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Research articles

The relationship between allelic variations of *Vrn-1* and *Ppd-1* and agronomic traits in Korean wheat cultivars

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Abstract

The allelic variations at the *Vrn-1* and *Ppd-1* loci of Korean wheat cultivars were determined to evaluate their effects on agronomic traits and response to vernalization treatment. Korean wheat cultivars displayed high frequency of *Vrn-D1a* and *Ppd-B1b* alleles, but all of the tested cultivars carried *vrn-A1, vrn-B1, Ppd-A1b* and *Ppd-D1a* alleles at the corresponding loci. Regardless of vernalization treatments, Korean wheat cultivars carrying the *vrn-D1* allele showed longer days to flag leaf unfolding than those with the *Vrn-D1a* allele. Unvernalized cultivars carrying the *vrn-D1* allele also exhibited larger final leaf number than those with the *Vrn-D1a* allele. However, there were no significant differences in the response of the Korean wheat cultivars to vernalization treatment based on allelic variation at the *Ppd-1* loci. With respect to agronomic traits, the *Vrn-D1a* allele was related to increased grain yield and decreased thousand kernel weight compared to the *vrn-D1* allele. Cultivars carrying both *Vrn-D1a* and *Ppd-B1b* alleles produced higher grain yield (5.5 tons/ha) than those with the *vrn-D1* and *Ppd-B1b* alleles (5.0 tons/ha).

Key words: Wheat, vernalization, photoperiod, allelic variation, agronomic traits

Intorduction

Flowering time in wheat is mainly controlled by vernalization (*Vrn*) and photoperiod (*Ppd*), though flowering time involves complex processes (Karman et al. 2014). These response genes hasten or delay flowering in response to environmental stimuli, through which floral initiation is determined by their interactions with growth temperatures and photoperiod. *Vrn* and *Ppd* genes control flowering time of wheat in response to specific day length and temperature (Karman et al. 2014). Growth habits of wheat, either demonstrating sensitivity or insensitivity to vernalization, are mainly controlled by allelic variation at the *Vrn-1*, *Vrn-2*, *Vrn-3* and *Vrn-4* loci (Yoshida et al. 2010). Spring and facultative growth habits are manifested by the presence of one or more dominant alleles at *Vrn-1*, *Vrn-2, Vrn-3* or *Vrn-4* loci, whereas winter wheats tend to possess dominant alleles at the *Vrn-2* locus (Distelfeld et al. 2009). *Vrn-1* alleles include three orthologous genes, *Vrn-A1*, *Vrn-B1*, and *Vrn-D1,* located on chromosomes 5A, 5B and 5D, respectively. The *Vrn-2* alleles, *Vrn-A2* and *Vrn-B2*, were also mapped to chromosome 5, except in 5B in diploid and tetraploid wheat, while the *Vrn-3* alleles were mapped to chromosome 7 in hexaploid wheat (Distelfeld et al. 2009). *Vrn-3* alleles promote the transcription of *Vrn-1* alleles thereby accelerating flowering in wheat, but limited information is available on the *Vrn-4* alleles, though the *Vrn-D4* allele loci was mapped to chromosome 5D (Yoshida et al. 2010; Kippes et al. 2014). The spring habit allele, *Vrn-A1a,* is predominant in wheat cultivars grown at high latitudes and Indian spring wheat cultivars, while the *Vrn-D1* allele is predominantly found in cultivars from Asia, including Indian, Japanese and Chinese landraces, and particularly in sub-tropical regions where long growing seasons occur (Iwaki et al. 2000, 2001; Kumar et al. 2012).

Ppd genes play a key role in causing acceleration or delay of heading time under field conditions in vernalized wheats (Snape et al. 2001). The *Ppd-1*

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genes, well-known for their association with accelerating flowering under short photoperiods, are located on the homoeologous group 2 chromosomes, and include *Ppd-A1*, *Ppd-B1* and *Ppd-D1*, located on chromosomes 2A, 2B and 2D, respectively. Genes located on chromosome 1 are generally associated to delay heading in response to both vernalization and photoperiod, while a photoperiod insensitive genes are located on chromosome 3D (Snape et al. 2001). These genes play an important part in accelerating or delaying flowering time in the field. Under hot and dry summer conditions, as is usual in Southern and Eastern Europe, cultivars carrying photoperiod insensitive alleles displayed earlier flowering date and larger grains than cultivars with photosensitive alleles, consequently showing significantly higher yields (Snape et al. 2001). The pleiotropic influence of the *Ppd-D1* gene on the yield potential of the major wheat growing regions of Europe could be involved in reducing flowering time, plant height and number of spikelets per spike (Karman et al. 2014).

Early flowering time, with high grain yield, has been the most important selection target in Korean wheat breeding programs, because the harvest time of wheat overlapped with the rainy seasons and time for rice transplantation in Korea. However, the genetic information on Korean wheat cultivars relating to early flowering time is not yet available. Therefore, this study was conducted to investigate the distribution of *Vrn-1* and *Ppd-1* alleles in Korean wheat cultivars using molecular markers, and to elucidate the relationship between agronomic traits and allelic variation of these genes.

Materials and methods

Plant materials

Twenty-five Korean wheat cultivars were sown in randomized complete blocks with 3 replicates in the Upland Crop Experimental Farm of the National Institute of Crop Science, Rural Development Administration (Korea) for two years, from 2010/2011 to 2011/2012, on 50% clay loam soil. The seeds were sown on October 25. Each plot consisted of three 2-m rows spaced 25 cm apart, and plots were combine-harvested on June 20 each year.

Agronomic traits

Agronomic traits, including days to heading date and maturing date, kernel number per spike, and thousand kernel weight, were determined by the procedure described by Lee et al. (2014).

Response to vernalization treatment

Two sets of 25 Korean wheat cultivars were sown in pots and grown at 20°C with a photoperiod of 8 hours light/16 hours dark in greenhouse conditions for ten days. One set of cultivars continued to be grown at 20°C for the non-vernalization treatment with a photoperiod of 8 hours light/16 hour dark in greenhouse conditions until spike exertion. The other set of cultivars was transferred to a vernalization chamber at 4°C with a photoperiod of 8 hours light/16 hour dark for 4 weeks. After 4 weeks, plants were transferred back to a greenhouse at 20°C and placed in a photoperiod of 24 hours lights until flag leaf unfolding. Days to flag leaf unfolding was determined as the number of days to flag leaf exertion from the stem starting from the day of transfer to the green house after vernalization treatment, or the day sown in the greenhouse for the non-vernalization treatment. Final leaf number was determined as the number of leaves at the determined days to flag leaf unfolding.

PCR conditions

Genomic DNA was extracted from young leaf tissue (100 mg) using a genomic DNA prep kit (Solgent Co., Korea), according to the manufacturer's instructions. PCR was conducted with primers for *Vrn-1* allele-specific markers according to the methods illustrated in Zhang et al. (2008). PCR was conducted with primers for *Ppd-1* allele-specific markers according to the methods presented in Bentley et al. (2011) and Seki et al. (2011). Amplified PCR fragments were separated on 1.5% agarose gels, stained with ethidium bromide, and visualized using UV light.

Statistical analysis

Statistical analysis of the data was performed with SAS software (SAS Institute, NC, USA) using Fisher's least significant difference test (LSD) and analysis of variance (ANOVA). Heritability (h^2), on a progeny mean basis, was estimated from RCM analysis using the formula $h^2 = 1 - (M2/M1)$, as proposed by Knapp et al. (1985), where $M1$ is the mean square of genotype and $M2$ is the mean square for genotype by year interaction (G × Y) in the Korean wheat cultivars grown for two years.

Results and discussion

Allelic variation at Vrn-1 and Ppd-1 loci

Allelic variations at the *Vrn-1* loci in Korean wheat cultivars are shown in Fig. 1. Two different alleles,

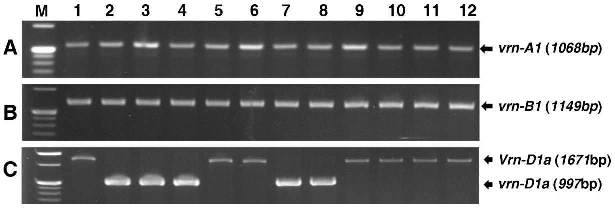

Fig. 1. PCR pattern of *Vrn-A1* (A), *Vrn-B1* (B), and *Vrn-D1* (C) alleles in Korean wheat cultivars. M=molecular size marker; 1 = Alchan; 2 = Baekjoong; 3 = Dahong; 4 = Gobun; 5 = Jeokjoong; 6 = Joeun; 7 = Jonong; 8 = Keumkang; 9 = Ol; 10 = Seodun; 11 = Shinmichal1 and 12 = Tapdong

vrn-D1 and *Vrn-D1a*, were found at the *Vrn-D1* locus in the cultivars tested (Table 1). All of the cultivars carried the *vrn-A1* and *vrn-B1* alleles, while 10 cultivars showed winter type at *Vrn-1* loci, *vrn-A1*, *vrn-B1* and *vrn-D1* alleles, in spite of the fact that Korean wheats are generally sown in the middle of October and early November. Fifteen of the cultivars carried the *vrn-D1* allele, while 10 displayed the *Vrn-D1a* allele at the *Vrn-D1* locus.

Seven different *Vrn-1* alleles, including *Vrn-A1a*, *Vrn-A1b* and *Vrn-A1c* at the *Vrn-A1* locus, *Vrn-B1a* and *Vrn-B1b* at the *Vrn-B1* locus and *Vrn-D1a* and *Vrn-D1b* at the *Vrn-D1* locus, are known in wheats with spring and facultative growth habits, occurring due to insertion and/or deletion mutations at the *Vrn-1* loci (Distelfeld et al. 2009). The *Vrn-A1a* allele was frequently found in spring wheats from Canada and India, with moderate frequency in Chinese, Pakistani and Turkish wheats (Iqbal et al. 2007, 2011; Zhang et al. 2008; Andeden et al. 2011; Singh et al. 2013). However, the *Vrn-A1b* and *Vrn-A1c* alleles have rarely been found in Indian, Pakistani and Turkish wheats The *Vrn-B1a* allele was frequently found in the spring wheats from Canada, India, and Russia and adjacent regions, while the *Vrn-B1c* alleles also displayed high presence in wheats from Russia and adjacent regions (Iqbal et al. 2007; Shcherban et al. 2012; Singh et al. 2013). The *Vrn-D1a* allele was found to be highly frequent in Indian wheats, whereas no Canadian spring wheats and only one cultivar from Russia and adjacent regions were found to harbor this allele (Iqbal et al. 2007; Shcherban et al. 2012; Singh et al. 2013).

Table 1. Allelic variations of 25 Korean wheat cultivars at the *Vrn-1* and *Ppd-1*

Cultivar	*Vrn-1* allele			*Ppd-1* allele		
				Ppd-A1	*Ppd-B1*	*Ppd-D1*
Alchan	*vrn-A1*	*vrn-B1*	*Vrn-D1a*	*b*	*a*	*a*
Anbaek	*vrn-A1*	*vrn-B1*	*vrn-D1*	*b*	*b*	*a*
Baekjoong	*vrn-A1*	*vrn-B1*	*Vrn-D1a*	*b*	*b*	*a*
Cheonggye	*vrn-A1*	*vrn-B1*	*Vrn-D1a*	*b*	*b*	*a*
Dahong	*vrn-A1*	*vrn-B1*	*vrn-D1*	*b*	*b*	*a*
Eunpa	*vrn-A1*	*vrn-B1*	*vrn-D1*	*b*	*b*	*a*
Gobun	*vrn-A1*	*vrn-B1*	*Vrn-D1a*	*b*	*b*	*a*
Hanbaek	*vrn-A1*	*vrn-B1*	*vrn-D1*	*b*	*b*	*a*
Jeokjoong	*vrn-A1*	*vrn-B1*	*Vrn-D1a*	*b*	*b*	*a*
Jinpoom	*vrn-A1*	*vrn-B1*	*Vrn-D1a*	*b*	*a*	*a*
Joeun	*vrn-A1*	*vrn-B1*	*vrn-D1*	*b*	*b*	*a*
Jokyung	*vrn-A1*	*vrn-B1*	*Vrn-D1a*	*b*	*b*	*a*
Jonong	*vrn-A1*	*vrn-B1*	*vrn-D1*	*b*	*b*	*a*
Jopoom	*vrn-A1*	*vrn-B1*	*Vrn-D1a*	*b*	*b*	*a*
Keumkang	*vrn-A1*	*vrn-B1*	*vrn-D1*	*b*	*b*	*a*
Milsung	*vrn-A1*	*vrn-B1*	*Vrn-D1a*	*b*	*b*	*a*
Ol	*vrn-A1*	*vrn-B1*	*vrn-D1*	*b*	*b*	*a*
Saeol	*vrn-A1*	*vrn-B1*	*Vrn-D1a*	*b*	*b*	*a*
Seodun	*vrn-A1*	*vrn-B1*	*Vrn-D1a*	*b*	*b*	*a*
Shinmichal	*vrn-A1*	*vrn-B1*	*vrn-D1*	*b*	*b*	*a*
Shinmichal1	*vrn-A1*	*vrn-B1*	*Vrn-D1a*	*b*	*a*	*a*
Sukang	*vrn-A1*	*vrn-B1*	*vrn-D1*	*b*	*b*	*a*
Tapdong	*vrn-A1*	*vrn-B1*	*Vrn-D1a*	*b*	*b*	*a*
Uri	*vrn-A1*	*vrn-B1*	*Vrn-D1a*	*b*	*b*	*a*
Younbaek	*vrn-A1*	*vrn-B1*	*Vrn-D1a*	*b*	*b*	*a*

Allelic variations at the *Ppd-1* loci in Korean wheat cultivars are also shown in Fig. 2. The presence of two different alleles in the cultivars was only observed at the *Ppd-B1* locus, showing *Ppd-B1a* and *Ppd-B1b* in various samples. The *Ppd-1a* alleles conferred insensitivity

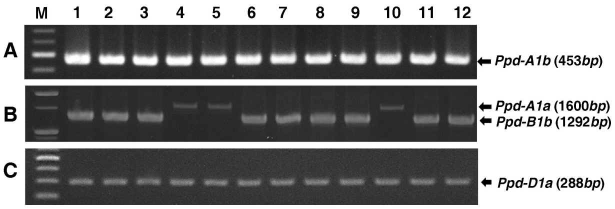

Fig. 2. PCR pattern of *Ppd-A1* (A), *Ppd-B1* (B) and *Ppd-D1* (C) alleles in Korean wheat cultivars. M = molecular size marker; 1 = Anbaek; 2 = Chunggye; 3 = Eunpa; 4 = Hanbaek; 5 = Jinpoom; 6 = Jokyung; 7 = Jopoom; 8 = Milsung; 9 = Saeol; 10 = Shinmichal; 11 = Sukang and 12 = Uri

in response to the photoperiod, while *Ppd-1b* alleles were related to sensitive response to the photoperiod (Snape et al. 2001). Winter wheats grown at more northern latitudes, such as in Canada, France and the UK, displayed high sensitivity to the photoperiod, whereas those grown in more southern latitudes, such as Italy and Yugoslavia, were highly insensitive (Worland et al. 1994). Photoperiod insensitive cultivars were also preferred in southern regions within Europe and North America, whereas cultivars grown in northern regions generally displayed photosensitivity (Worland et al. 1994; Dyck et al. 2004). *Ppd-D1* is the most photoperiod insensitive locus, followed by *Ppd-B1* and *Ppd-A1* (Seki et al. 2011). The *Ppd-D1a* allele is also wide spread in most of the European, Canadian and Chinese insensitive cultivars (Yang et al. 2009; Kamran et al. 2013).

Year, genotype and their interactions displayed significant influence on the agronomic traits of the Korean wheat cultivars tested, which agrees with the previous report (Brancourt-Hulmet et al. 2003). Year accounted for the largest proportion of the variation in measured agronomic traits (69.6-96.7%) while interaction of year and genotype accounted negligible proportions of the variation (0.2-4.6%). The estimated heritability of Korean wheat cultivars for agronomic traits was over 0.81, except for kernel number per spike, which displayed similar values as observed from studies on Chinese and Japanese wheat populations (Heidari et al. 2011; Jia et al. 2013). These results indicate that the measured agronomic traits in this study were primarily influenced by genotype rather than cultivation year and/or the interactions among year and genotype, although the proportion of the variation in these traits was mainly accounted for by cultivation year.

Effect of allelic variation on agronomic traits

Vernalized Korean wheat cultivars showed shorter mean values of days to flag leaf unfolding and final leaf number with vernalization treatment than Korean wheat cultivars without treatment (Table 2). The wheat cultivars carrying the *vrn-D1* allele showed longer days to flag leaf unfolding than those with *Vrn-D1a* allele, with or without vernalization. Unvernalized cultivars

Table 2. Days to flag leaf unfolding and final leaf number of Korean wheat cultivars with or without 4 weeks vernalization, followed by growth under 24 h light at 22°C in a greenhouse

Cultivar	Days to flag leaf unfolding		Final leaf number	
	Vernalization	No treatment	Vernalization	No treatment
Alchan	37.3	61.5	6.0	8.0
Anbaek	37.0	78.5	6.0	8.2
Baekjoong	30.3	59.2	6.2	9.0
Cheonggye	35.8	62.2	7.0	8.0
Dahong	38.0	60.8	6.3	8.0
Eunpa	33.0	60.0	6.0	7.0
Geuru	50.7	94.0	8.0	8.5
Gobun	32.2	60.7	6.8	8.2
Hanbaek	38.0	67.3	7.0	8.7
Jeokjoong	33.5	58.0	7.2	8.0
Jinpoom	32.3	63.2	7.0	8.0
Joeun	31.0	56.3	7.0	8.0
Jokyung	28.0	48.3	6.0	7.0
Jonong	37.2	68.8	7.0	8.7
Jopoom	28.7	55.0	6.0	8.0
Keumkang	36.7	66.7	7.0	8.0
Milsung	32.2	52.5	7.0	7.8
Ol	40.0	61.2	7.2	8.0
Saeol	30.7	51.5	7.0	7.0
Seodun	34.0	58.5	7.0	7.5
Shinmichal	34.2	58.2	8.0	8.0
Shinmichal1	34.8	62.0	7.0	8.0
Sukang	31.5	66.0	7.0	9.2
Tapdong	33.0	65.7	6.0	7.5
Uri	34.5	60.7	6.0	7.0
Younbaek	38.7	62.5	7.2	8.0
LSD[a]	1.2	3.2	0.3	0.5

[a] Least significant difference ($P < 0.05$)

carrying the *vrn-D1* allele also exhibited larger final leaf number than those harboring the *Vrn-D1a* allele, but the difference was not significant for the vernalization treatment. No differences in the days to flag leaf unfolding or final leaf number were found based on the allelic variations at the *Ppd-B1* locus in cultivars with or without vernalization. The days to flag leaf unfolding and final leaf number also showed no difference according to allelic variation of both the *Vrn-D1* and *Ppd-B1* alleles. Allelic variation at *Vrn-D1* locus was also not cause significant difference in heading time under field conditions. However, Japanese cultivars carried *Ppd-B1a* allele were accelerated heading compared with those with *Ppd-D1b* allele (Seki et al. 2011). This discrepancy between the cultivars originating from two countries, despite similar growing conditions of wheat. This could be caused by narrow genetic background in *Ppd-B1* alleles in Korean wheat cultivars.

Reduction in the flowering time and final leaf number was reported to be related to the sensitivity of wheats following vernalization, in which vernalization sensitive cultivars showed lower final leaf number and shorter duration to flowering time than the unvernalized samples because the vernalization shortened the vegetative phase and accelerated the reproductive phase (Snape et al. 2001; Foulkes et al. 2004). Cultivars carrying the alleles for insensitivity to photoperiod, including *Ppd-A1a*, *Ppd-B1a* and *Ppd-D1a* alleles, displayed earlier heading date under short days than those with sensitive photoperiod alleles. This earliness is generally mediated through developmental acceleration, such as emergence, floral initiation, shortening of the spikelet primordial initiation or terminal spikelet to flowering time, or short thermal duration from crop emergence to stem extension (Snape et al. 2001; Foulkes et al. 2004). Almost all high-yield improved cultivars are insensitive to photoperiod, because selection for the photoperiod insensitive trait has enhanced the adaptability of the improved cultivars in a wide range of environments in comparison with the photoperiod-sensitive wheat cultivated under short day lengths or in the higher latitude of North America and Europe (Worland et al. 1994, 1998; Worland and Snape 2001; Dyck et al. 2004).

The mean values of days to heading date and maturation date of Korean wheat cultivars were 190.3 and 227.3, respectively, with ranges of 182.7-193.7 and 221.5-231.0. Mean values of kernel number per spike and thousand kernel weight were 37.4 and 38.7g, respectively, with ranges of 30.4-43.1 for kernel number per spike and 32.7-49.0g for thousand kernel weight. Grain yield displayed mean values of 5.3 tons/ha with ranges from 4.4-6.1 tons/ha. The Korean wheat cultivars carrying the *vrn-D1* allele exhibited higher thousand kernel weight and lower grain yield than those harboring *Vrn-D1a* (Table 3). However, no significant differences were found in any of the other traits based on allelic variation at the *Vrn-D1* locus. In addition, differences in the agronomic traits according to allelic variation at the *Ppd-B1* locus were also not observed.

Vernalization could have an influence on kernel number per spike and spike fertility, as well as days to flowering time. The *Vrn-D1* allele or *Vrn-A1* and *Vrn-D1* alleles influenced variation of these traits in wheats (Kamran et al. 2014). The possibility of combining specific *Vrn-1* alleles should be considered to improve grain yield potential while maintaining their earliness, and the incorporation of the *Vrn-D1* allele should be

Table 3. Differences in agronomic traits of Korean wheat cultivars carrying different combinations of *Vrn-1* and *Ppd-1* alleles

Allelic variation	No.	Days to heading date	Days to maturing date	Kernel No./ spike	Thousand kernel weight (g)	Yield (tons/ha)	Protein (%)
vrn-D1	9	190.2^{a*}	227.6^{a}	37.7^{a}	40.9^{a}	5.0^{b}	13.5^{a}
Vrn-D1a	16	190.3^{a}	227.2^{a}	37.3^{a}	37.4^{b}	5.5^{a}	12.6^{a}
Ppd-B1a	3	191.5^{a}	229.4^{a}	39.5^{a}	35.2^{a}	5.3^{a}	12.6^{a}
Ppd-B1b	22	190.0^{a}	227.0^{a}	37.2^{a}	39.2^{a}	5.3^{a}	13.0^{a}
vrn-D1, Ppd-B1b	9	190.2^{a}	227.6^{ab}	37.7^{a}	41.0^{a}	5.0^{b}	13.5^{a}
Vrn-D1a, Ppd-B1a	3	192.1^{a}	229.6^{a}	39.4^{a}	35.0^{b}	5.4^{ab}	12.5^{a}
Vrn-D1a, Ppd-B1b	13	189.9^{a}	226.6^{b}	36.8^{a}	38.0^{ab}	5.5^{a}	12.7^{a}

*Values followed by the same letter are not significantly different at $P < 0.05$

also considered in wheat breeding programs. The *Vrn-D1* allele provides advantages to the grain yield through accelerating or delaying flowering time in order to avoid heat, drought and frost injury, and the CIMMYT-derived Mexican wheat cultivars carrying this allele have predominantly displayed longer growth seasons because of the increase in grain yield (Kamran et al. 2014). Wheat cultivars carrying two *Vrn-1* alleles in combination at two *Vrn-1* loci tended to mature early and with high yield, whereas those carrying triple *Vrn-1* alleles displayed early maturation but low yield in spring wheats (Stelmakh 1998).

Cultivars carrying the *Ppd-A1a* allele had a greater number of spikelets and higher grain weight than those harboring the *Ppd-A1b* allele (Stelmakh 1998). Cultivars carrying the *Ppd-D1a* allele displayed shortening of the flowering days by about 6 days in spring wheats and up to 12 days in winter wheat, with up to 8 days observed in UK wheats (Foulkes et al. 2004; Karman et al. 2013). The *Ppd-B1* allele has been related to reduction of heading time, tiller number, plant height and spikelet number, but these effects seem to be less pronounced than those of the *Ppd-D1* allele (Worland et al. 1998). Grain yield of wheats carrying photoperiod insensitive alleles was higher than those with photoperiod sensitive alleles, from 8 to 35%, in Germany, Southern Europe, and former Yugoslavia (Worland et al. 1994, 1998). However, there was no significant difference in grain yield over the years, though grain yield was reduced by 1.8% during cool humid summers but increased by 5 % in hot dry summers in European wheats (Worland et al. 1994, 1998).

Herein, cultivars carrying the *Vrn-D1a* allele combined with the *Ppd-B1a* allele showed longer days to maturation than those with the *Vrn-D1a* and *Ppd-B1b* alleles. Cultivars harboring the *vrn-D1* and *Ppd-B1b* alleles showed higher thousand kernel weight and lower grain yield than those with the *Vrn-D1a* allele combined with the *Ppd-B1a* or *Ppd-B1b* allele. However, no significant differences were observed in any of the other agronomic traits. These results indicate that the *Ppd-B1b* allele, when combined with *Vrn-D1b* alleles, could be involved in shortening the days to maturation and increasing grain yield in Korean wheat cultivars. Further investigation is needed to make general recommendations regarding the relationship between specific alleles combined with *Vrn-1* and *Ppd-1* alleles and major agronomic traits in Korean wheat breeding programs.

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