



Vernalisation and photoperiod sensitivity in wheat: Impact on canopy development and yield components



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ABSTRACT

Genetic variation in the *VERNALIZATION1* (*VRN1*) and *PHOTOPERIOD1* (*PPD1*) genes, which control the vernalisation and photoperiod response, underpin wheat adaptation to different environments. Near isogenic lines were used to investigate the role of allelic combinations of *VRN1* and *PPD1*, including new alleles for *VRN1*-A1, on the length of developmental phases, dynamics of leaf and tiller appearance and yield components in complementary irrigated field trials relevant to low latitude wheat growing areas and controlled conditions. Allelic differences in *VRN1* had a stronger effect on the duration of the vegetative phase, while photoperiod sensitivity at *PPD1* lengthened the stem elongation phase (SE) by up to 23%. If a phase was lengthened, flowering was delayed. The level of response to daylength during stem elongation (SE) introduced by photoperiod sensitive alleles was dependent on the *VRN1* composition and vernalisation status. A longer SE under short days was achieved by *PPD1* sensitive genotypes when one *VRN1* spring allele was present and plants were vernalised. The duration of SE was weakly related to spike dry weight m^{-2} at DC65 in the field but did not translate into higher grain number m^{-2} . In the field, lines with two to three *VRN1* spring alleles had shortest development phases, including SE, close flowering dates, sampled similar temperature environments at different stages, and achieved high yields. Yield advantage was explained by higher biomass, harvest index, grain number m^{-2} and thousand kernel weight. Genotypes with three winter *VRN1* alleles were comparatively disadvantaged, with a longer vegetative phase placing SE under higher temperatures. Allelic differences in both genes caused large variation in leaf and tiller number generation but also in tiller mortality and individual leaf size, lessening the impact on leaf area. Changes in plant morphology and yield components that did not seem mediated via the influence of development genes on the duration of different stages and their impact on resource capture deserve further investigation.

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1. Introduction

Wheat has been able to adapt to a wide range of environmental conditions thanks to the selection of plants with differing

Abbreviations: DC31, decimal code detection of the first node on the Zadoks scale; DC65, anthesis defined by the Zadoks scale; LD, long day; LSD, least significant difference; NILs, near isogenic lines; PAR, photosynthetically active radiation; *PPD1*, *PHOTOPERIOD1*; PTQ, photothermal quotient; SD, short day; SD1, first sowing date; SD2, second sowing date; SE, stem elongation; *VRN1*, *VERNALIZATION1*.

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flowering behaviour. The *VRN1* (*VERNALISATION1*) and photoperiod *PPD1* (*PHOTOPERIOD1*) genes, which control the vernalisation and photoperiod responses, were held responsible for this successful adaptation by having a strong influence in determining the duration of developmental phases leading to flowering, influencing organ generation and yield components.

Allelic differences at the *VRN1* gene have allowed the adaptation of wheat to different climates and its classification into winter and spring genotypes (Flood and Halloran 1986; Trevaskis et al., 2007). Wheat has three sets of homeologous chromosomes A, B and D, which have different expression patterns (Leach et al., 2014). *VRN1* is located on the long arm of chromosome 5 and their alleles are denoted as *VRN*-A1, *VRN*-B1 and *VRN*-D1. Winter wheats can be sown in autumn and winter and they require the exposure to cold

temperatures to promote flowering. Without vernalisation, winter wheats delay flowering (Trevaskis et al., 2003; Oliver et al., 2013) however, when the exposure to cold temperatures saturates the vernalisation requirement, they flower at similar time to spring wheats (Trevaskis et al., 2003), which are adapted to be grown in the absence of cold temperatures.

VRN1 winter alleles require low temperatures to be expressed and promote flowering while the spring alleles have high levels of expression regardless of temperature (Trevaskis et al., 2003). Which combination a particular wheat cultivar has, will determine how fast it will flower in response to a particular sowing date in a given environment. Experiments carried out by Allard et al. (2012) with near isogenic lines (NILs) differing in the *VRN1* gene, have shown that plants with a single spring allele at VRN-A1, VRN-D1 and VRN-B1, in the absence of vernalisation treatment, produced 7, 8 and 9.6 leaves, respectively, reducing the duration of the vegetative phase with respect to the winter alleles. This suggests that VRN-A1 has the highest expression in the absence of cold followed by VRN-D1 and VRN-B1, as a lower leaf number indicates a faster transition to floral initiation.

PPD1 is located in chromosome 2 and their alleles are known as PPD-A1, PPD-B1 and PPD-D1 (Law et al., 1978; Scarth and Law 1983; Worland and Law 1986). Shaw et al. (2012), working with NILs differing in *PPD1* sensitivity, agreed that the photoperiod response in terms of time to flowering is dependent on the nature of the acquired mutation in each allele. In that experiment, under short days, the photoperiod insensitive alleles at PPD-D1, PPD-A1 and PPD-B1 reduced the time to anthesis in that order, and when combined, time to anthesis was reduced by at least 15 days compared to the control. This suggests that the photoperiod insensitive allele at PPD-D1 has the highest expression in the absence of long days.

The vernalisation response mainly affects the duration of the vegetative phase until the initiation of floral primordia or double ridge (Flood and Halloran 1986), photoperiod has a lower magnitude effect in this phase (Rawson and Richards, 1993; Miralles and Richards 2000; Brooking and Jamieson 2002). Vernalisation and photoperiod also influence the duration of the early reproductive phase, from double ridge to terminal spikelet, and the stem elongation (SE) phase, from terminal spikelet to anthesis (Rawson and Richards 1993; Miralles and Richards 2000; Gonzalez et al., 2002, 2003). Plants sensitive to vernalisation and photoperiod exposed to optimal vernalising conditions and long days will have less leaves related to a shorter time to reach double ridge; lower number of leaves have also been related to increases in the phyllochron (Rawson & Richards, 1993; Miralles and Richards, 2000; Brooking and Jamieson 2002; Gonzalez et al., 2002, 2003). Additionally, vernalisation decreased the time required to complete the early reproductive and SE phases, advancing anthesis date by up to 60% in vernalisation sensitive lines when vernalised compared

to non-vernalised plants, in a field study carried by Gonzalez et al. (2002, 2003) and an experiment under controlled conditions by Brooking and Jamieson (2002). When shorter early reproductive and SE phases were triggered by long days, the number of spikelets per spike decreased together with a reduction in the number of fertile florets per spike and per spikelet in photoperiod sensitive plants (Miralles and Richards 2000; Gonzalez et al., 2003). From several studies showing the effects of vernalisation and photoperiod on crop development and yield components, it has been proposed that increases in yield potential can be achieved by exploiting genotypic differences in the major genes controlling flowering time. Allelic combinations of these genes would allow the fine tuning of the timing of phenological events before flowering, without substantial changes in flowering date (Slafer and Rawson 1994; Slafer 1996; Miralles and Richards 2000; Gonzalez et al., 2011). In particular, increasing the duration of SE is expected to lengthen the duration of the spike growth period resulting in heavier spikes with a higher number of fertile florets, leading to more grains and higher yields (Slafer 1996; Miralles et al., 2000; Gonzalez et al., 2011), possibly via higher cumulative assimilate supply to the spike (Gonzalez et al., 2005a; Ghigliione et al., 2008). The majority of the studies cited so far were based on cultivar differences or NILs for either *VRN1* or *PPD1*.

This study used a set of NILs with different allelic combinations of *VRN1* (including a new allele for VRN1-A1) and *PPD1* within the same spring wheat background to determine their single and combined effect on the duration of developmental phases leading to flowering, and their influence on the dynamics of canopy development and biomass production and partitioning relevant to yield and yield components. Plants were exposed to controlled environments to achieve contrasting vernalisation and photoperiod treatments and irrigated field conditions relevant to low latitude wheat growing areas.

2. Materials and methods

2.1. Germplasm

NILs developed from the wheat spring cultivar Sunstate (B. Trevaskis, pers. comm.) (Tables 1 and 2) were grown in glasshouse and field experiments. The NILs were made by crossing donors of different *VRN1* or *PPD1* alleles to Sunstate followed by four rounds of recurrent backcrossing and selection of targeted donor alleles using molecular markers. The parent line is not fixed for PPD-B1. Primers and conditions for allelic detection are presented in Appendix A. Novel alleles were detected by screening 3000 wheats for novel deletion alleles with the primer set BT472/BT474 (Appendix C). The genotypes included different combinations of the VRN-A1, VRN-B1 and VRN-D1 spring (A, B and D) and winter (a, b

Table 1
Nomenclature for genes and allelic variation for *VRN1*, *PPD-D1* and *PPD-B1*. ¹bp: base pair.

Alleles	Symbol	Description	Reference
<i>VRN1</i>			
VRN-A1	a	Full-length winter type, A genome.	
VRN-A1a	A	Promoter insertion, gene duplication. High activity; reduces vernalisation requirement.	Yan et al. (2004)
VRN-A1 Langdon.	Ai1	Deletion 1 st intron A genome, Langdon. Deletion: bp ¹ 1080–8536. High activity; reduces vernalisation requirement.	Fu et al. (2005)
VRN-A1AUS28709	Ai2	Novel deletion intron A genome. Deletion: bp 1807–7804. High activity, reduces vernalisation requirement	This study
VRN-B1	b	Full-length winter type, B genome.	
VRN-B1a	B	Deletion 1 st intron B genome. Common allele. Deletion: bp 1105–8885	Fu et al. (2005)
VRN-D1	d	Full-length winter type, D genome.	
VRN-D1a	D	Deletion 1 st intron D genome. Common allele.	Fu et al. (2005)
<i>PPD1</i>			
PPD-B1a	3×	Three copies of <i>PPD1</i> , B genome (insensitivity)	Diaz et al. (2012)
PPD-B1b	1×	One copy of <i>PPD1</i> , B genome. Wildtype.	Diaz et al. (2012)
PPD-D1	s1	Full length <i>PPD1</i> , D genome.	Beales et al. (2007)
PPD-D1a	i	Promoter deletion <i>PPD1</i> , D genome (insensitivity)	Beales et al. (2007)

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