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Effect of *Ppd-1* photoperiod sensitivity genes on dry matter production and allocation in durum wheat

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ABSTRACT

Understanding the effect of genetic factors controlling flowering time is essential to fine-tune phenological development and to maximize yield. Thirty-four spring durum wheat genotypes classified in five allelic combinations for *Ppd-A1/Ppd-B1* loci were grown for two years at three contrasting latitudes: Mexico-North, Spain-South and Spain-North. In all them, a delay in flowering date due to the presence of photoperiod sensitivity alleles *Ppd-A1b* and *Ppd-B1b* resulted in lower yields. The number of days to flowering, determined by an increasing number of photoperiod sensitivity alleles, accounted in all sites for more than 80% of the variation in the contribution of translocation of pre-flowering assimilates to grain yield. In Mexico and Spain-North late-flowering resulted in decreased harvest index as influenced by high temperatures during grain filling. In Mexico, where grain filling occurred under high temperatures and solar radiation, translocation of pre-flowering assimilates accounted from 55 to 63% of yield, independently of the flowering date of the genotype. In Spain-North, where water was available during grain filling, current photosynthesis was the main contributor to yield (57–73%), with independence of the allelic combination at *Ppd* loci. In Spain-South, the relative contribution of photosynthesis and translocation depended on the allelic composition at *Ppd* loci, with translocation increasing by 24% in the latest-flowering genotypes compared with the earliest ones. In all sites the limiting factor for attaining high yields was the capacity of the plant canopy to photosynthesize after anthesis. This study suggests that the expression of genes *Ppd-A1* and *Ppd-B1* regulating the response to photoperiod modulates the physiological strategy adopted by durum wheat to fill its grains, underlining the importance of phenology fitting in maximizing grain yield.

1. Introduction

Wheat is one of the major grain crops in the world and provides about 20% of the calories of the world's population (FAOSTAT, 2016). Durum wheat (*Triticum turgidum* L. var. *durum*) represents about 10% of total wheat production (Kantety et al., 2005), playing an important role in food security for urban populations in small geographical areas (Ammar et al., 2006). The Mediterranean Basin is the largest durum producing area worldwide, the most significant import market and the largest consumer of durum wheat products.

Durum wheat yield can only be maximized by growing varieties which flowering time allows the crop to avoid stresses during vegetative and grain-filling periods (Kamran et al., 2014). Flowering time is a critical stage that delimits the duration of spike formation and marks the transition into the grain-filling period during which kernels per spike and kernel weight are defined. Wheat grain growth is mainly supported by transient photosynthesis (primarily in the flag leaf and the inflorescence) and translocation of stored reserves accumulated in vegetative organs prior to flowering (Ehdaie et al., 2006Blum, 1988). Dry matter accumulated prior to flowering is of particular importance when grain filling takes place under hot and dry conditions that limit photosynthesis (Papakosta and Gagianas, 1991; Villegas et al., 2001; Ehdaie et al., 2006; Álvaro et al., 2008). The relative proportion of stem reserves to wheat grain yield ranges from 6 to 100%, depending on the environment and genotypes under cultivation (Borrell et al., 1993; Blum et al., 1994). Under optimal conditions, stem carbohydrate reserves have been estimated to contribute from 10 to 12% of the final grain yield in wheat, but more than 40% under drought or heat stress

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during the grain filling period (Wardlaw and Porter, 1967; Bidinger et al., 1977; Ehdaie et al., 2008). Van Herwaarden et al. (1998) reported a 75–100% share of stem reserves in the grain yield of wheat under drought. It has been estimated that total dry matter remobilized from the main stem to the filling grains is greater in the modern durum wheat cultivars than in the landraces (Álvaro et al., 2008), possibly providing one basis for the increased harvest index of modern cultivars.

The genetic control of flowering time in wheat is complex. It is controlled primarily by three groups of loci: photoperiod sensitivity genes (*Ppd*), vernalization requirement genes (*Vrn*) and 'earliness *per se*' (*Eps*) or 'narrow-sense earliness'. The latter act on the developmental rate independently of vernalization and photoperiod (Snape et al., 2001; Distelfeld et al., 2009). Vernalization requirement is controlled by the *Vrn-1* genes, which in durum wheat consist of homoelogous copies designated as *Vrn-A1* and *Vrn-B1*, located on the long arms of chromosomes 5A and 5B, respectively (Yan et al., 2004; Fu et al., 2005).The major elite durum wheat gene pools are spring types showing no major vernalization requirements.

Photoperiod sensitivity in durum wheat is determined at the *Ppd-A1* and *Ppd-B1* loci, located on chromosomes 2AS and 2BS, respectively (Laurie, 1997). Wilhelm et al. (2009) found two large deletions within the *Ppd-A1* gene in durum wheat (1027 and 1117 bp, designated as allele 'GS-100′ and 'GS-105′, respectively), which remove a common region from the wild-type sequence. The presence of either deletion accelerated flowering, which led to the conclusion that these deletions are the likely causal basis of photoperiod insensitivity in tetraploid wheat (Wilhelm et al., 2009).

Ppd-1 genes play an important role in the regulation of wheat growth and development (Kirby, 1988; Miralles and Richards, 2000; Kamran et al., 2014). Allelic combinations at these loci modulate plant development, interacting with the environmental stimuli to advance or delay flowering time (Snape et al., 2001). This may affect indirectly the accumulation and distribution of dry matter within the wheat plant, modifying source-sink equilibrium (Foulkes et al., 2004). The intensive selection for photoperiod insensitivity conducted during the 20th century, particularly in the CIMMYT breeding programs, resulted in the selection of early types, most of them with little to no photoperiod sensitivity. The breeding-generated reduction in the number of days to flowering in durum wheat has been estimated to amount to 8 days in Spain and 2 days in Italy (Álvaro et al., 2008). Yield advantages resulting from photoperiod insensitivity in bread wheat have been estimated to represent up to 35% in Europe (Worland, 1996).

Current climate change scenario, predicting more drought events and increased temperature in Europe and northern latitudes (DePauw et al., 2011), require from wheat breeders to develop cultivars achieving high yields in spite of less than optimal growing conditions in order to ensure food security (Curtis and Halford, 2014). In this context, understanding the effect of allelic combinations at *Ppd-1* on flowering time and yield formation under different environmental conditions, through the analysis of the main physiological processes involved, becomes of prime importance to select allelic combinations, or fine tuning phenological development, to maximize yield.

This study was conducted with a set of 34 spring durum wheat genotypes encompassing five of the six possible allelic combinations at *Ppd-A1* and *Ppd-B1* loci to estimate the contribution of current photosynthesis after flowering and translocation of stored reserves accumulated in vegetative organs prior to flowering on grain yield, as it is affected by flowering time.

2. Materials and methods

2.1. Plant material

Thirty-four spring durum wheat (*Triticum turgidum* L. var. *durum*) genotypes were used in this study. Thirty inbred lines resulted from a divergent selection process within the offspring of crosses between parents with contrasting flowering time. Five late-flowering German genotypes provided by the University of Hohenheim, Stuttgart, Germany ('Durabon', 'Megadur', 2716-25.94.01, 2805-49.94.02 and 2905-13.93-04), were crossed with five early-flowering advanced lines (Sooty_9/Rascon_37, Cado/Boomer_33, Dukem_12/2*Rascon_21, 'Guanay' and 'Snitan') from the CIMMYT (International Centre for Wheat and Maize Improvement, Mexico) durum wheat breeding program. The F_1, F_2 and F_3 populations were advanced in bulk at CIMMYT. From each F_4 population, an early-flowering and a late-flowering plants were selected in order to capture the maximum range for time to flowering. From generations F_5 to F_7, selected lines were selfed, purified and increased at the Institute for Food and Agricultural Research and Technology (IRTA) in Spain. At generations F_8 and F_9, the seed of fixed lines with contrasting flowering dates was used in field experiments. Two additional CIMMYT sister lines, derived from the cross CF4-JS 40/3/Stot//Altar84/Ald, and two commercial cultivars ('Simeto' and 'Anton') were also included in the collection.

The selected genotypes were analysed with a set of molecular markers associated with key *Vrn* and *Ppd* alleles as described in Royo et al. (2016). The molecular characterization revealed that all of the 34 genotypes were spring types, carrying the dominant allele *Vrn-A1c* with a deletion in intron-1 of *Vrn-A1* (Yan et al., 2004), and the recessive alleles *vrn-B1* and *vrn-B3* (Fu et al., 2005; Yan et al., 2006). The analysis of the allelic composition for *Ppd-1* identified three alleles at *Ppd-A1* (i.e. *Ppd-A1b* conferring photoperiod sensitivity in 16 genotypes, and alleles 'GS-105′ and 'GS-100′ causing photoperiod insensitivity in 12 and 6 genotypes, respectively), and two alleles at *Ppd-B1* (the wild-type allele *Ppd-B1b* conferring photoperiod sensitivity in 13 genotypes, and the mutation conferring photoperiod insensitivity *Ppd-B1a* in 21 genotypes (Table 1). Details on the allelic combinations present on each genotype at *Ppd-A1* and *Ppd-B1* loci is shown in Supplementary Table 1.

2.2. Experimental details

Field experiments were conducted in 2007 and 2008 at three sites, two in Spain: Lleida in the north (Spain-North), and Jerez de la Frontera

Table 1
Mean phenotypic values of 34 durum wheat genotypes classified according allelic combinations for *Ppd-A1/Ppd-B1* loci across three sites (Spain-North, Spain-South, and Mexico) and two years (2007 and 2008). (S) and (I) stand for sensitive and insensitive photoperiod response, respectively. DM_F = dry matter at flowering, DMT = dry matter from translocation, DMP = dry matter in grain from current photosynthesis during grain filling, and CT = contribution of pre-anthesis assimilates to grain yield.

Ppd-A1 allele[1]	*Ppd-B1* allele	Acronym	Number of lines	Days emergence-flowering	Yield ($g\ m^{-2}$)	DM_F ($g\ m^{-2}$)	Harvest index	DMT ($g\ m^{-2}$)	DMP ($g\ m^{-2}$)	CT (%)
Ppd-A1b (S)	*Ppd-B1a* (I)	SI	9	117^{a}	597^{b}	1019^{b}	0.456^{b}	316^{a}	282^{b}	54.5^{a}
Ppd-A1b (S)	*Ppd-B1b* (S)	SS	7	117^{a}	622^{b}	1077^{a}	0.456^{b}	328^{a}	294^{b}	53.6^{a}
GS-105 *Ppd-A1a* (I)	*Ppd-B1b* (S)	I5S	6	112^{b}	611^{b}	991^{c}	0.470^{a}	315^{a}	296^{b}	52.6^{a}
GS-105 *Ppd-A1a* (I)	*Ppd-B1a* (I)	I5I	6	107^{c}	623^{b}	971^{c}	0.467^{ab}	251^{b}	372^{a}	42.9^{b}
GS-100 *Ppd-A1a* (I)	*Ppd-B1a* (I)	I0I	6	105^{d}	664^{a}	975^{c}	0.478^{a}	260^{b}	404^{a}	40.8^{b}

Means within columns with the same superscript latin letters are not significantly different ar $P < 0.05$

[1] Nomenclature described in Wilhelm et al. (2009).