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Effect of allele combinations at *Ppd-1* loci on durum wheat grain filling at contrasting latitudes

Jose M. Arjona[1] (iD) | Conxita Royo[1] (iD) | Susanne Dreisigacker[2] (iD) | Karim Ammar[2] |
Joan Subirà[1] | Dolors Villegas[1] (iD)

[1]Sustainable Field Crops Programme, Institute for Food and Agricultural Research and Technology (IRTA), Lleida, Spain

[2]International Maize and Wheat Improvement Centre (CIMMYT), Mexico City, Mexico

Correspondence
Dolors Villegas, Sustainable Field Crops Programme, Institute for Food and Agricultural Research and Technology (IRTA), Lleida, Spain.
Email: dolors.villegas@irta.cat

Abstract

Flowering time is the most critical developmental stage in wheat, as it determines environmental conditions during grain filling. Thirty-five spring durum genotypes carrying all known allele variants at *Ppd-1* loci were evaluated in fully irrigated field experiments for three years at latitudes of 41°N (Spain), 27°N (northern Mexico) and 19°N (southern Mexico). Relationships between weight of central grains of main spikes (W) and thermal time from flowering to maturity were described by a logistic equation. Differences in flowering time between the allele combination causing the earliest (GS100/*Ppd-B1a*) and the latest (*Ppd-A1b/Ppd-B1a*) flowering were 7, 20 and 18 days in Spain, northern Mexico and southern Mexico, respectively. Flowering delay drastically reduced the mean grain filling rate (R) and W at all sites. At autumn-sowing sites, an increase of 1°C in mean temperature during the first half of the grain filling period decreased W by 5.2 mg per grain. At these sites, W was strongly dependent on R. At the spring-sowing site (southern Mexico), W depended on both R and grain filling duration. Our results suggest that incorporating the allele combinations GS100/*Ppd-B1a* and GS105/*Ppd-B1a* (alleles conferring photoperiod insensitivity) in newly released varieties can reduce the negative effects of climate change on grain filling at the studied latitudes.

KEYWORDS
flowering time, grain filling rate, grain weight, photoperiod sensitivity, solar radiation, temperature

1 | INTRODUCTION

Wheat is one of the staple foods of humankind, with global consumption during the last ten years reaching around 700 million tons per year. About 10% of total wheat production corresponds to durum wheat (*Triticum turgidum* L. var. *durum*) (Kantety, Diab, & Sorrells, 2005). Though a record wheat production was achieved in 2018, the forecast for 2019 suggests that use will exceed production

(FAO, 2018). In most wheat-growing regions, around 36% of the annual variation in grain yield can be explained by climate changes (Ray, Gerber, MacDonald, & West, 2015). The mean temperature of the Earth's surface has increased by between 0.8 and 1.2°C since the second half of the 18th century, and climate change models predict a mean increase of 0.2°C per decade in the next century (Allen et al., 2018). It has been estimated that an increase of 1°C could reduce wheat production by 6% (Asseng et al., 2015), so a decrease in wheat

TABLE 1 Allele combinations for *Ppd-A1* and *Ppd-B1* loci present in the collection of 35 durum wheat genotypes used in the current study, acronyms used and frequencies within the collection

Allele combination acronym	Number of genotypes	*Ppd-A1*		*Ppd-B1*	
		Allele[a]	Photoperiod response	Allele	Photoperiod response
I0I	5	GS−100/*Ppd-A1a*	Insensitive	*Ppd-B1a*	Insensitive
I5I	7	GS−105/*Ppd-A1a*	Insensitive	*Ppd-B1a*	Insensitive
I5S	10	GS−105/*Ppd-A1a*	Insensitive	*Ppd-B1b*	Sensitive
SI	5	*Ppd-A1b*	Sensitive	*Ppd-B1a*	Insensitive
SS	8	*Ppd-A1b*	Sensitive	*Ppd-B1b*	Sensitive

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

stocks is expected in the future. Continuous efforts in crop and specifically yield improvement are therefore required (FAO, 2018).

Grain number per unit land and grain weight are the main components of wheat yield. Grain weight is not only an essential yield component but also an important quality trait that interacts with other quality standards, such as protein content and yellowness, which are usually negatively correlated with grain weight (Rharrabti, Villegas, Royo, Martos-Núñez, & García del Moral, 2003). Grain weight is also highly correlated with flour and semolina yield, bigger grains having higher milling yields per kg of grain than smaller grains (Baasandorj, Ohm, Manthey, & Simsek, 2015; Matsuo & Dexter, 1980).

In the context of climate change, yield reductions will be led by a significant decrease in one or both yield components. Reductions in grain number per unit land area due to an increase in temperature have been widely reported, as has a reduction in grain weight, which depends on the conditions before flowering and during grain filling (Bergkamp, Impa, Asebedo, Fritz, & Jagadish, 2018; Ferris, Ellis, Wheeler, & Hadley, 1998; Hlaváčová et al., 2018; Prasad, Pisipati, Momčilović, & Ristic, 2011; Terrile, Miralles, & González, 2017; Ugarte, Calderini, & Slafer, 2007). Although the environmental conditions in the pre-flowering period can have an effect on grain weight (Ugarte et al., 2007), the grain filling period is considered critical for the final grain weight (Royo et al., 2006). The two components of the grain filling period are the mean rate of grain filling (R) and the grain filling duration. Weather conditions such as drought and heat stress can modify the duration and the rate of grain filling. Crop senescence is usually accelerated and the starch accumulation phase is shortened, so R is reduced (Bergkamp et al., 2018; Dias & Lidon, 2009; García, Serrago, Dreccer, & Miralles, 2016; Royo et al., 2006). The effect of heat stress induced either during a short period of time or extended throughout the grain filling has been studied under controlled and semi-controlled conditions (Bergkamp et al., 2018; Dias & Lidon, 2009; Shirdelmoghanloo, Cozzolino, Lohraseb, & Collins, 2016). However, field studies analysing the effect of flowering date on grain filling are lacking in durum wheat.

Strategies that could be followed to improve grain filling in wheat under climate change conditions include the development of heat-tolerant varieties and the use of avoidance mechanisms (Shavrukov et al., 2017). The most common among these are (a) adapting sowing

dates to allow the crop to fill its grains under favourable environmental conditions (Ortiz-Monasterio, Dhillon, & Fischer, 1994) and (b) adjusting wheat phenology by modifying alleles of major genes responsible for crop development. Flowering time is controlled in wheat by three groups of loci affecting vernalization requirement (*VRN*), photoperiod sensitivity (*Ppd-1*) and earliness per se (*Eps*). Though vernalization genes exert the greatest influence on crop phenology (Kamran, Iqbal, & Spaner, 2014), most cultivated durum wheat has a spring growth habit, so flowering time is controlled by *Ppd-1* and *Eps* genes.

In spring durum wheat, there are two known genes of photoperiod response (*Ppd-1*), *Ppd-A1* and *Ppd-B1*, located in chromosome 2 of the A and B genomes, respectively (Maccaferri et al., 2008; Wilhelm, Turner, & Laurie, 2009). It has been reported that *Ppd-A1* insensitive alleles shorten the pre-flowering phase to a greater extent than the insensitive allele of *Ppd-B1* (*Ppd-B1a*), which in turn shortens pre-flowering time in comparison with the sensitive alleles of both genes at low to medium latitudes (Royo, Dreisigacker, Alfaro, Ammar, & Villegas, 2016). It is also known that *Ppd-A1a* 'GS100' allele has a stronger effect than *Ppd-A1a* 'GS105' (Arjona, Royo, Dreisigacker, Ammar, & Villegas, 2018; Royo et al., 2016; Wilhelm et al., 2009).

The objective of this study was to explore the effect of *Ppd-1* genes on durum wheat development and yield formation at a range of northern latitudes. Results regarding the effect of *Ppd-1* genes on flowering time (Royo et al., 2016), yield formation (Arjona et al., 2018; Royo et al., 2018) and yield constraints induced by environmental features (Villegas et al., 2016) have been published previously. As the shortening of the pre-flowering phase due to the presence of alleles causing photoperiod insensitivity may modify the environmental conditions after flowering, this study was carried out to examine the effect of allele combinations at *Ppd-1* loci on grain filling in durum wheat.

2 | MATERIALS AND METHODS

2.1 | Plant material

Thirty-five spring durum wheat genotypes were used in this study (Table S1). The genotypes included 5 late-flowering German varieties and inbred lines from the University of Hohenheim, 5

TABLE 2 Location and environmental descriptions of the three experimental sites

| Site | Location (state or province) | Experimental station (institution's acronym) | Coordinates | | Altitude (m.a.s.l) | Environmental characteristics |
			Lat	Long		
Spain	Gimenells, (Lleida)	Gimenells (IRTA)	41°38'N	0°23'E	200	Moderate terminal stress. High-to-medium productivity
Northern Mexico	Cd. Obregón, (Sonora)	CENEB (CIMMYT)	27°21'N	109°54'W	40	Very high terminal stress. Mandatory full irrigation. Very high productivity
Southern Mexico	El Batán, (Mexico)	El Batán (CIMMYT)	19°31'N	98°50'W	2,249	Initial stress eliminated with irrigation. Medium productivity
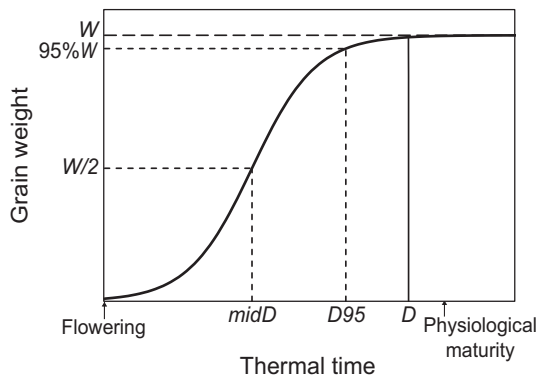
FIGURE 1 Representation of the logistic curve: *D95*, point where 95% of *W* is reached; *D*, total grain filling duration; *W*, asymptote value; and *W/2*, inflection point, where half the asymptote value is reached and corresponds to mid-duration of grain filling (*midD*)

early-flowering inbred lines from the CIMMYT-Mexico breeding programme, and 25 lines obtained from crosses between a late genotype (used as a female parent) and an early genotype (used as a pollen donor). The set of markers and the methodologies used for the molecular characterization of the collection at *Vrn-1* and *Ppd-1* loci are described in Royo et al. (2016). The results revealed that the 35 genotypes used in this study were spring types, carrying the dominant allele *Vrn-A1c*. For *Ppd-1* allele combinations, 8 genotypes carried the alleles conferring photoperiod sensitivity and 12 carried the mutations conferring photoperiod insensitivity at both *Ppd-1* loci (*GS100/Ppd-A1a* and *Ppd-B1a*; *GS105/Ppd-A1a* and *Ppd-B1a*). Fifteen genotypes carried the photoperiod-insensitive allele only at one of the two loci (Table 1).

2.2 | Field experiments and phenotypic measures

Nine field experiments were conducted at three sites with contrasting latitude: 41°N (Spain), 27°N (northern Mexico) and 19°N (southern Mexico) (Table 2) during the growing seasons in the years 2010, 2011 and 2012. The experiments consisted of field plots of 12 m^2 size with three replicates, arranged in a randomized

complete block design. The plots were kept free of diseases, weeds and pests and were fully irrigated. Field management was conducted according to standard agronomic practices at each site. Sowing density was fitted to obtain an approximate density of 450 spikes/m^2. The six experiments performed in Spain and northern Mexico were autumn-sowing (17 November–23 December), while in southern Mexico the experiments were spring-sowing (17–28 May). Daily maximum, minimum and mean temperatures (°C), as well as solar radiation (MJ/m^2 day^{-1}), were recorded during the entire crop cycle with meteorological stations located on the field or nearby.

Zadoks, Chang, and Konzak (1974) growth stages 65 (flowering) and 87 (physiological maturity) were determined for each plot. At flowering, up to 60 main spikes in synchronous development and with similar size were tagged in the central part of each plot. On a weekly basis, five tagged spikes were removed at random, and six grains per spike were extracted from the central spikelets of each spike. The grains were oven-dried for 48 hr at 70°C and weighed with a precision scale (Mettler B-2002-S). For each plot, thermal time (growing degree days, GDD) was calculated from flowering to physiological maturity, assuming a base temperature of 9°C and a maximum temperature of 37°C (Weir, Bragg, Porter, & Rayner, 1984).

In each experiment, changes in dry weight per grain were fitted for each individual plot to a logistic model with three parameters (Figure 1), chosen on the basis of previous studies (Robert, Huet, Hennequet, & Bouvier, 1999) and with the modification suggested by Davidian and Giltinan (1995). The model (Equation 1) was fitted with the 'NLIN' procedure and the Marquardt method of the SAS software (SAS RRID:SCR_008567, 2009):

$$GW_{ij} = \frac{W_i}{1 + \exp\{-Rt_i(x_{ij} - midD_i)\}} \quad (1)$$

where

　　GW_{ij} is the weight of the grain for a sample *i* at time *j*;

　　W_i is the asymptote of the curve for sample *i*;

　　Rt_i is the factor that relates in constant proportion the growing rate and the current size of sample *i*;

　　x_{ij} are the growing degree days of sample *i* at time *j*; and

TABLE 3 Percentage of the sum of squares (SS) of the ANOVA for the number of days from emergence to flowering, and results of MANOVA for the curve coefficients final grain weight (*W*), mean rate of grain filling (*R*) and thermal time from flowering to 95% *W* (*D95*)

| Source of variation | ANOVA (days emergence to flowering) | | MANOVA (*W, R, D95*) | | | | |
	%SS	−Log *P*	Wilks' λ	*F*	*n*	*d*	−Log *P*
Site	84.7	>999	0.024	1,096.95	6	1,194	>999
Year	3.2	>999	0.144	325.56	6	1,194	246
Site × Year	6.1	>999	0.050	277.73	12	1,579.8	>999
Genotype	4.4	>999	0.016	52.24	102	1,788.5	>999
Between *Ppd-1*	58.5	7.6	0.148	139.33	12	1,579.8	237
Within Genotype(*Ppd-1*)	41.5	>999	0.022	50.81	90	1,787.5	>999
Site × Genotype	1.2	>999	0.078	11.75	204	1,791.1	214
Site × *Ppd−1*	36.0	4.2	0.390	27.67	24	1,732.1	103
Site × Genotype(*Ppd-1*)	64.0	>999	0.132	9.62	180	1,790.8	162
Year × Genotype	0.2	141.5	0.100	10.15	204	1,791.1	186
Year × *Ppd-1*	42.8	6.1	0.534	17.44	24	1,732.1	64
Year × Genotype(*Ppd-1*)	57.2	96.5	0.139	9.25	180	1,790.8	155
Site × Year ×Genotype	0.2	141.2	0.038	8.62	408	1,791.8	232
Site x Year × *Ppd-1*	28.9	4.2	0.400	13.35	48	1,776.4	87
Site × Year ×Genotype(*Ppd-1*)	71.1	114.4	0.056	8.04	360	1,791.7	203
Rep(Site × Year)	0.0	5.5	0.887	1.35	54	1,779.6	1

Abbreviations: d, degrees of freedom of the denominator; *n*, degrees of freedom of the numerator.

$midD_i$ is the value of growing degree days at the inflection point of the curve (mid-point of duration of the grain filling).

Final grain weight (*W*) was estimated in mg. Grain filling duration (*D95*) was considered to be the thermal time (GDD) required for grain weight to reach 0.95 W. The mean rate of grain filling (*R*, mg GDD^{-1}) was calculated as $R = W/D$.

2.3 | Statistical analyses

Combined ANOVA across sites (latitudes), experiments, years and genotypes were performed using a fixed model to analyse the number of days from emergence to flowering and from flowering to physiological maturity, as well as the mean temperature and solar radiation from flowering to *midD*. The genotype effect was partitioned into differences between allele combinations at the *Ppd-1* loci and differences between genotypes within each allele combination. This last factor was considered as the error term used to test differences between allele combinations (SAS Institute Inc., 2010). Multivariate analysis of variance (MANOVA) was used to analyse *W*, *R* and *D95* to deal with the association between variables. The GLM procedure of the SAS software (SAS RRID:SCR_008567, 2009) was used for these analyses, and the Wilks lambda (λ) values and the log *P* for the *F*-values were obtained. Means of allele combinations were compared using the protected Fisher's least significant differences method at *P* = .05. A photo-thermal ratio was calculated at each site for the first part of the grain filling period (flowering to *midD*) as the ratio between solar radiation and temperature (MJ m^{-2} day^{-1}°C^{-1}). Linear regression equations were used to study the relationships between variables at each site (JMP RRID:SCR_008567 14242, 2007).

3 | RESULTS

3.1 | Phenology

The ANOVA for the number of days from emergence to flowering revealed that all factors in the analysis were statistically significant, but the site effect explained most of the variation of the model (84.7%), followed by the site × year interaction (6.1%) and the genotype (4.4%) effect (Table 3). Differences between allele combinations accounted for 58.5% of the variation induced by the genotype and 2.6% of the total variation of the model, while the site × allele combination interaction explained 36% of the site × genotype interaction (Table 3).

On average across sites and years, the number of days from emergence to flowering ranged from 90 for the allele combination I0I to 105 for the combination SI (Table 4). The same pattern of flowering delay derived from photoperiod-sensitive alleles was observed at each site. Differences in the number of days to flowering between the allele combinations showing the earliest and the latest flowering dates were 7 days in Spain, 20 days in northern Mexico and 18 days in southern Mexico. At all sites, allele combinations I0I, I5I and I5S led to similar earlier flowering dates in comparison with allele combinations SS and SI. Only in southern Mexico were flowering dates of allele combinations SI and SS significantly different (Table 4).

TABLE 4 Mean values for each allele combination at *Ppd-1* across sites and at each site for days from emergence to flowering, final grain weight (*W*), mean rate of grain filling (*R*), thermal time from flowering to 95% *W* (*D95*), days from flowering to 95% *W*, mean temperature and mean solar radiation from flowering to mid–grain filling duration (*midD*). See Table 1 for acronym list

Ppd-1 allele combination	Days emergence to flowering	W (mg)	R (mg GDD⁻¹)	D95 (GDD)	Days to D95	Mean temperature from flowering to *midD* (°C)	Mean solar radiation from flowering to *midD* (MJ m⁻² day⁻¹)
IOI	90 b	55.7 a	0.140 a	366 a	41.5 a	17.2 b	23.5 b
ISI	94 b	55.0 a	0.139 a	362 a	40.6 a	17.5 b	23.7 b
ISS	94 b	51.3 a	0.132 a	362 a	40.2 a	17.5 b	23.8 b
SS	100 a	49.8 a	0.125 a	367 a	39.5 ab	18.0 a	24.2 a
SI	105 a	46.7 a	0.120 a	358 a	37.9 b	18.4 a	24.3 a
Ppd-1 × site interaction							
Spain							
IOI	132 b	55.3 a	0.150 a	350 a	35.0 a	17.6 d	25.9 c
ISI	134 b	55.9 a	0.152 a	345 a	33.7 a	18.2 cd	26.3 b
ISS	135 b	54.2 a	0.150 a	345 a	33.6 a	18.2 bc	26.3 b
SS	138 a	53.0 a	0.139 a	360 a	34.3 a	18.8 ab	26.6 a
SI	139 a	51.5 a	0.134 a	360 a	33.9 a	19.3 a	26.8 a
Northern Mexico							
IOI	81 b	59.9 a	0.140 a	388 a	41.7 a	17.5 b	24.2 b
ISI	85 b	59.3 ab	0.139 ab	386 a	40.1 ab	17.8 b	24.5 b
ISS	87 b	54.6 abc	0.129 abc	388 a	39.7 ab	17.9 b	24.8 b
SS	95 a	52.7 bc	0.124 bc	395 a	37.4 bc	18.7 a	25.9 a
SI	101 a	49.5 c	0.116 c	395 a	35.1 c	19.2 a	26.6 a
Southern Mexico							
IOI	58 c	51.9 a	0.129 a	361 a	48.0 a	16.4 a	20.5 a
ISI	62 bc	49.8 ab	0.127 a	356 a	48.0 a	16.4 a	20.3 a
ISS	62 bc	45.1 bc	0.117 a	353 a	47.3 a	16.5 a	20.3 a
SS	67 b	43.7 bc	0.113 a	347 a	46.6 a	16.5 a	20.1 a
SI	76 a	39.4 c	0.110 a	321 a	44.6 a	16.6 a	19.6 a

Note: Different letters within columns and sites indicate significant differences according to protected Fisher's least significant difference at $p = .05$.

TABLE 5 Summary of the regression models fitted to the relationships between variables

Dependent variable	Independent variable	Spain			Northern Mexico			Southern Mexico		
		b	SE	R^2	b	SE	R^2	b	SE	R^2
W	$Days_{EF}$	−0.95	0.201	0.40***	−0.59	0.091	0.56***	−0.57	0.090	0.55***
R	$Days_{EF}$	−0.00028	0.0005	0.51***	−0.0012	0.0002	0.47***	−0.0009	0.0003	0.25**
D95	$Days_{EF}$	0.14	0.66	0.01^{ns}	0.23	0.32	0.02^{ns}	−2.19	0.38	0.50***
W	R	355	28.0	0.82***	409	31.2	0.84***	382	38.3	0.75***
W	D95	0.108	0.066	0.07^{ns}	0.001	0.074	0.01^{ns}	0.127	0.038	0.04**

Abbreviations: D95, thermal time from flowering to 95% W (GDD); $Days_{EF}$, number of days from emergence to flowering; R, mean rate of grain filling (mg GDD^{-1}); W, final grain weight (mg grain^{-1}). Genotype mean data across years was used at each site ($n = 35$). The slope of the linear regression equation (b), its standard error (SE), the coefficient of determination (R^2) and the statistical significance (*$p < .05$; **$p < .01$; ***$p < .001$; ^{ns} $p > .05$) are shown.

3.2 | Grain filling curve coefficients

The results of MANOVA showed that although all effects and interactions were statistically significant, the site, year and genotype effects and the site × year interaction resulted in a p-value close to zero (Table 3). Mean values of the allele combinations across sites and years showed no significant statistical differences for W, R or D95 (Table 4). However, differences between allele combinations were significant in northern Mexico for W and R and in southern Mexico for W, with the allele combinations leading to an earlier flowering date showing higher values for both coefficients. All allele combinations led to a similar D95 at all sites (Table 4).

3.3 | Relationships between traits

Exploring the relationships between flowering time and the coefficients in the grain filling curve revealed that flowering time accounted for 40%–56% of W variations depending on the site (Table 5). The values of the slopes of the regression equations fitted to these relationships indicated that each day of delay in flowering resulted in a decrease of 0.57 mg per grain in southern Mexico and 0.95 mg per grain in Spain. In northern Mexico and Spain, this was due to a significant reduction in R, as D95 was not significantly affected by flowering time. However, in southern Mexico both W and R were significantly reduced when flowering date was delayed (Table 5).

Variations in R explained 75%–84% of W, depending on the site. Grain filling duration had no effect on W at the two autumn-sowed sites, but a longer grain filling period significantly increased W in southern Mexico (Table 5).

3.4 | Allele combinations and associated environmental conditions during grain filling

The ANOVA revealed that the allele combination affected flowering time and thus the mean temperature and solar radiation during the first half of the grain filling period of the crop (Table 4). On average across sites and years, genotypes carrying allele combinations SS and SI received higher temperatures and solar radiation levels during the first part of the grain filling period than genotypes carrying allele combinations I0I, I5I and I5S. Though this tendency was observed at the two autumn-sowing sites, it was not observed in southern Mexico, where allele combinations did not significantly affect temperature or solar radiation to *midD* (Table 4).

To further explore the influence of flowering time on the shift of temperature and solar radiation during the first half of the grain filling period, regression models were fitted for each site to the relationships between them, and the same methodology was used subsequently to analyse the effect of the two environmental variables on R and W. The results showed that, in Spain and northern Mexico, flowering delay increased significantly the temperature and solar radiation to *midD* and reduced R and W drastically (Figures 2 and 3). The slopes of the regression equations showed that each day of delay in flowering time caused an increase in the mean temperature
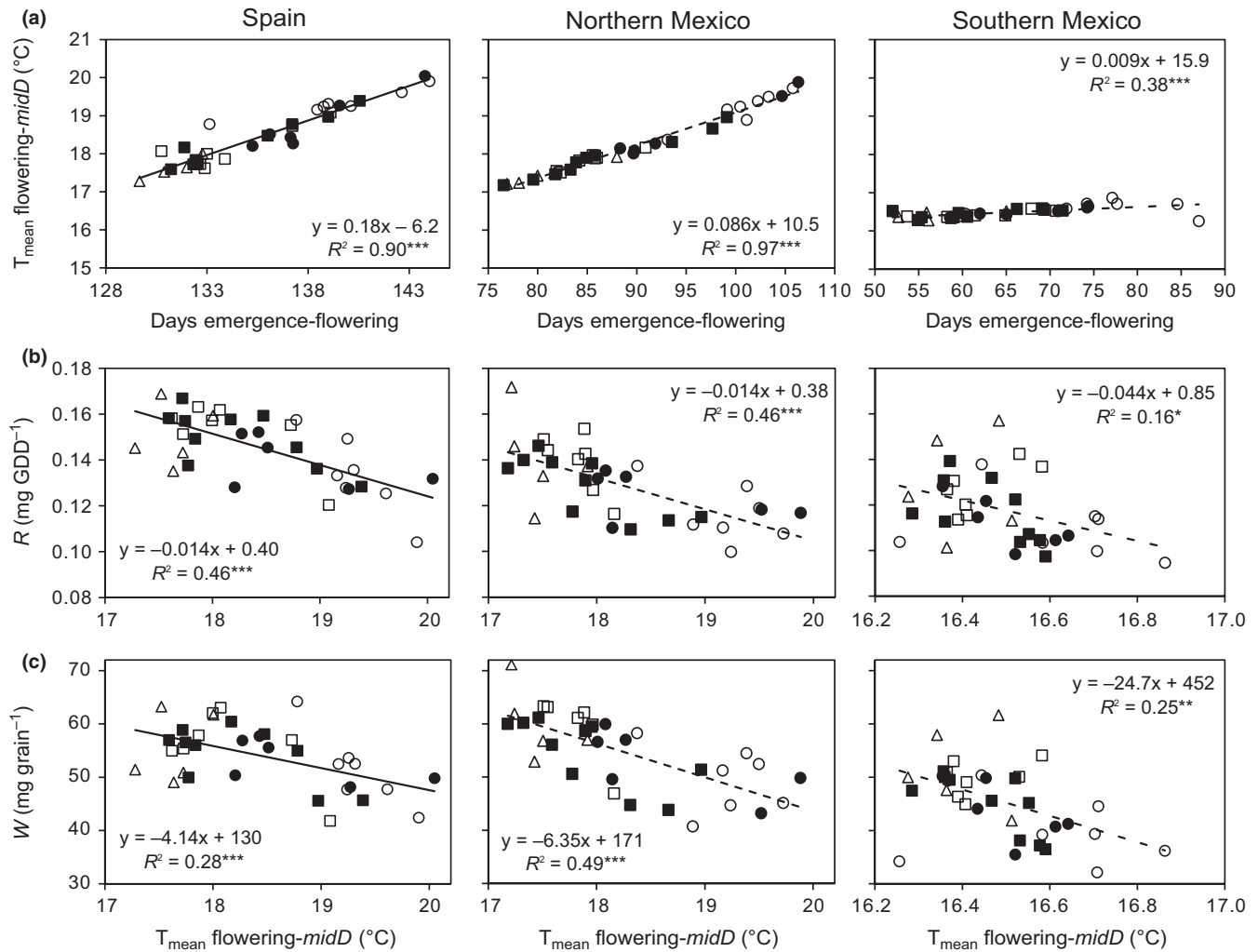
FIGURE 2 Relationships between (a) days from emergence to flowering and mean temperature (Tmean) from flowering to mid-grain filling (*midD*), (b) Tmean from flowering to *midD* and mean grain filling rate (*R*) and (c) Tmean from flowering to *midD* and final grain weight (*W*) in field experiments conducted in Spain (— continuous line), northern Mexico (---) and southern Mexico (- - -), involving 35 durum wheat genotypes grouped according to their allele combination at *Ppd-A1* and *Ppd-B1* loci. Allele combinations are represented according to the acronyms shown in Table 1 as △ = I0I, □ = I5I, ■ = I5S, ● = SS, ○ = SI. *$p < .05$; ** $p < .01$; *** $p < .001$

during the first half of the grain filling period of 0.18°C in Spain and 0.09°C in northern Mexico (Figure 2a). Moreover, an increase of 1°C in this period caused a decrease in *R* of 0.014 mg GDD^{-1} at both sites (Figure 2b) and a decrease in *W* of 4.14 mg per grain in Spain and 6.35 mg per grain in northern Mexico (Figure 2c). In southern Mexico, genotypes consistently experienced the lowest temperatures during *midD*. At this site, a delay in flowering time did not always cause a clear pattern of temperature increase. However, mean data across years revealed a temperature increase of about 0.01°C per day (Figure 2a). The effect of this temperature increase was also year-dependent, but on average it was associated with higher decreases of *R* and *W* than in the other two sites. However, the model was not as explanatory as in Spain and northern Mexico, with a worse R^2 value (Figure 2b,c).

A longer pre-flowering period significantly increased the solar radiation during *midD*, which had a similar effect as temperature on reducing *R* and *W* in both Spain and northern Mexico

(Figure 3a–c). In southern Mexico, the effect of flowering delay on solar radiation depended on the year. However, data across years showed significant increases in *R* and *W* as solar radiation increased (Figure 3b,c).

Given that both temperature and solar radiation significantly affected *R* and *W* at all sites, we tried to ascertain which of them had the greatest effect at each site. For this purpose, the relationship between the photo-thermal ratio during *midD* and *W* was calculated at each site with the mean values of each allele combination across genotypes and years. The results showed that the relationships were significant and positive in Spain and southern Mexico, with the allele combinations causing a regular decrease in the photo-thermal ratio associated with a delay in flowering time (Figure 4). At these two sites, the photo-thermal coefficient increased steadily for genotypes with allele combinations SI to I0I, but in northern Mexico, it was similar for all five combinations (Figure 4).
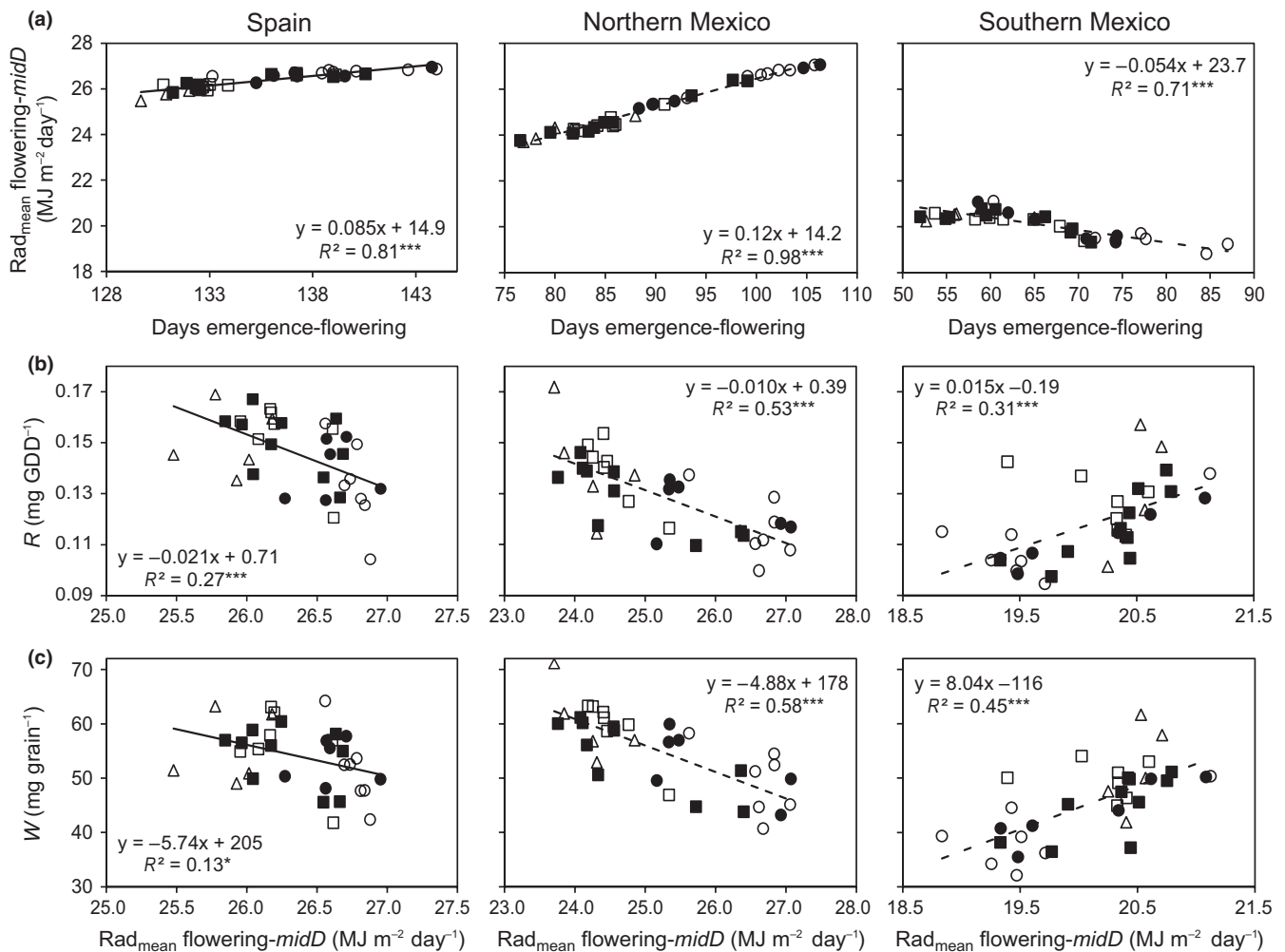
FIGURE 3 Relationships between (a) days from emergence to flowering and mean radiation (Rad_{mean}) from flowering to mid-grain filling (*midD*), B) Rad_{mean} from flowering to *midD* and mean grain filling rate (*R*) and C) Rad_{mean} from flowering to *midD* and final grain weight (*W*) in field experiments conducted in Spain (— continuous line), northern Mexico (---) and southern Mexico (- - -), involving 35 durum wheat genotypes grouped according to their allele combination at *Ppd-A1* and *Ppd-B1* loci. Allele combinations are represented according to the acronyms shown in Table 1 as △ = IOI, □ = I5I, ■ = I5S, ● = SS, ○ = SI. * $p < .05$, ** $p < .01$, *** $p < .001$

4 | DISCUSSION

It has been demonstrated that *Ppd-1* genes have a significant influence on flowering time (Royo et al., 2016). Early and late genotypes could be expected to experience different weather conditions close to flowering and during the grain filling period, particularly in environments where springs have an increasing pattern of temperature. Under this assumption, nine experiments were carried out at three contrasting latitudes for three years with the aim of quantifying the effect of allelic combination for *Ppd-1* (*Ppd-A1* and *Ppd-B1*) on grain filling traits and final grain weight.

Two important aspects must be considered when interpreting the results of the current study. First, drought stress was avoided in our experiments, so the impact of temperature and solar radiation on grain filling traits was not associated with water scarcity, as generally occurs in many environments such as the Mediterranean (Royo, Nazco, & Villegas, 2014). Second, it has been reported that grains from the lower and upper parts of main spikes and from spikes at

tillers are more affected by temperature than grains from the centre of the main spikes (Tashiro & Wardlaw, 1990). Therefore, the effect of the allele combinations on *W* described here could underestimate the average grain weight corresponding to all grains and spikes of crop canopies.

The environmental effect on the coefficients of the grain filling curve observed in this study was a consequence of the contrasting latitudes and weather conditions at the experimental sites, such as day-length and temperature during the grain filling period (Villegas et al., 2016). As reported previously, allele variants that cause photoperiod insensitivity exert a significant effect on flowering time (Royo et al., 2016). When we compared the mean values of five allele combinations across sites and years, we observed no significant effect on *W*, *R* or *D95*. The lack of statistical significance was assumed to be due to the great annual variability. Consistent and negative correlations were found between the days from emergence to flowering and *W* and *R* at the three experimental sites, thus indicating that a delay in flowering time significantly reduced *R* and *W*. Although the
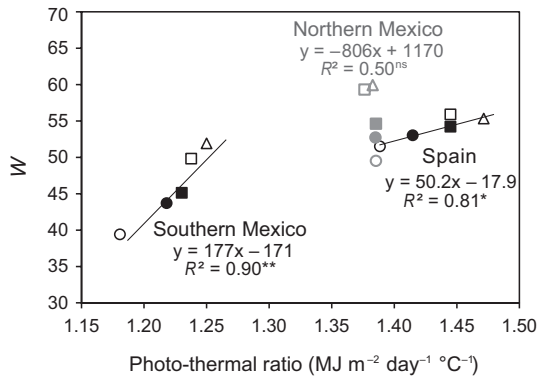
FIGURE 4 Relationship between the photo-thermal ratio from flowering to mid-grain filling (*midD*) and final grain weight (*W*) in field experiments conducted in Spain, northern Mexico and southern Mexico, involving durum wheat genotypes grouped in five allele combinations at *Ppd-A1* and *Ppd-B1* loci. Allele combinations are represented according to the acronyms shown in Table 1 as △ = I0I, □ = I5I, ■ = I5S, ● = SS, ○ = SI. * $p < .05$, ** $p < .01$, *** $p < .001$

differences between allele combinations were not significant for *W* and *R* in Spain, or for *R* in southern Mexico, the tendency was the same at all three sites and across sites. The differences in days to flowering between the allele combinations causing the earliest (I0I) and the latest flowering date (SI) were 7, 20 and 18 days in Spain, northern Mexico and southern Mexico, respectively. The flowering time delay resulted in decreases in *R* of 10.7%, 17.1% and 14.7% in Spain, northern Mexico and southern Mexico, respectively, and decreases in *W* of 6.8%, 17.4% and 24.1% at the same sites. Our results indicated that the effect of the allele combination on flowering time differed between sites, but at all sites the flowering delay reduced *R* and *W*, although with different intensity, so the site × allele combination interaction was quantitative in nature for the two traits.

On the other hand, *D95* measured in thermal time was not affected by flowering time in Spain and northern Mexico, as only small increases in *D95* (≤2.8%) were caused by a flowering delay at these two sites. However, in southern Mexico each day of flowering delay reduced *D95* by 2.19 GDD. The positive and significant relationship between *D95* and *W* found at this site reveals that the short grain filling period of spring planting in southern Mexico constrained the achievement of high grain weight. The analyses of the relationships between *W* and its components, *R* and *D95*, showed that *W* strongly depended on *R* in Spain and northern Mexico, but in southern Mexico the two components were important for final grain weight, though *R* was more important.

The relationship between flowering time, temperature and solar radiation that occurred during the first half of the grain filling period showed clear differences between the two sowing times. In Spain and northern Mexico, where sowing was carried out in autumn, both temperature and solar radiation increased significantly after flowering, and these increases significantly reduced *R* and *W* in the late-flowering genotypes. At the spring-sowing site in southern Mexico, the effect of flowering delay on temperature and solar radiation depended strongly on the year, as it

coincided with the rainy season. However, on average, a slight increase in temperature after flowering also caused reductions in *R* and *W* in the late-flowering genotypes. The negative effect of high temperatures on grain weight has been previously reported in wheat, either durum (Ferrise, Triossi, Stratonovitch, Bindi, & Martre, 2010) or bread wheat (Gibson & Paulsen, 1999; Ortiz-Monasterio et al., 1994; Shirdelmoghanloo et al., 2016; Tashiro & Wardlaw, 1990; Thomason et al., 2018). The effect of temperature on grain development has been deeply studied in bread wheat. Lower grain weight has been attributed to a shorter grain filling period (Bergkamp et al., 2018; García et al., 2016) and to both shorter grain filling periods and lower grain filling rates (Liu et al., 2016). Previous studies conducted in bread and durum wheat also reported lower grain filling rates as a consequence of temperature rises after flowering when grain filling rate was measured in mg GDD⁻¹ (Dias & Lidon, 2009; Liu et al., 2016). However, increased grain filling rates were described when measured in mg day⁻¹ (García et al., 2016; Shirdelmoghanloo et al., 2016). The lower *R* could be due to temperature effects on starch enzymes, stability of membranes and photosynthetic activity (Jener, 1994; Keeling, Banisadr, Barone, Wasserman, & Singletary, 1994; Thomason et al., 2018). The fact that our results agree with the reported by studies conducted on bread wheat indicates that the effect of temperature on grain filling is a general trend for both species. However, the effect of allele combinations presented in this study cannot be translated directly to bread wheat. The absence of the D genome in durum wheat is the main difference, as it has been reported to have the strongest effect on bread wheat development (Beales, Turner, Griffiths, Snape, & Laurie, 2007). While any allele combination leading to earlier flowering time would be desirable both in durum and in bread wheat under the environmental conditions considered in the current study, the specific allele combination would therefore be species-dependent.

The relationship between the photo-thermal ratio and *W* was useful to understand the relative effect of changes in temperature and solar radiation on final grain weight at each site. In Spain, where both temperature and solar radiation increased after flowering, the photo-thermal ratio decreased significantly when flowering was delayed, suggesting that the increase in temperature was more important for reducing *W* than the increase in solar radiation. In northern Mexico, this ratio remained stable independently of the flowering date, which indicates that temperature and radiation had a similar impact on reducing *W*. In southern Mexico, as in Spain, the photo-thermal ratio decreased as flowering was delayed. At this site, both reductions in solar radiation and increases in temperature contributed to the reduction of the photo-thermal ratio, but the greater effect of flowering date on decreasing radiation than on increasing temperature shown by the slopes of the regression models fitted to these relationships suggests that limiting radiation contributed the most to reducing final grain weight at this site. This result is supported by previous studies demonstrating that solar radiation was a limiting factor at the spring-sowing site in southern Mexico (Arjona et al., 2018; Villegas et al., 2016).

The allele combinations I0I and I5I tended to cause the earliest flowering time, hence associated with the most favourable environmental conditions for grain filling and increased *W* values. However, it has been demonstrated that *Ppd-B1a* allele, causing photoperiod insensitivity, reduces the number of grains per unit area (Arjona et al., 2018). Therefore, this should be taken into account in sites where increasing grain number would be desirable. This is the case of the southern Mexico site where the high minimum temperatures cause a very low grain number that constrains yield (Villegas et al., 2016).

This study was carried out at three sites with contrasting conditions of photoperiod, temperature and solar radiation. In order to extrapolate the results to other locations worldwide, it is worth mentioning that the northern Mexico site (CENEB in Ciudad Obregón) has been considered representative of high-yielding irrigated sites. On the other hand, the Spain site (Gimenells) has a typical Mediterranean climate and is representative of the Mediterranean regions, where durum wheat is a widely grown crop (Ammar et al., 2008). Broadly, when facing the unfavourable conditions during and after flowering time predicted by climate change models, two different strategies could be considered to avoid crop stress: tolerance and escape. In this study, we focused on the escape strategy: the early-flowering genotypes performed better in terms of grain filling because of more favourable environmental conditions. An earlier flowering time could also be achieved by an earlier sowing time, but too early sowing may also cause yield reductions caused by frost or unfavourable conditions during the growth cycle (Fischer, 2016; Ortiz-Monasterio et al., 1994). Furthermore, changing the sowing date is not always an option for farmers. It may depend on precipitation after a dry summer, an unsuitable temperature regime or a previous crop still to be harvested. The selection of the optimum sowing date for each particular site will be an important crop operation, jointly with the variety selection for each site.

Fine-tuning flowering time for each site by using developmental important genes such as *Ppd-1* will become one of the important choices in future farming (Wasson et al., 2012). The results obtained in the current study are in line with predicted declines of grain yield in wheat caused by temperature increases as a consequence of climate change (Asseng et al., 2015; Bergkamp et al., 2018; García et al., 2016; Gibson & Paulsen, 1999; Liu et al., 2016; Vignjevic, Wang, Olesen, & Wollenweber, 2015).

On average, across the two autumn-sowing sites, a temperature increase of 1°C during the first half of the grain filling period resulted in a decrease in the mean rate of grain filling of 0.014 mg GDD^{-1} and in a reduction of about 5.2 mg per grain, which is about 10% of the average weight of the grains from the central main spikes. In this context, the late-flowering genotypes would be the most damaged by temperature rises during the grain filling period. Our results therefore suggest that incorporating the allele combinations GS100/*Ppd-B1a* (I0I) and GS105/*Ppd-B1a* (I5I), which confer photoperiod insensitivity, at the two *Ppd-1* loci in newly released varieties could help reduce the negative effects of climate change.

ORCID

Jose M. Arjona [iD] https://orcid.org/0000-0002-7386-1560

Conxita Royo [iD] https://orcid.org/0000-0001-7939-1451

Susanne Dreisigacker [iD] https://orcid.org/0000-0002-3546-5989

Dolors Villegas [iD] https://orcid.org/0000-0003-2961-6346

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