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Associations between Plant Density and Yield Components Using Different Sowing Times in Wheat (*Triticum aestivum* L.)

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The yield potential of wheat depends not only on genetic × environmental interactions, but also on various agronomic factors such as sowing date or the seed rate used for sowing. The main aim of this work was to determine possible correlations between the effects of different sowing dates and plant densities on the yield components of a collection of 48 wheat genotypes. Two-way analysis of variance on the data revealed that both sowing date and plant density, as main components, only had a minor effect on the yield component patterns. Correlation analysis, however, indicated that the sowing date had a greater effect on the yield components, while plant density was in closer correlation with the heading time (r = 0.90). The patterns determined for individual yield components at two different sowing dates and plant densities showed significant differences for spike length, spike fertility, grain number in the main spike, number of productive tillers, grain number on side tillers, mean grain number and grain weight. Genotypes that carry the winter (recessive) alleles of genes regulating vernalisation processes (*VRN-A1, VRN-B1, VRN-D1*) and the sensitive (recessive) alleles of the two genes responsible for photoperiod sensitivity (*PPD-B1, PPD-D1*) may have better tillering and consequently higher grain yield, though this may depend greatly on the year.

Keywords: seeding density, yield components, sowing time experiment, wheat (*T. aestivum* L.)

Introduction

Bread wheat is a staple cereal not only in Hungary, but throughout the world. Its ability to adapt to a wide range of environments can be attributed to its great genetic variability, one important component of which is the plant developmental pattern, especially the heading date. The plant development pattern plays a role not only in environmental adaptation, but also in the determination of yield potential. The start date and duration of each phenophase are greatly influenced by environmental factors (particularly temperature and photoperiod), the genetic composition of the plants and interactions between the two (Borras et al. 2009; Chen et al. 2010). A close relationship has also been detected between the yield potential of wheat and certain agronomic factors, such as sowing date and the seed rate used for sowing (Kabesh et al. 2009; Nakano and Morita 2009). It was observed that

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early sowing leads to higher yields than later sowing dates, since the longer vegetative phase means that more time is available for the production and storage of larger quantities of nutrients (Whitechurch and Slafer 2001; Gonzalez et al. 2003; Kiss et al. 2011). It was found by Yan et al. (2008) that a wisely chosen sowing date ensures higher protein content in the grain. Ragasits (1998) reported that an over-dense stand increased the damaging effect of various fungal diseases, while also leading to greater competition between individual plants, which could result in yield reductions. It was stated by Pan et al. (1994) that an increase in plant density had a negative effect in the case of early and optimum sowing dates, while using a higher seed rate for late sowing might compensate for this negative effect.

In the case of wheat one of the most important adaptation factors is the heading date, which is determined to the greatest extent by the cold treatment required for the vegetative/generative transition, i.e. the vernalisation requirement (*VRN* genes), and photoperiod sensitivity, regulated by the *PPD* genes (Slafer and Rawson 1994; Worland, 1996; Dubcovsky et al. 1998). Several gene families are involved in the genetic regulation of the vernalisation requirement, among which the *VRN-A1, VRN-B1* and *VRN-D1* genes exert the greatest effect (Pugsley 1971, 1972; McIntosh et al. 1998). The most important genes responsible for regulating photoperiod sensitivity are *PPD-A1, PPD-B1* and *PPD-D1* (Law et al. 1978; Börner et al. 1993), among which *PPD-D1* is the most effective. It can be said that the duration and start of the vegetative phase in individual genotypes can be influenced by inducing changes in photoperiod sensitivity and cold treatment (Slafer et al. 1996; Miralles et al. 2000; Gonzalez et al. 2002). Under field conditions, however, the diverse environmental parameters arising in different years result in considerable variability in the phenotypic effects of the various alleles of these genes, often resulting in contradictory results (Snape et al. 1985; Worland 1996; Kato et al. 2000). Knowledge of the temporal course of individual phenophases may provide breeders with information on the expected yield potential of a given genotype (Gonzalez et al. 2005; Chen et al. 2009). The use of these data in breeding programmes is still somewhat limited, as the genetic control mechanisms have not been adequately clarified. Many authors have studied the effect of photoperiod and temperature on the duration and starting date of individual phenophases and their influence on yield components (Gonzalez et al. 2002, 2003, 2005; Whitechurch et al. 2007; Kiss et al. 2014), but little information is available, however, on possible correlations between environmental factors (photoperiod and temperature) and individual yield components after the vernalisation requirement of wheat has been satisfied in field experiments including sowing date and plant density. In addition, little information is available for tillering ability of individual genotypes, which could have a substantial influence on yield potential. Our results can provide important information for various crossing programs, because in these cases the determination of ability of the selected parental genotypes might also be a serious aspect. Here can be mentioned, that during the process of hybrid wheat breeding the tillering ability is an important aspect as genotypes which are able to produce large tiller numbers by low plant density can achieve higher yield potential. Furthermore in the future there may be a greater call for the optimum plant density and sowing date of individual cultivars to be determined in breeding programmes, in order to compensate to some extent for the negative consequences of global climate change.

The main aim of the present research was to analyse a group of wheat cultivars with varying heading patterns and characterised for the allele compositions of major genes for vernalisation requirement and photoperiod sensitivity in order to (1) reveal how the gene allele effects are modified by plant density, and (2) to identify correlations between sowing dates, plant density and yield components.

Materials and Methods

Plant material, DNA isolation and genotyping of VRN and PPD genes

The 48 wheat genotypes included in the analysis were obtained from the winter wheat gene bank in the MTA-ATK Agricultural Institute (Table S1*). Genomic DNA was extracted from young leaves (100 mg) using a DNeasy® Plant Mini Kit (Qiagen) according to the manufacturer's instructions. The individual alleles of the *VRN-A1, VRN-B1, VRN-D1, PPD-B1* and *PPD-D1* genes were determined using functional molecular markers (Yan et al. 2004; Fu et al. 2005; Yang et al. 2009; Beales et al. 2007; Faure et al. 2007; Díaz et al. 2012). The aim was to use a heterogeneous gene pool in the experiments that might result in different heading. The allele patterns of the plant materials included in the analysis are summarised in Supplemental Table 1.

Characterization of yield components

The characteristic features of heading and yield components of the genotypes were tested in a field experiment in Martonvásár (Central Hungary) in 2013 on chernozem soil with average N, P_2O_5 and K_2O content. The cultivars were sown with normal and low seed rates at two sowing dates in autumn (mid-October, mid-November), sowing the cultivars in 1-metre rows with a 20 cm row distance. A seed quantity of 90 seeds/m (450 seeds/m^2) was used in the normal plant density treatment, and 20 seeds/m (100 seeds/m^2) for the thin stands. Two cultivars (Mv Toborzó, Mv Verbunkos) were each sown in four replications as a control in each treatment. In all four treatments five healthy, nearly uniform plants were chosen from each row and scored for heading /DEV59/ (spike completely emerged from the leaf sheath), as described by Tottman and Makepeace (1979). The heading time were expressed as the number of days required for spike appearance from 1 January 2013. The plants were raised till full maturity and the following yield components were scored for each plant: number of productive side tillers, number of spikelets, grain number and grain weight in the main spike, grain number and grain weight in the side spikes. The mean plant height was determined at the end of the physiological maturity phenophase as follows: (1) height from the base of the main tiller to the flag-leaf sheath (PH1) and (2) from the base of the main tiller to the base of the main spike (PH2). The lengths of the spikes and the last internode were also measured in this phenophase.

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*Further details about the Electronic Supplementary Material (ESM) can be found at the end of the article.

Table 1. Two-way ANOVA on the morphological, plant developmental traits and yield components measured for 48 wheat genotypes sown on two different dates with two plant densities

Trait	Total SS	SS (%)				1st sowing date with normal seeding density	1st sowing date with low seeding density	2nd sowing date with normal seeding density	2nd sowing date with low seeding density	LSD (0.05)
		Cultivar (C)	Treatment (T)	(C) × (T)	Error					
DEV59 [day]	6780	60.2***	31.6***		8.2	136	136	142	143	3.9
Plant height 1 [cm]	149299	55.0***	25.4***	7.8***	11.8	67	53	55	51	8.4
Plant height 2 [cm]	220892	75.5***	10.6***	5.9***	8.1	77	65	66	65	8.4
Length of the last internode [cm]	58830	73.4***	2.9***	9.5***	14.2	29	31	29	32	5.8
Spike length [cm]	2846	47.7***	16.9***	13.5***	21.9	9.4	10.4	8.6	8.8	1.6
Spike density [%]	150	54.8***	3.2***	18.4***	23.7	2.3	2.1	2.3	2.3	0.4
Number of spikelets	6262	46.2***	18.0***	15.8***	20.1	21.4	21.9	19.3	19.7	2.2
Seeds/spikelets	282	33.0***	5.9***	28.4***	32.8	2.4	2.6	2.7	2.8	0.6
Seeds/main ear	141605	32.2***	3.9***	29.4***	34.5	51.4	57.3	51.9	54.9	14.0
TKW/main ear [g]	42394	62.4***	2.1***	16.0***	19.6	44.9	46.7	44.2	44.8	5.8
RT (productive tillers)	21908	13.2***	44.3***	23.9***	18.6	9	14	5	7	4.0
Seeds/side tiller	51380373	9.7***	41.4***	27.7***	21.3	295	556	143	289	209.1
Average seeds/ear	115524	33.9***	4.8***	28.4***	32.8	41	46	41	46	12.3
Average TKW [g]	34058	67.3***	2.8***	16.4***	13.6	42.1	44.2	41.8	43.6	4.3
Grain yield [g]	100247	8.3***	42.7***	26.9***	22.1	14.5	26.6	8.1	15.0	9.4

Plant height 1: measured from the base of the main stem to the flag-leaf sheath; Plant height 2: measured from the base of the main stem to the base of the main spike; TKW: thousand-kernel weight; *** denotes significant relationships at the $P \leq 0.001$ probability level

Statistical analysis

The analyses were performed using one- and two-way analysis of variance (Microsoft, Redmond, WA, USA), multiple regression analysis and multi-variable analysis, using the Statistica 6 software package (StatSoft Inc., Tulsa, OK, USA). Five measurements were made for the two-way analysis of variance of traits recorded directly on the plants, while two-way analysis without replications was applied for data originating from various regression equations.

Results

Effects of different seeding densities and sowing dates on the phenotypic manifestation of the VRN-1 and PPD-1 genes

An analysis of correlations between the individual gene alleles and the heading time proved that the gene alleles had different phenotypic roles in the sowing date × plant density experiment. *PPD-B1* and *PPD-D1* genes were found to have a significant effect on DEV59, but this was strongly dependent on the sowing date and plant density. In stands sown with the normal seed rate at the first sowing date, both of these photoperiod sensitivity genes had a significant effect on DEV59; the *PPD-D1* gene explained 21% ($P \leq 0.01$) of phenotypic variance, and the *PPD-B1* gene 30.2% ($P \leq 0.05$). When sown with a lower seed rate or later with either a normal or low seed rate, DEV59 was only significantly affected by the *PPD-D1* gene, the effect of which was larger in the case of normal plant density irrespective to the sowing time. These values were 21% at normal plant density versus 17.1% ($P \leq 0.01$) at low plant density in the first sowing, while they were 31% ($P \leq 0.001$) and 19.1% ($P \leq 0.01$), respectively, in the later sowing. On average, genotypes carrying the dominant, insensitive alleles of the *PPD-B1* and *PPD-D1* genes reached DEV59 sooner, irrespective of treatments. The allele composition of these genes was not found to have any detectable effect on the yield components in any of the treatments.

Comparison of yield components

Two-way analysis of variance on the yield components revealed that the main effect of sowing date and plant density influenced these parameters to a lesser extent than via their interactions with the genotypes. The variance was only influenced to a greater extent by the sowing date and plant density for three yield components (productive tillers, seeds/side tiller and grain yield), these factors explaining 44.3%, 41.4% and 42.7% of the phenotypic variance, respectively. The sowing date and plant density had the least effect on the thousand-kernel weight of the main spike, the mean thousand-kernel weight and the length of the last internode (2.1%, 2.8% and 3.7%, respectively). Apart from the plant height (PH2) the genotype had the greatest effect on the length of the last internode (accounting for 73.4% of the phenotypic variance) and the least effect on the grain yield (8.3%). As a function of the two different sowing dates and plant densities significant differences were demonstrated in the patterns of certain yield components, namely the spike length, spike fertility, grain number on the main spike, number of productive tillers, grain number in side-spikes, mean grain number and grain weight (Table 1).

The mean spike length was 10.4 cm for the first sowing date with low seeding density, which differed significantly ($P \leq 0.001$) from the values recorded for the first sowing date with normal seeding density (9.4 cm), and for normal (8.6 cm) and low (8.8 cm) seeding density for the second sowing date. The spike fertility had a mean value of 2.8 grains/spikelet for the second sowing date with low seeding density, which differed significantly ($P \leq 0.01$) from the mean value recorded for the first sowing date with normal seeding density (2.4). The mean grain number in the main spike was highest for the first sowing date with low seeding density (57.3), differing significantly ($P \leq 0.01$) from that recorded for the first sowing date with normal seeding density and the second sowing date with normal seeding density (51.4 and 51.9, respectively). The mean number of productive side-tillers was highest for the first sowing date with low seeding density (14), with significantly lower values ($P \leq 0.001$) in the case of the first sowing date with normal seeding density (6), and for the second sowing date with normal (9) or low seeding density (5). The mean grain number in the side-spikes was highest for the first sowing date with low seeding density (556), which was significantly different ($P \leq 0.001$) from the values for the first sowing date with normal seeding density (295), and the second sowing date with normal (143) or low seeding density (289). At the same time, for the second sowing date,

Table 2. Correlation data on the morphological, plant developmental traits and yield components measured for 48 wheat genotypes as a function of sowing dates and seeding densities

Trait	Sowing date	Seeding density
Plant height 1 [cm]	0.85***	0.73***
Plant height 2 [cm]	0.89***	0.84***
Length of the last internode [cm]	0.89***	0.86***
Spike length [cm]	0.72***	0.76***
Spike density [%]	0.58***	0.77***
Number of spikelets	0.69***	0.82***
Seeds/spikelets	0.42***	0.46***
Seeds/main ear	0.47***	0.35***
TKW/main ear [g]	0.78***	0.74***
RT (productive tillers)	0.65***	0.53***
Seeds/side tiller	0.59***	0.33***
Average seeds/ear	0.56***	0.38***
Average TKW [g]	0.82***	0.74***
Grain yield [g]	0.57***	0.27**
DEV59 [day]	0.88***	0.90***

**, ***denote significant relationships at the $P \leq 0.01$ and $P \leq 0.001$ probability levels, respectively.

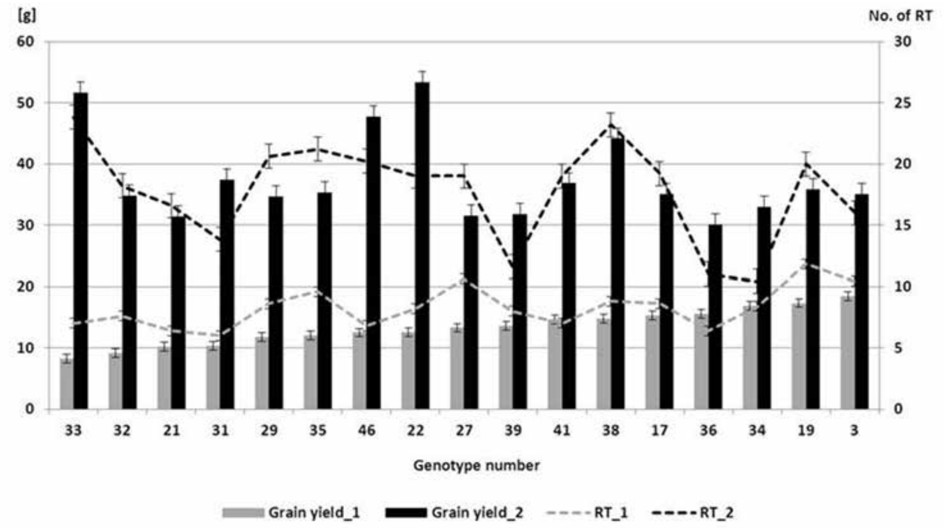

Figure 1. Distribution of the values of grain yield and productive tillers for 17 wheat genotypes measured in the first sowing date experiment (1: normal seeding density, 2: low seeding density)

too, the grain number in the side-spikes was significantly greater ($P \leq 0.001$) in the case of low seeding density than for normal seeding density. In both experiments involving low seeding density, the mean grain number (46) was significantly different from that recorded with normal seeding density (41) for both sowing dates. The mean grain weight was the greatest for the first sowing date with low seeding density (26.6 g), exhibiting a highly significant difference ($P \leq 0.001$) from the mean values recorded for the first sowing date with normal seeding density (14.5 g) and for the second sowing date with normal (8.1 g) or low seeding density (15.0 g). The difference in grain weight between the two seeding densities was also significant ($P \leq 0.001$) for the second sowing date, the grain weight again being higher in the case of low seeding density.

Correlation analysis revealed that the sowing date was significantly correlated with numerous traits. These were the following: plant height (PH1: $r = 0.85$; PH2: $r = 0.89$), length of the last internode ($r = 0.89$), grain number in the main spike ($r = 0.47$), thousand-kernel weight of the main spike ($r = 0.78$), number of productive side-tillers ($r = 0.65$), grain number in side-tillers ($r = 0.59$), mean grain number in the main spike ($r = 0.56$), mean thousand-kernel weight ($r = 0.82$), and grain yield ($r = 0.57$) (Table 2). At the same time the plant density treatments exhibited a highly significant correlation ($P \leq 0.001$) with spike length ($r = 0.76$), spike density ($r = 0.77$), number of spikelets ($r = 0.82$), grain number per spikelet ($r = 0.46$), and DEV59 ($r = 0.90$) (Table 2).

Among the 48 genotypes tested, 17 (35%) were found to have a grain weight of over 30 g in the first sowing date treatment with low seeding density (Fig. 1). In the case of the 17 cultivars with the best tillering ability, the mean number of productive side-tillers was 8 and the mean grain weight 13 g for the first sowing date with normal seeding density, while in the low seeding density experiment these values were 18 and 38 g, respectively. For both parameters, the differences were highly significant ($P \leq 0.001$). For the two cultivars with the highest grain weight, this value exceeded 50 g. These two genotypes carried the winter alleles of all three *VRN1* genes and the photoperiod-sensitive alleles of the *PPD-B1* and *PPD-D1* genes.

Discussion

The determination of the best plant density and sowing date for individual genotypes could provide important information to breeders for predicting tillering ability, which has a significant influence on yield potential.

The results obtained in the present work show that different sowing dates and plant densities caused substantial differences in the plant development and yield component patterns of the genotypes tested. The vegetative phase was longer for the first sowing date, resulting in better tillering, especially in plots with low seeding density. A considerable proportion of the side-tillers later proved to be productive. The extra leaves and side-tillers formed due to the intensive tillering also increased the nutrient-producing biomass (Slafer et al. 1996; Araus et al. 2002). As main components, both sowing date and plant density had a significant influence on almost all the yield components, but the effect was greatest for productive tillers, seeds/side-tiller and grain yield, particularly in the case of sowing date.

Significant differences were detected in the yield component patterns recorded for the two different sowing dates and seeding densities in the case of spike length, spike fertility, grain number in the main spike, number of productive side-tillers, grain number in side-spikes, mean grain number and grain weight.

Data on correlations between sowing date and seeding density revealed that the sowing date had a greater effect on the yield components tested, while the spike length, spike density, number of spikelets, grain number per spikelet and DEV59 exhibited a closer relationship with the plant density. It was reported by Wilson and Swanson (1962) that the number of secondary tillers may be exceptionally high in plots with low seeding density irrespective of the genotype, so that the full maturity phase is reached later, resulting in small and shrivelled grains. However, this finding was not confirmed by the present study, as the thousand-kernel weights recorded for the outstandingly high grain number recorded in plots with low seeding density were not lower than those found for normal seeding density. Although the genotypes differed with respect to tillering ability, this was not significantly correlated with the dominant or recessive alleles of the *VRN* and *PPD* genes. Nevertheless, genotypes that carried the recessive (winter) allele of all three *VRN1* genes and the recessive (sensitive) allele of both photoperiod sensitivity genes had better tillering and consequently higher grain yield.

Further work is planned on a genotype collection exhibiting broad genetic variability in order to establish how genes influencing plant development and yield components are correlated with environmental and agronomic parameters. The conclusions drawn from the present research will form a useful background for this work.

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Electronic Supplementary Material (ESM)

Electronic Supplementary Material (ESM) associated with this article can be found at the website of CRC at http://www.akademiai.com/content/120427/

Electronic Supplementary *Table S1*. Origin and allele types of the genotypes tested