, A. Pan, T.H. Chen, E. Baird, W. Powell, W. Thomas, R. Waugh, and Z. Bedo, The Dicktoo×Morex Population, in Plant Cold Hardiness. 1997, Springer, New York, US. p. 77–87.

[90] Francia, E., F. Rizza, L. Cattivelli, A. Stanca, G. Galiba, B. Toth, P. Hayes, J. Skinner, and N. Pecchioni, Two loci on chromosome 5H determine low-temperature tolerance in a 'Nure'(winter)×'Tremois'(spring) barley map. Theoretical and Applied Genetics, 2004. 108(4): p. 670–680.

[91] Trevaskis, B., D.J. Bagnall, M.H. Ellis, W.J. Peacock, and E.S. Dennis, MADS box genes control vernalization-induced flowering in cereals. Proceedings of the National Academy of Sciences, 2003. 100(22): p. 13099–13104.

[92] Loukoianov, A., L. Yan, A. Blechl, A. Sanchez, and J. Dubcovsky, Regulation of VRN-1 vernalization genes in normal and transgenic polyploid wheat. Plant Physiology, 2005. 138(4): p. 2364–2373.

[93] Fu, D., P. Szucs, L. Yan, M. Helguera, J.S. Skinner, J. Von Zitzewitz, P.M. Hayes, and J. Dubcovsky, Large deletions within the first intron in VRN-1 are associated with spring growth habit in barley and wheat. Molecular Genetics and Genomics, 2005. 273(1): p. 54–65.

[94] Shitsukawa, N., C. Ikari, S. Shimada, S. Kitagawa, K. Sakamoto, H. Saito, H. Ryuto, N. Fukunishi, T. Abe, and S. Takumi, The einkorn wheat (Triticum monococcum) mutant, maintained vegetative phase, is caused by a deletion in the VRN1 gene. Genes and Genetic Systems, 2007. 82(2): p. 167–170.

[95] Cuesta-Marcos, A., P. Szucs, T.J. Close, T. Filichkin, G.J. Muehlbauer, K.P. Smith, and P.M. Hayes, Genome-wide SNPs and re-sequencing of growth habit and inflorescence genes in barley: implications for association mapping in germplasm arrays varying in size and structure. BMC Genomics, 2010. 11(1): p. 707.

[96] Yan, L., D. Fu, C. Li, A. Blechl, G. Tranquilli, M. Bonafede, A. Sanchez, M. Valarik, S. Yasuda, and J. Dubcovsky, The wheat and barley vernalization gene VRN3 is an orthologue of FT. Proceedings of the National Academy of Sciences, 2006. 103(51): p. 19581–19586.

[97] Dubcovsky, J., D. Lijavetzky, L. Appendino, and G. Tranquilli, Comparative RFLP mapping of Triticum monococcum genes controlling vernalization requirement. Theoretical and Applied Genetics, 1998. 97(5–6): p. 968–975.

[98] Mahfoozi, S., A. Limin, P. Hayes, P. Hucl, and D. Fowler, Influence of photoperiod response on the expression of cold hardiness in wheat and barley. Canadian Journal of Plant Science, 2000. 80(4): p. 721–724.

[99] Yan, L., A. Loukoianov, A. Blechl, G. Tranquilli, W. Ramakrishna, P. SanMiguel, J.L. Bennetzen, V. Echenique, and J. Dubcovsky, The wheat VRN2 gene is a flowering repressor down-regulated by vernalization. Science, 2004. 303(5664): p. 1640–1644.

[100] Slafer, G., Genetic basis of yield as viewed from a crop physiologist's perspective. Annals of Applied Biology, 2003. 142(2): p. 117–128.

[101] Appendino, M. and G.A. Slafer, Earliness per se and its dependence upon temperature in diploid wheat lines differing in the major gene Eps-A m 1 alleles. The Journal of Agricultural Science, 2003. 141(02): p. 149–154.

[102] Kuchel, H., G. Hollamby, P. Langridge, K. Williams, and S. Jefferies, Identification of genetic loci associated with ear-emergence in bread wheat. Theoretical and Applied Genetics, 2006. 113(6): p. 1103–1112.

[103] Zikhali, M., M. Leverington-Waite, L. Fish, J. Simmonds, S. Orford, L.U. Wingen, R. Goram, N. Gosman, A. Bentley, and S. Griffiths, Validation of a 1DL earliness per se (eps) flowering QTL in bread wheat (Triticum aestivum). Molecular Breeding, 2014. 34(3): p. 1023–1033.

[104] Griffiths, S., J. Simmonds, M. Leverington, Y. Wang, L. Fish, L. Sayers, L. Alibert, S. Orford, L. Wingen, and L. Herry, Meta-QTL analysis of the genetic control of ear emergence in elite European winter wheat germplasm. Theoretical and Applied Genetics, 2009. 119(3): p. 383–395.

[105] Faricelli, M., M. Valarik, S. Lewis, L. Appendino, and J. Dubcovsky, Physical map of the Eps-Am1 gene region in Triticum monococcum L. 11th International Wheat Genetics Symposium, 2008. http://ses.library.usyd.edu.au//bitstream/2123/3333/1/P266.pdf.

[106] Slafer, G.A., D.F. Calderini, and D.J. Miralles, Yield Components and Compensation in Wheat: Opportunities for Further Increasing Yield Potential: Increasing Yield. Potential in Wheat, Breaking the Barriers Conference Proceedings of a Workshop Held in Ciudad Obregon, Sonora, Mexico. Edt by M.P. Reynolds, S. Rajaram, and A. McNab., 1996(CIMMYT): p. 101–133.

[107] Hoogendoorn, J., A reciprocal F1 monosomic analysis of the genetic control of time of ear emergence, number of leaves and number of spikelets in wheat (Triticum aestivum L.). Euphytica, 1985. 34(2): p. 545–558.

[108] Slafer, G., J. Araus, C. Royo, and L. Moral, Promising eco-physiological traits for genetic improvement of cereal yields in Mediterranean environments. Annals of Applied Biology, 2005. 146(1): p. 61–70.

[109] Zikhali, M. and S. Griffiths, The effect of Earliness per se (Eps) genes on flowering time in bread wheat. Advances in Wheat Genetics, From Genome to Field. Proceeding of the 12th International Wheat Genetic Symposium, 2015.

[110] Herndl, M., J. White, S. Graeff, and W. Claupein, The impact of Vernalization requirement, photoperiod sensitive and earliness per se on grain protein content of bread wheat. Euphytica, 2008. 163(2): p. 309–320.

[111] Castro, A., P. Hayes, L. Viega, and I. Vales, Transgressive segregation for phenological traits in barley explained by two major QTL alleles with additivity. Plant Breeding, 2008. 127(6): p. 561–568.

[112] Takahashi, R. and S. Yasuda. Genetics of earliness and growth habit in barley. in Proceedings of the International Barley Genetics Symposium. 1971.

[113] Gallagher, L., K. Soliman, and H. Vivar, Interactions among loci conferring photoperiod insensitivity for heading time in spring barley. Crop Science, 1991. 31(2): p. 256–261.

[114] Boyd, W., Li, C.-D., and Grime, C. (2008). Genetic control of heading date in spring barley. The Proceedings of 13th Australian Barley Technical Symposium, Esplanade Hotel, Fremantle, Western Australia, 26–30 August 2007.

[115] APSIM, 2015. http://www.apsim.info/Documentation/Model,CropandSoil/CropModuleDocumentation/AgPasture.aspx.

[116] Keating, B.A., P.S. Carberry, G.L. Hammer, M.E. Probert, M.J. Robertson, D. Holzworth, N.I. Huth, J.N. Hargreaves, H. Meinke, and Z. Hochman, An overview of APSIM, a model designed for farming systems simulation. European Journal of Agronomy, 2003. 18(3): p. 267–288.

[117] CCIA/CSIRO, Projections: climate change in Australia. Technical Report, 2015. 1: p. 1–222.

[118] Anwar, M.R., D. Li Liu, R. Farquharson, I. Macadam, A. Abadi, J. Finlayson, B. Wang, and T. Ramilan, Climate change impacts on phenology and yields of five broadacre crops at four climatologically distinct locations in Australia. Agricultural Systems, 2015. 132: p. 133–144.

[119] Harrison, M., B. Cullen, and R. Rawnsley, Modelling the sensitivity of agricultural systems to climate change and extreme climatic events, Agricultural Systems, 2016, 148: p. 135–148.

[120] Harrison, M.T., F. Tardieu, Z. Dong, C.D. Messina, and G.L. Hammer, Characterizing drought stress and trait influence on maize yield under current and future conditions. Global Change Biology, 2014. 20(3): p. 867–878.

[121] Van Gool, D., L. Vernon, and W. Australia, Potential impacts of climate change on agricultural land use suitability: wheat. 2005: Department of Agriculture.

[122] Phelan, D.C., M.T. Harrison, E.P. Kemmerer, and D. Parsons, Management opportunities for boosting productivity of cool-temperate dairy farms under climate change. Agricultural Systems, 2015. 138: p. 46–54.

[123] Bogard, M., C. Ravel, E. Paux, J. Bordes, F. Balfourier, S. Chapman, J. Le Gouis, and V. Allard, Predictions of heading date in bread wheat (Triticum aestivum L.) using QTL-based parameters of an ecophysiological model. Journal of Experimental Botany, 2014. 65 (20): p. 5849–5865.

[124] Asseng, S., B. Keating, I. Fillery, P. Gregory, J. Bowden, N. Turner, J. Palta, and D. Abrecht, Performance of the APSIM-wheat model in Western Australia. Field Crops Research, 1998. 57(2): p. 163–179.

[125] Jamieson, P., M. Semenov, I. Brooking, and G. Francis, Sirius: a mechanistic model of wheat response to environmental variation. European Journal of Agronomy, 1998. 8(3): p. 161–179.

[126] Yin, X., P.C. Struik, F.A. van Eeuwijk, P. Stam, and J. Tang, QTL analysis and QTL-based prediction of flowering phenology in recombinant inbred lines of barley. Journal of Experimental Botany, 2005. 56(413): p. 967–976.

[127] Meinke, H. and G. Hammer, Climatic risk to peanut production: a simulation study for Northern Australia. Animal Production Science, 1995. 35(6): p. 777–780.

[128] Zheng, B., S. Chapman, J. Christopher, T. Frederiks, and K. Chenu. Predicting heading date and frost impact in wheat across Australia. in 17th Australian Agronomy Conference. 2015.

[129] Zheng, B., S.C. Chapman, J.T. Christopher, T.M. Frederiks, and K. Chenu, Frost trends and their estimated impact on yield in the Australian wheatbelt. Journal of Experimental Botany, 2015. 66 (12): p. 3611–3623.

[130] APSIM, Barley, 2015. https://www.apsim.info/Documentation/Model,CropandSoil/CropModuleDocumentation/Barley.aspx.

[131] Manschadi, A., Z. Hochman, G. Mclean, P. DeVoil, D. Holzworth, and H. Meinke. APSIM-Barley model–Adaptation of a wheat model to simulate barley growth and development. in 13th Australian Agronomy Conference: Perth, Western Australia. 2006.

[132] Eticha, F., H. Grausgruber, and E. Berghoffer, Multivariate analysis of agronomic and quality traits of hull-less spring barley (Hordeum vulgare L.). Journal of Plant Breeding and Crop Science, 2010. 2(5): p. 81–95.

[133] Zeng, X., Genetic variability in agronomic traits of a germplasm collection of hulless barley. Genetics and Molecular Research: GMR, 2015. 14(4): p. 18356.

[134] Nuttall, J. G., G. J. O'Leary, J. F. Panozzo, C. K. Walker, K. M. Barlow and G. J. Fitzgerald. Models of grain quality in wheat-A review. Field Crops Research, 2016. doi:10.1016/j.fcr.2015.12.011

[135] Asseng, S., S. Milroy, and M. Poole, Systems analysis of wheat production on low water-holding soils in a Mediterranean-type environment: I. Yield potential and quality. Field Crops Research, 2008. 105(1): p. 97–106.

[136] Goyne, P., H. Meinke, S. Milroy, G. Hammer, and J. Hare, Development and use of a barley crop simulation model to evaluate production management strategies in north-eastern Australia. Crop and Pasture Science, 1996. 47(7): p. 997–1015.

[137] Asseng, S., F. Ewert, P. Martre, R. Rötter, D. Lobell, D. Cammarano, B. Kimball, M.J. Ottman, G. Wall, and J. White, Rising temperatures reduce global wheat production. Nature Climate Change, 2015. 5(2): p. 143–147.

[138] Barlow, K., B. Christy, G. O'Leary, P. Riffkin, and J. Nuttall. Simulating the impact of extreme heat and frost events on wheat production: The first steps. in 20th International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand, Adelaide, Australia. 2013.

[139] Shorter, R., R. Lawn, and G. Hammer, Improving genotypic adaptation in crops–a role for breeders, physiologists and modellers. Experimental Agriculture, 1991. 27(02): p. 155–175.

[140] Wu, R. and D. O'Malley, Nonlinear genotypic response to macro-and microenvironments. Theoretical and Applied Genetics, 1998. 96(5): p. 669–675.

[141] Bondari, K., Statistical analysis of genotype x environment interaction in agricultural research. Paper SD15, SESUG: The Proceedings of the SouthEast SAS Users Group, St Pete Beach, 2003.

[142] FAO, Plant breeding and farmer participation. (Eds) Ceccarelli, S., Guimaraes, EP and Weltzien, E. 2009.

[143] Garcıa del Moral, L., D.J. Miralles, and G.A. Slafer, Initiation and appearance of vegetative and reproductive structures throughout barley development. Barley Science: Recent Advances from Molecular Biology to Agronomy of Yield and Quality, 2002: p. 243–268.

[144] Ceccarelli, S., W. Erskine, J. Hamblin, and S. Grando, Genotype by environment interaction and international breeding programmes. Experimental Agriculture, 1994. 30(02): p. 177–187.

[145] Löffler, C.M., J. Wei, T. Fast, J. Gogerty, S. Langton, M. Bergman, B. Merrill, and M. Cooper, Classification of maize environments using crop simulation and geographic information systems. Crop Science, 2005. 45(5): p. 1708–1716.

[146] Vargas, M., F.A. van Eeuwijk, J. Crossa, and J.-M. Ribaut, Mapping QTLs and QTL× environment interaction for CIMMYT maize drought stress program using factorial regression and partial least squares methods. Theoretical and Applied Genetics, 2006. 112(6): p. 1009–1023.

[147] Duvick, D.N., The contribution of breeding to yield advances in maize (Zea mays L.). Advances in Agronomy, 2005. 86: p. 83–145.

[148] Hammer, G., Pathways to prosperity: breaking the yield barrier in sorghum. Agricultural Science, 2006. 19(2): p. 16–22.

[149] Bakhsh, A., S. Malik, M. Aslam, U. Iqbal, and A. Haqqani, Response of chickpea genotypes to irrigated and rain-fed conditions. International Journal of Agriculture and Biology (Pakistan), 2007. Volume 9, (4): p. 590–593.

[150] Hunt, J. and N. Poole. Simulating leaf area duration to predict yield response to foliar fungicide in wheat and barley. in Proceedings of 15th Agronomy Conference on Food Security from Sustainable Agriculture. 2010.

[151] Klepper, B., T. Tucker, and B. Dunbar, A numerical index to assess early inflorescence development in wheat. Crop Science, 1983. 23(2): p. 206–208.

[152] SolarTopo, Day length, sunrise and sunset calculator, 2016. http://www.solartopo.com/daylength.htm.