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Effect of Different Sowing Times on the Plant Developmental Parameters of Wheat (*Triticum aestivum* L.)

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Studies on plant development phases and yield component patterns of wheat are essential for a better understanding of adaptation in wheat. Our main aim was to carry out detailed phenological analyses of 18 wheat genotypes in three sowing times for determining the effect of sowing date on individual phenophases, and yield components. Sowing date had the single greatest effect on the start of intensive stem elongation. The longer vegetation period had a favourable effect on main spike length and on the spikelet number per spike, but had no influence on thousand-kernel weight and grain number per spike. The time between the first node appearance and start of intensive stem elongation had a significant effect on the number of reproductive tillers. A close association ($R^2 = 0.191$) was observed during the second phase of intensive stem elongation between the boot stage-to-heading interval and the number of spikelets per spike. Two-way analysis of variance on the yield components showed that the sowing date, as a main factor, had a weaker effect on the phenophases than on morphological and developmental parameters. The insensitive allele of the *Ppd-D1* gene shortened the time required for first node appearance and heading both in autumn and spring sowing.

Keywords: plant developmental phases, yield components, sowing time, *Ppd-D1,* wheat (*T. aestivum* L.)

Introduction

One of the methods most widely used to determine the adaptation of cereals to various ecological conditions is to study the developmental pattern and flowering date of the plants. Plant growth and development can be divided into three major phases (Hay and Kirby 1991; Snape et al. 2001; Gonzalez et al. 2002), the first being the vegetative period from germination to intensive stem elongation, the second the generative period from intensive stem elongation to heading and the third the grain filling period from heading to physiological maturity. The starting date and length of each developmental phase are greatly influenced by environmental factors (especially temperature and day length), by the genetic constitution of the plants and by interactions between these parameters (Borras et al. 2009; Chen et al. 2010). Knowledge of the time course of each phase can thus provide breeders with important information on the yield potential of a given genotype

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(Gonzalez et al. 2005; Chen et al. 2009). A shift in the starting date of the intensive stem elongation phase could allow the plants to avoid frost damage in early spring, while early grain filling could contribute to the avoidance of heat and drought in early summer (Chen et al. 2010). At the same time, the duration of the individual developmental phases may have a substantial influence on the yielding ability of wheat. A longer vegetative phase results in more biomass (due to the longer nutrient storage period), a longer stem growth phase may increase the number of fertile florets/spikelets, and a longer grain-filling period may lead to higher average grain weight in the spikes (Whitechurch and Slafer 2001; Gonzalez et al. 2003a; Kiss et al. 2011). The use of data on individual growth phases in breeding programmes is still limited, as the mechanism of genetic regulation is not yet sufficiently understood. In the case of wheat one of the most important adaptation factors is the flowering date, which depends on the vernalization requirement (*Vrn* genes), i.e. the cold treatment necessary for the vegetative-to-generative transition, and on the *Ppd* genes responsible for photoperiod sensitivity (Slafer and Rawson 1994; Dubcovsky et al. 1998; Worland 1996; Worland et al. 1998). Among the gene families involved in the genetic regulation of the vernalization requirement in wheat, the genes *Vrn-A1, Vrn-B1* and *Vrn-D1* have the greatest effect (Yan et al. 1998; Fu et al. 2005), while the most important photoperiod sensitivity genes are *Ppd-A1, Ppd-B1* and *Ppd-D1* (Börner et al. 1993), of which *Ppd-D1* has the strongest effect. Depending on the distribution of the dominant and recessive alleles of the *Vrn* genes on the three separate genomes of hexaploid wheat, it is possible to distinguish winter (recessive) and spring (dominant) growth habits of cereal cultivars, together with genotypes with facultative habit, carrying various combinations of dominant and recessive alleles. Cereals in the temperate zone can be divided into photoperiod-sensitive and -insensitive groups depending on the allele distribution of the *Ppd* genes. The heading of genotypes carrying the photoperiod-insensitive allele proceeds rapidly under both short- and long-day photoperiod. The photoperiod-sensitive allele, on the other hand, causes a considerable delay in heading under short-day photoperiod. The latest models designed to describe the genetic regulation of flowering in cereals suggest a functional relationship between these genes (Cockram et al. 2007; Distelfeld et al. 2009).

Many authors have dealt with the effect of the starting date and length of individual phenophases on yield components in terms of photoperiod and temperature (Gonzalez et al. 2002, 2003a, 2005; Whitechurch et al. 2007). By contrast, very little information is available on possible correlations between environmental factors (photoperiod, temperature) and yield components in field sowing date experiments carried out after the vernalization requirement has been fully satisfied. The aim of the present work, performed on wheat genotypes having very varied heading patterns, was (i) to use a non-destructive phenotyping method to make a detailed study of how the sowing date influenced the yield components and the morphological and phenotypic traits determining individual phenophases, (ii) to use molecular markers to identify the alleles of major genes responsible for vernalization requirement and photoperiod sensitivity and to reveal their possible effects on the patterns of plant development and yield components, and (iii) to find correlations between sowing dates, phenophases and yield components.

Materials and Methods

All the plant samples (18 wheat genotypes) were obtained from the winter wheat gene bank at the Agricultural Institute (MTA-ATK) and were chosen on the basis of previously determined flowering data. The *Vrn-1* and *Ppd-D1* alleles were determined using gene-specific molecular markers (Yan et al. 1998; Fu et al. 2005; Yang et al. 2009). The main data obtained for the genotypes are summarised in Table 1.

Table 1. Origin and allele types of the genotypes tested

Genotype	Country	Alleles of *Vrn-A1* gene	Alleles of *Vrn-B1* gene	Alleles of *Vrn-D1* gene	Alleles of *Ppd-D1* gene
KT Hasáb	Hungary	winter	winter	winter	**insensitive**
Bajnok	Czech Republic	winter	winter	winter	**insensitive**
Fleming	USA	winter	**spring**	winter	sensitive
GK Göncöl	Hungary	winter	winter	winter	**insensitive**
Gruia	Romania	winter	winter	winter	**insensitive**
Plainsman V	Israel	winter	winter	winter	**insensitive**
Mv Apród	Hungary	winter	winter	winter	**insensitive**
Mv Bodri	Hungary	winter	winter	winter	**insensitive**
Mv Csárdás	Hungary	winter	winter	winter	sensitive
Mv Kokárda	Hungary	winter	**spring**	winter	sensitive
Mv Kolompos	Hungary	winter	winter	winter	**insensitive**
Mv Pálma	Hungary	winter	winter	winter	sensitive
Mv Tallér	Hungary	winter	winter	winter	**insensitive**
Mv Toborzó	Hungary	winter	winter	winter	**insensitive**
Mv Verbunkos	Hungary	winter	winter	winter	sensitive
Mv Walzer	Hungary	winter	winter	winter	sensitive
Mv213-10	Hungary	winter	**spring**	winter	sensitive
Marquis	Canada	**spring**	**spring**	winter	sensitive

The plant growth and development phases were characterised in 2012 in field experiments (Martonvásár, Central Hungary), involving two sowing dates in autumn (14 Oct. 2011: Experiment 1, and 14 Nov. 2011: Experiment 2) and one in spring (22 March 2012: Experiment 3). In the case of spring sowing the genotypes were previously submitted to artificial vernalization treatment at +3°C for 60 days to fully satisfy the vernalization requirement. The experimental plots measured 4 × 1 m and each genotype was planted in one row, with a distance of 20 cm between rows. Five healthy, near-uniform plants were chosen from each row for the regular scoring of plant height (twice a week) and three development phases (Tottman and Makepeace 1979): DEV31 (first node appearance at the base of the main stem), DEV49 (when the spike was in the top part of the flag-leaf sheath) and DEV59 (when the spike had completely emerged from the leaf sheath). All three development phases were given in terms of the number of days from 1 Jan. 2012. Regression equations fitted to the plant height measurements over time allowed the determination of the start (DEV30), end (DEVSEend) and the length (LSE) of intensive stem elongation (Kiss et al. 2011). The steepness of the regression lines is indicative of the rate of stem

elongation, thus allowing the rates of initial stem elongation (bph_ini) and of intensive stem elongation (bph_max) to be determined, together with the plant height at the start of intensive stem elongation (PH_DEV30). The plants were grown to 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, and grain number and grain weight in the side spikes. The mean plant height at the end of the physiological maturity phase was determined as follows: (1) from the base of the main stem to the collar of the flag leaf sheath (PH1) and (2) from the base of the main stem to the base of the main spike (PH2).

One- and two-way analysis of variance (Microsoft, Redmond, WA, USA), and the multiple regression analysis and multi-variable analysis modules of the Statistica 6 software package (StatSoft Inc., Tulsa, OK, USA) were used for the statistical analysis. For traits that were measured directly on the plants, two-way analysis of variance was carried out in 5 replications, while data originating from regression functions were analysed without replications.

Results

Changes in wheat growth dynamics as a function of the three sowing dates

Based on the results of two-way analysis of variance, the morphological and plant developmental traits examined were greatly influenced by the genotype, the sowing date, and the interaction between these two factors (Table 2). The cultivar, as a main factor, had the greatest effect on DEVSEend and on PH1 and PH2, while its effect on bph_ini, on DEV30 and on LSE was not significant. These latter traits were mainly influenced by the sowing date and to a slighter extent by the cultivar × sowing date interaction. Among the developmental phases, the cultivar, as a main factor, had a substantial effect not only on DEVSEend but also on the DEV49 phase. The mean values of these data indicate that in the first and second experiments (sown in autumn) bph_ini was twice as fast, averaged over the genotypes, as in the third (spring sown) experiment (Table 1). LSE was similar in the two autumn sown experiments (25 and 24 days), while it was the largest in the spring sown experiment. In the spring sown experiment bph_max was also larger than in the autumn sown experiments, resulting in significantly larger PH1, PH2 and length of the last internode.

In the spring sown experiment the plants required a fewer number of days (105) on average before DEV30, while these values were 110 and 114 days in the two autumn sown experiments, respectively. The time required for DEV31 was the shortest in the first autumn sown experiment, averaging 103 days, and the longest in the second autumn sown experiment (108 days), while there was no difference in the range (Fig. 1a). In the two autumn sown experiments there was almost a week between DEV31 and DEV30 (7 and 6 days, respectively), while in the spring sown experiment DEV31 coincided with DEV30, averaged over the cultivars. The lowest values of DEV49 and DEV59 were found in the spring sown experiment. In the case of DEV49 this was 124 days (range: 116–132 days),

Table 2. Two-way ANOVA on the morphological, and plant developmental traits measured for 18 winter wheat cultivars sown on three different dates

Trait	Total SS	SS (%)				1st autumn sown	2nd autumn sown	Spring sown	LSD (0.05)
		Cultivar (C)	Sowing (S)	(C)×(S)	Error				
DEV30 [day]	1335	20.4	54.5***	25.1	110	114	105	2.9	
DEV31 [day]	3968	40.0***	22.1***	24.8***	13.1	103	108	105	3.5
DEV49 [day]	5716	59.4***	20.6***	14.1***	5.9	127	130	124	2.9
DEV59 [day]	9251	41.1***	39.3***	13.7***	5.9	136	141	130	3.6
DEVSEend [day]	1178	79.7***	5.1	15.2		135	138	136	2.1
bph_ini	1.7	19.3	**42.2***	38.5		0.42	0.36	0.20	0.1
bph_max	4.32	**52.4****	13.7**	33.9		1.46	1.51	1.71	0.2
LSE [day]	1486	30.5	**31.5***	38.1		25	24	31	3.8
PH_DEV30 [cm]	967	15.0	**49.3***	35.7		13.2	10.0	5.9	2.9
Plant height 1 [cm]	15578	**62.7***	11.8***	12.9***	12.7	44	42	49	6.9
Plant height 2 [cm]	28908	**60.6***	22.9***	10.3***	6.2	51	48	61	6.6
Length of the last internode [cm]	10134	**51.4***	26.7***	10.4***	11.6	23	22	30	5.3

For traits measured on individual plants: df of cultivars = 17, df of sowing time = 2, df of (C) × (S) = 34, df of Error = 162.
For traits calculated from regression equations: df of cultivars = 17, df of sowing time = 2, df of (C) × (S) and error together = 34.
, * denote significant relationships at the P ≤ 0.001 and 0.0001 probability levels, respectively.
LSE: length of the intensive stem elongation phase.
PH_DEV30: plant height at the onset of the intensive stem elongation phase.

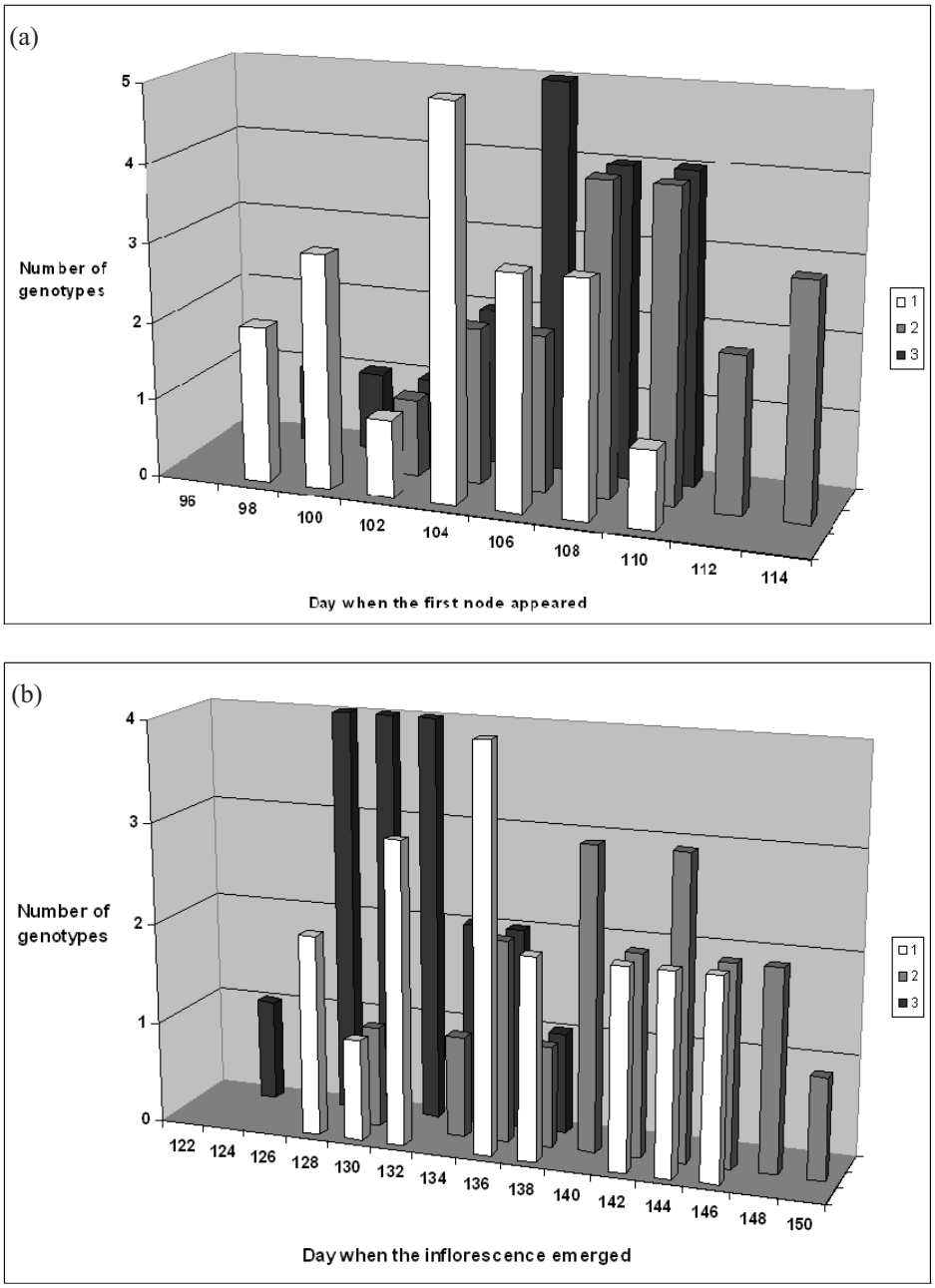

Figure 1. Distribution of the days required to reach the (a) DEV31, and (b) DEV59 phenophases for 18 wheat cultivars sown on three different dates (1: first autumn sown, 2: second autumn sown, 3: spring sown experiment)

compared with 127 days (122–138) in the first autumn sown experiment and 130 days (124–140) in the second autumn sown experiment. The differences between the experiments were even greater for DEV59, with a mean value of 130 days (124–138) in the spring sown experiment, compared with 136 (128–146) in the first and 140 (130–150) in the second autumn sown experiments (Fig. 1b).

Based on the mean values of the number of days between DEV49 and DEV59, heading proceeded more rapidly in the spring sown experiment (6 days on average) than in the autumn sown ones (9 and 10 days on average).

While for DEV49, values between the earliest and latest heading genotypes was the same in all three sowing date experiments (16 days), for DEV59 this difference was smaller in the spring sown experiment (14 days) compared to those in the two autumn sown experiments (18 and 20 days, respectively).

Interactive effect of the Vrn-1 *and* Ppd-1 *genes on the phenophases tested*

The analysis of correlations between the gene alleles and DEV31, DEV49 and DEV59 proved that the winter or spring allele types of the *Vrn-A1* and *Vrn-B1* genes had no significant effect on the three phenophases. When the rarely occurring *Vrn-B1* and *Vrn-A1* alleles were omitted from the analysis, the *Ppd-D1* gene was found to have a significant effect on the DEV31 and DEV49 phenophases, but this was greatly dependent on the sowing date. The DEV31 phenophase was only significantly influenced by this gene in the first autumn sown experiment, when it explained 23.1% of the phenotypic variance ($P = 0.05$). In the second autumn sown experiment the allele composition of the *Ppd-D1* gene had no influence on any of the phenophases, while in the spring sown experiment its effect was manifested in the later phenophases, explaining 23.6% of the phenotypic variance in the case of DEV49 ($P = 0.05$), while a close but non-significant ($P = 0.06$) correlation was found for DEV59. Genotypes carrying the semi-dominant insensitive allele of this gene reached the given phenophase in a shorter time. The allele composition of this gene was not found to have significant effects on any of the yield components tested.

Comparison of yield components

Two-way analysis of variance on the yield components revealed that the sowing date, as a main factor, had a smaller influence on these traits than on the morphological traits and phenophases (Table 3). Only three of the traits with a decisive effect on yield components (productive tillers, seeds/side tiller and grain yield) were influenced to a greater extent by the sowing date than by the genotype, but even for these traits the genotype × sowing date interaction had a greater influence, explaining 38.7, 40.8 and 43.8% of the phenotypic variance in the three traits. The sowing date had the least effect on the thousand-kernel weight in the main spike, the number of grains per spikelet and the grain number in the main spike. The cultivar had the greatest effect on the number of spikelets per spike (being responsible for 65.5% of the phenotypic variance) and the least effect on the grain yield per plant (14.9%).

Significant differences were detected for the number of productive tillers, the grain number in the side-spikes and the grain yield per plant between the sowing dates (Table 3).

Table 3. Two-way ANOVA on the yield components measured for 18 winter wheat cultivars sown on three different dates

Trait	Total SS	SS (%)				1st autumn sown	2nd autumn sown	Spring sown	LSD (0.05)
		Cultivar (C)	Sowing (S)	(C)×(S)	Error				
Spike length [cm]	500	37.6***	**37.6***	13.2***	11.7	11.7	10.9	9.5	1.2
Spike density [%]	17.9	66.0***	9.5***	12.6***	11.9	1.9	2.0	2.1	0.2
Number of spikelets	1573	65.5***	15.7***	7.3***	11.6	21.9	21.9	19.6	2.1
Seeds/spikelet	50.5	52.1***	2.4***	33.2***	12.2	2.8	2.7	2.9	0.4
Seeds/main ear	27453	44.4***	3.7***	35.6***	16.3	61.5	59.0	56.2	10.4
TKW/main ear [g]	10761	**53.3***	1.0***	28.7***	17.0	41.1	39.3	40.1	6.7
RT (reproductive tillers)	5355	24.1***	24.5***	**38.7***	12.6	15	11	9	4.0
Seeds/side tiller	7633249	19.8***	26.4***	**40.8***	13.2	524	347	301	156
Average seeds/ear	16581	**47.1***	5.8***	35.4***	11.6	39	34	38	6.8
Average TKW [g]	7475	**56.2***	7.5***	25.9***	10.5	39.6	36.4	36.0	4.4
Grain yield [g]	14612	14.9***	30.3***	**43.8***	11.1	23.2	15.0	12.7	6.3

For traits measured on individual plants: df of cultivars = 17, df of sowing time = 2, df of (C) × (S) = 34, df of Error = 162.
TKW: thousand-kernel weight.
*** denotes significant relationships at the $P \leq 0.001$ probability level.

The number productive tillers were highest in the first autumn sown experiment (15), and the lowest in the spring sown experiment (9). In the first autumn sown experiment the mean number of grains in the side-spikes was 524, which was significantly higher from that of the spring sown experiment (301). Likewise, the grain yield per plant was highest in the first autumn sown experiment (23.2 g), with significantly lower values in the second (15 g; $P = 0.01$) and in the spring sown (12.7 g; $P = 0.001$) experiments.

An analysis was also made of whether the length of the phenophases and the various developmental parameters were correlated with the yield components for the three sowing dates (Table 4). Of the phenophases, the length of the vegetative phase, characterised by the number of days from sowing to DEV31, had a significant influence on the spike length (explaining 39.6% of phenotypic variance), the number of reproductive tillers (24.2%), the number of side-spikes (22.8%), the grain yield (24.3%) and to a lower extent the spike density (7.6%). The time elapsing between DEV30 and DEV31 had a significant effect on heading (29.3%) and a less pronounced effect on the number of productive tillers (8.3%), while that between the DEV30 and DEV49 had a significant influence on the spike density (17%) and the number of grains per spikelet (11.6%). The length between DEV49 and DEV59 influenced the number of spikelets and the spike density, explaining 19.1 and 8.9%, respectively, of the phenotypic variance. PH_DEV30 had a significant effect on the number of productive tillers (34.3%), the number of grains in the side-spikes (22.4%), the grain yield (29.2%) and to a lesser extent the mean thousand-kernel weight (10%), while the length of the last internode influenced the number of grains in the main ear (13.3%).

Discussion

The application of three sowing dates caused substantial differences in the growth dynamics of the wheat genotypes and in the patterns of plant development and yield components. As the yield is fundamentally determined by the quantity of assimilates produced by the plant and their distribution among the plant organs, it is obvious that the relative lengths of the various development phases have a decisive influence on the yield components (Slafer et al. 1996). This was clearly reflected by the present findings. In all three sowing date variants the vernalization requirement of the cultivars was completely satisfied, either naturally or by means of artificial vernalization treatment. A substantial difference existed in the length of the vegetative phase, expressed indirectly as the time between sowing and first node appearance (Tottman and Makepeace 1979). Analysis of the correlation between individual phenophases and the grain yield indicated that the length of the vegetative phase and the plant height at the end of this phenophase had the greatest effect. The vegetative phase was longer after autumn sowing, as the environmental conditions (short day length, low temperature) did not promote the initiation of stem elongation even after the cold requirement of the genotypes had been saturated. Thus, the assimilates produced were used for the formation of leaves and tillers, further increasing the biomass available to produce assimilates (Slafer et al. 1996). The vegetative phase was the longest in the first autumn sown experiment, resulting in a large number of tillers, a large proportion of which later proved to be productive. By contrast the vegetative phase was considerably

Table 4. Associations between plant developmental phases and yield components, based on the combined data sets of 18 wheat cultivars for three sowing dates

Trait	R^2 of single trait regression									Multi R^2
	VEG	DEV30–DEV31	DEV49–DEV30	DSE49	DEV59–DEV49	LSE	PH_DEV30	bph_max	Length of the last internode	
	All the sowing times combined									
Spike length	39.6***	29.3***	–	0.1	–	–	–	2.0	0.3	58.2***
Spike density	7.6*	–	17.0**	–	8.9*	–	–	–	1.1	44.2***
No. of spikelets	–	–	2.5	–	19.1***	–	5.7	–	–	39.4***
Seeds/spikelet	–	0.3	11.6*	0.1	1.3	–	–	–	7.0	32.6**
Seeds/main ear	–	–	–	0.8	–	–	–	–	13.3**	16.6**
TKW/main ear	0.1	5.0	–	1.5	0.9	–	–	0.3	–	29.1**
Reproductive tillers	24.2***	8.3*	0.1	–	–	0.8	34.3***	–	–	54.6***
Seeds/side tiller	22.8***	–	–	–	–	1.1	22.4***	–	0.1	36.7***
Average seeds/ear	–	–	–	–	–	–	–	–	–	ns
Average TKW	–	6.9	–	0.6	0.3	–	10.0*	0.9	–	26.2*
Grain yield	24.3***	–	–	–	–	2.1	29.2***	–	–	41.5***

VEG: vegetative period (from sowing to the onset of the intensive stem elongation phase, DEV30).
DSE49: end of the intensive stem elongation phase.
LSE: length of the intensive stem elongation phase.
PH_DEV30: plant height at the onset of the intensive stem elongation phase (DEV30) of the intensive stem elongation phase.
TKW: thousand-kernel weight.
*, **, *** denote significant relationships at the $P \leq 0.05$, $P \leq 0.01$, $P \leq 0.001$ probability levels, respectively.

shorter after spring sowing, as the plants were in an inductive environment immediately after sowing, resulting in the rapid initiation of stem elongation, parallel with a considerable decline in tillering and thus in the number of productive tillers, while the plant height increased. The longer vegetation period characteristic of autumn sown crops also had a favourable effect on the length of the main spike and the number of spikelets per spike, but had no influence on the thousand-kernel weight or the mean number of grains per spike, which were mostly determined by the genotypes. The significant difference in grain yield detected between the three sowing dates could be attributed primarily to the decrease in the number of productive tillers.

In addition to the vegetative phase, the length of three other phenophases also had a notable effect on certain yield components. The period between the start of intensive stem elongation and the appearance of the first node (DEV30–DEV31) also had a significant effect on the number of productive tillers. In the autumn sown experiments the length of the vegetative phase was further increased by the fact that, on average, intensive stem elongation did not begin until a week after first node appearance. In addition, of all the phenophases, the start of intensive stem elongation was influenced to the greatest extent by the sowing date, while the effect of the genotype was not significant. After spring sowing, development was much more rapid, as shown by the simultaneous occurrence of first node appearance and the start of intensive stem elongation. Averaged over the cultivars, the time between the start of intensive stem elongation and the boot stage did not differ significantly for the three sowing times, indicating that this phase was more dependent on the genotype than on the environmental conditions. The length of this phenophase was significantly correlated with the spike density and the number of grains per spikelet. Numerous authors have demonstrated that in the course of wheat spike differentiation the development of new spikelets ceases once the terminal spikelet has been formed, indicating that the maximum number of spikelets is genetically determined, while no such determination was observed for the number of flowers within the spikelets (Kirby 1988; Miralles et al. 1998; Gonzalez et al. 2003b, 2005). The final number of flowers per spikelet is then thought to be determined during the intensive stem elongation phase, depending on the quantity of assimilates accumulated as a function of the environment and the plant status, while the fertilisation rate of the flowers determines the number of grains per spikelet (Miralles et al. 2000; Gonzalez et al. 2003a, 2005). This hypothesis is contradicted, however, by the close correlation observed in the present work in the second stage of intensive stem elongation, between the period from booting to heading and the number of spikelets per spike.

It was established that the time course of the DEV59 phenophase was greatly influenced not only by the genotype, but also by the sowing date, which caused considerable changes in the spring sown experiment, where the average value but also the difference between the earliest and latest heading genotypes was much less than in the two autumn sown experiments. This phenomenon can probably be attributed to the complex interactions between weather factors, as the location was the same for all three experiments.

Molecular marker-assisted analysis demonstrated that the semi-dominant (insensitive) allele type of the *Ppd-D1* gene not only shortened the time required for heading (Beales

et al. 2007), but also caused the first node on the main stem to appear earlier (DEV31) after both autumn and spring sowing, averaged over the genotypes bearing this allele. This proved that this allele type plays an important role in plant development not only in later development stages, but also prior to the intensive stem elongation phase.

The conclusions drawn from the present results will be of assistance in future research on a genotype collection exhibiting broad genetic variability, aimed at detecting further correlations between the genes influencing plant development and yield components and various environmental parameters.

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