Spanish Journal of Agricultural Research
16 (3), e0903, 13 pages (2018)
eISSN: 2171-9292
https://doi.org/10.5424/sjar/2018163-11388
Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, O.A, M.P. (INIA)

RESEARCH ARTICLE

OPEN ACCESS

Grain number and grain weight as determinants of triticale, wheat, two-rowed and six-rowed barley yield in the Pannonian environment

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Abstract

Climate significantly affects cropping systems across Europe. Knowledge of the variability in grain number per unit area and grain weight across different growing seasons and its association with grain yield is important for further improving small grain crop production. The main aim of this study was to compare grain yield and its numerical components among triticale, wheat, two-rowed and six-rowed barley cultivars across different growing seasons in a typical Pannonian location (south-eastern part of Central Europe). Trials with twelve winter cereal genotypes (three two-rowed barley, three six-rowed barley, three wheat and three triticale genotypes) were carried out in four successive seasons in Novi Sad, Serbia. Results of this study showed that growing season, species, cultivar, and species × growing season interaction significantly (p<0.01) affected grain yield and its determinants. Generally, triticale had higher average grain yield, while the lowest grain yield was recorded in six-rowed barleys. Grain yield was more associated with the number of grains/m^2 than with grain weight. Heading date was recognized as one of the important adaptive traits in crop development and yield determination. Short duration of the pre-anthesis phase in early cultivars and delayed anthesis in late cultivars significantly decreased the number of grains/spike in different species/spike types, reducing the final grain yield. Medium early cultivars had the highest number of grains/spike due to optimal duration of the pre-anthesis period and heading date and are suggested as recommendable for large scale production in the Pannonian environments.

Additional keywords: cultivars; heading date; Pannonian plain.

Abbreviations used: C (cultivar); GDD (growing degree days); GN (number of grains/m^2); GW (grain weight); GY (grain yield); OF (from October to February); PCA (principal component analysis); S (species); Y (year of the growing season).

Authors' contributions: Conceived and designed the experiments: MM and NP. Performed the experiments, material support and analysis tools: MM, VM, SM and DT. Analyzed and interpretation of data: MM, VM, NP and SD. Statistical analysis: MM and VM. Wrote the paper: MM, VM and NP.

Citation: Mirosavljević, M.; Momčilović, V.; Denčić, S.; Mikić, S.; Trkulja, D.; Pržulj, N. (2018). Grain number and grain weight as determinants of triticale, wheat, two-rowed and six-rowed barley yield in the Pannonian environment. Spanish Journal of Agricultural Research, Volume 16, Issue 3, e0903. https://doi.org/10.5424/sjar/2018163-11388

Received: 14 Mar 2017. **Accepted:** 31 Jul 2018.

Funding: Ministry of Education, Science and Technological Development of the Republic of Serbia (project TR-31066 "Modern breeding of small grains for present and future needs").

Competing interests: The authors have declared that no competing interests exist.

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Introduction

Grain yield (GY) represents one of the most important and complex traits, and its constant increase remains the main priority worldwide when developing new varieties (Yan *et al.*, 2007; Araus *et al.*, 2008). In small grain cereals, GY is determined by two main components, number of grains/m^2 (GN) and grain weight (GW). The former is generated during the pre-anthesis period in barley (Arisnabarreta & Miralles, 2008), wheat (Ferrante *et al.*, 2013) and triticale (Giunta *et al.*, 1993; Estrada-Campuzano *et al.*, 2008), while the final GW is result of the grain filling duration and the grain filling rate (Koutroubas *et al.*, 2014; Xie *et al.*, 2015). Furthermore, numerous studies indicated the importance of the period between booting and anthesis for potential GW determination (Calderini *et al.*, 1999; Ugarte *et al.*, 2007). Other developmental stages (*e.g.* duration of tillering and stem elongation phase; Borràs *et al.*, 2009; Foulkes *et al.*, 2011), plant morphology (number of grains/spike, plant height; Mladenov *et al.*, 2011) and physiological traits (chlorophyll content, stomatal conductance and pre/post-anthesis photosynthetic rate; Beche *et al.*, 2014) have also been reported to have close association with GY.

A positive relationship between GW and GY has been shown in various studies (Garcia del Moral *et* *al.*, 2003; Pržulj & Momčilović, 2012) especially in drought prone environments (Royo *et al.*, 2006). Nevertheless, GY is mainly associated with GN in different cereal crops and generally genetic gain in GY has resulted from the increase in GN (Peltonen-Sainio *et al.*, 2007; Abeledo *et al.*, 2008; Lizana & Calderini, 2013; Zhou *et al.*, 2014). Grain number/m^2 is a result of the establishment of different numerical subcomponents, including plants/m^2, spikes/plant, spikelets/spike and grains/spikelet (Slafer *et al.*, 2014). In general, wheat and barley have different strategies of GN establishment (Alvarez-Prado *et al.*, 2017). In two-rowed barley, variation in GN is less related to the number of grains/spike than in wheat and six-rowed barley cultivars (Peltonen-Sainio *et al.*, 2009). However, these numerical subcomponents are often negatively related to each other (Slafer, 2003). Thus, it is necessary to identify traits that determine GN, and understand their connections in order to manipulate them for further GY improvement.

The Pannonian region, which lies in the south-eastern part of Central Europe, represents one of the major cereal growing regions in Europe. In Serbia, the southern part of the Pannonian plain, wheat is the main winter cereal crop with a harvested area over 550,000 ha, followed by barley and triticale, with harvested areas over 90,000 and 25,000 ha, respectively (FAOSTAT, 2014). In the Pannonian environment, GY of many cereal crops significantly varies across different growing seasons (Hristov *et al.*, 2011; Pržulj *et al.*, 2015). The agricultural areas of the Pannonian basin are characterized by a relatively short growing season, winter frosts, occasional spring heats and frequent drought stresses at the end of the grain filling period (Smith *et al.*, 2009; Olesen *et al.*, 2011). Similarly to cropping systems across Europe, this region is threatened by the adverse effects of climate change, reflected in the mean temperature increase of 0.7 to 2.0 °C and precipitation decrease, according to the future climate projections (EEA, 2012; IPCC, 2013), and with more frequent occurrence of unfavourable growing conditions (Ebrahimi *et al.*, 2016). Some recent studies have reported that the Pannonian environmental zone (rather than the Mediterranean) is the most vulnerable area of Europe to the influence of climate change (Olesen *et al.*, 2012). Projected changes in climatic conditions will overload crop with additional stress conditions during different developmental phases such as anthesis and/or the grain filling period (Olesen *et al.*, 2011). Moreover, the gap between potential GY (defined as the GY achieved under non-limiting conditions, *i.e.* a crop growing without biotic and abiotic stresses, such as water and nutrients deficiencies; van Ittersum *et al.*, 2013) and actual GY (achieved in a farmer's field) influences winter cereal production. In order to minimize this GY gap, it is necessary to improve our knowledge about crop development and its relationship with different GY determinants in main cereal crops. Therefore, the main objective of this study was to compare GY and its numerical components (GN and GW) in wheat, triticale, two-rowed and six-rowed barley under different growing seasons in order to (i) analyse differences among species in GY generation and (ii) to define the ideotypes of small grain cereal cultivars which should be recommended for production in the Pannonian environment.

Material and methods

Plant materials and growing conditions

The trial was conducted in four successive growing seasons (Y) (2008/09 - 2011/12) at Rimski Šančevi experimental station of the Institute of Field and Vegetable Crops, Novi Sad (45°20´N and 19°51´E), Serbia, on a non-carbonate chernozem soil. A growing season refers to a time period from sowing to crop maturity. Plots were sown from October 10 to 25 each growing season, which is the recommended sowing period for the agroecological conditions in the southern Pannonian plain, at the density of 400 seeds/m^2 for all species and cultivars. Twelve winter cereal genotypes were evaluated in each growing season: three two-rowed barley (*Hordeum vulgare* subsp. *distichum* L.), three six-rowed barley (*H. vulgare* subsp. *hexastichon* L.), three wheat (*Triticum aestivum* L.) and three triticale (× *Triticosecale* spp. Wittmack) cultivars (Table 1). The plots (12 m^2) were arranged in a randomized complete block design with three replications, within each growing season. A fertilizer combining N, P, and K (containing 15% N, 15% P_2O_5 and 15% K_2O) was applied before sowing in each growing season to avoid N, P and K deficit (the average applied dose was ca. 60 kg/ha N, 60 kg/ha P and 60 kg/ha K). In early February, additional nitrogen fertilizer (ammonium-nitrate - 33% N) was top dressed according to N-min analysis in average doses of 80, 100, 60 and 80 kg/ha N in 2009, 2010, 2011 and 2012, respectively. When necessary, weeds were periodically removed by hand. As required during spring, deltametrine was applied for pest control at the beginning of insect colonies formation (aphids and cereal leaf beetles), while tebuconazole and protiokonazol were used for diseases management (rusts, *Septoria tritici* blotch and powdery mildew), when the first symptoms appeared and before they spread to the upper leaves. The chemical control was applied in all plots.

Table 1. Species, cultivar, country of origin, spike type and relative maturity group of the tested cultivars.

Species	Cultivar	Country of origin	Spike type	Maturity group
Barley	'NS 525'	Serbia	Two-rowed	Early
	'NS 565'	Serbia	Two-rowed	Medium early
	'Monaco'	France	Two-rowed	Late
	'Dorat'	Croatia	Six-rowed	Early
	'Nonius'	Serbia	Six-rowed	Medium early
	'NS 150'	Serbia	Six-rowed	Late
Wheat	'Prima'	Serbia		Early
	'Pobeda'	Serbia		Medium early
	'Diplomat'	Germany		Late
Triticale	'Odisej'	Serbia		Early
	'NS tritikale'	Serbia		Medium early
	'Garne'	Ukraine		Late

The studied cultivars have been widely grown in Serbia and the surrounding countries (Table 1). They were grouped according to their heading time as early, medium early and late, where each species/spike type was represented by one cultivar from each group. Although six-rowed and two-rowed barley cultivars belong to the same species, due to significant differences in agronomical traits (number of grains/spike, number of spikes/m^2, GW, etc.), they were analysed separately.

Data recording and analyses

The dates of emergence (Z10), heading (Z55) and anthesis (Z61) were recorded in each plot when 50% of plants reached those stages (Zadoks *et al.*, 1974). Each experimental plot was divided into two equal subplots, where one (6 m^2) was used for destructive sampling and the other (6 m^2) was left intact for assessment of GY. At maturity, 1 m long sample was taken from two central rows of one of the subplots of each experimental unit. From the sample, twenty spikes were collected, dried and weighed in order to calculate GY components (number of spikes/m^2, number of grains/spike, GN and GW). Grain yield was determined at maturity, after mechanical harvesting from the second intact subplots and calculated at 10% moisture level. The number of fertile florets/spike was counted at anthesis (Z61) in ten randomly selected spikes, and only florets that developed green and yellow anthers and stigmatic branches spread wide were considered fertile. The percentage of grain setting was calculated as the ratio between the number of grains/spike at maturity and the number of fertile florets/spike at anthesis. To evaluate crop development rates, thermal time (growing degree-days, GDD) was calculated from emergence as $GDD=\sum((T_{max}+T_{min})/2-T_b$, where T_{max} is maximum daily temperature, T_{min} is minimum daily temperature, and T_b is the base temperature (0 °C). The limits for the minimum and maximum temperatures were established at 0 °C (Gallagher, 1979) and 37 °C, respectively.

Meteorological records were obtained from a station located approximately 300 m away from the experimental field. From these data, twenty meteorological variables were constructed: level of precipitation accumulated in winter period (from October to February - OF), March, April, May and June; average daily temperature in OF, March, April, May and June; the number of days with maximum temperatures below 0 °C in OF and March; the number of days with maximum temperature over 25 °C in OF, March, April, May and June; the number of days with maximum temperature over 30 °C in April, May and June. Principal component analysis (PCA) was performed on the set of the meteorological indices and a biplot of the first two PCA axes was constructed to visualize associations between growing seasons, meteorological variables and GY. The growing seasons, GY and meteorological data were standardized and positioned on a biplot according to their scores from the PCA. The distances between growing seasons corresponded to the differences in meteorological conditions. For the analysis of variance (ANOVA), a split-plot model with blocks combined over years was used, treating the growing season as the main plot and the species as the subplot. The cultivars were nested within species. Means were compared using the Tukey test ($p<0.05$). All analyses were performed in STATISTICA 10.

Results

Meteorological variables

In the environmental conditions of the Pannonian Plain, tillering phase begins mid-November when sowing is completed in the recommended period, during the first and second decades of October. In spring, early cultivars enter the stem elongation phase at the end of March, while beginning of stem elongation phase of late cultivars occurs approximately in the second half of April. In our study, heading of the early cultivars occurred at the end of April ('Odisej' and 'NS 525') and at the beginning of May ('Prima' and 'Dorat'), while heading of the late cultivars was recorded in the second or the third decade of May. Anthesis occurs only a few days (usually 2-5) after heading. The cultivars explored variable weather conditions throughout their cycle in the different growing seasons. The PCA analysis of the meteorological data and GY across four growing seasons is shown in a biplot (Fig. 1) with first two principal components. The meteorological variables, GY and the growing seasons were placed on the biplot according to their PCA scores. The first principal component (PCA1) accounted for 62.25%, while the second principal component (PCA2) accounted for 23.80% of the total variation. The highest average daily temperature, the number of days with maximum temperature over 25 °C and over 30 °C in April, May and June, the number of days with maximum temperatures below 0 °C in the winter period, and the lowest level of precipitation were observed in the growing season 2011/12. The growing seasons 2008/09 and 2010/11 were characterized by high precipitation in the winter period, March and June and increased average temperature in April. Similar conditions with higher temperatures in March and winter, and higher precipitations in April and May were recorded in the season 2009/10. Temperatures in March (number of days with maximum temperature over 25 °C and average daily temperature) did not affect GY, as indicated by near perpendicular vectors. High temperatures in April, May and June and number of days with <0 °C in OF had high negative association with GY. The number of days with maximum temperature over 25 °C in OF had a weak negative association with GY. Although GY was positively related to precipitation during the growing season, the level of association varied between periods. Therefore, the biplot showed that GY was mostly related to precipitation during March, June and the winter period.

Main grain yield components

Growing season (Y), species (S), cultivar (C), and Y × S had a significant (p<0.01) influence on GY (Table 2). Growing season had the most important effect on GY, while the effect of cultivar, cultivar by growing

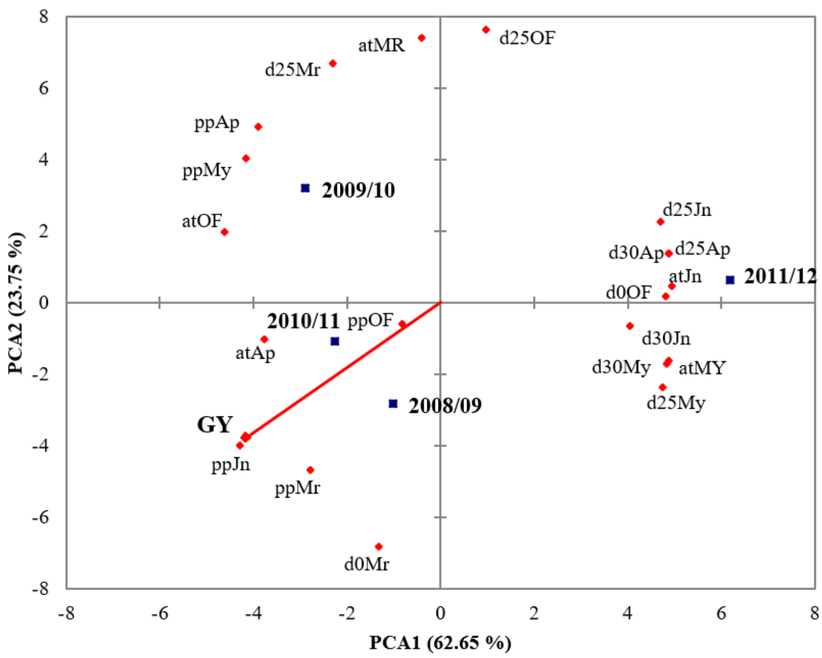

Figure 1. Biplot presentation of 20 environmental variables and grain yield (GY) across four growing seasons (2008/09-2011/12). Accumulated precipitation (pp) in winter (from October to February: OF), March (Mr), April (Ap), May (My) and June (Jn); average daily temperature (at) in OF, Mr, Ap, My and Jn; number of days with maximum temperatures below 0 °C (d0) in OF and Mr; number of days with maximum temperature over 25 °C (d25) in OF, Mr, Ap, My and Jn; number of days with maximum temperature over 30 °C (d30) in Ap, My and Jn.

Table 2. ANOVA for the main analysed traits: grain yield (GY), mean individual grain weight (GW), number of grains/m^2 (GN), number of spikes/m^2 (NSSM), number of grains/spike (NGS), number of fertile florets/spike (NFS), grain setting percentage (GS); duration in days of the period from emergence to heading (HD), for growing season (Y), species (S), species by growing season interaction (Y×S) and cultivar within species (C(S)) as source of variation.

Source of variation	DF	GY	GW	GN	NSSM	NGS	NFS	GS	HD
Y	3	40486013**[a] (89.6%)[b]	101.3** (11.2%)	132120168** (51.3%)	12767** (1.2%)	553.5** (10.6%)	405.6** (4.1%)	0.17** (80.6%)	73414** (24.7%)
S	3	570780** (1.3%)	720.4** (79.3%)	104424600** (40.6%)	1035860** (96.5%)	4551.6** (87.4%)	9173.6** (92.3%)	0.01** (4.7%)	81307** (27.3%)
Y×S	9	1562577** (3.5%)	29.4** (3.2%)	8330728** (3.2%)	15587** (1.5%)	81.6** (1.6%)	155.9** (1.6%)	0.01** (4.7%)	2254** (0.8%)
C(S)	8	2409424** (5.3%)	53.2** (5.9%)	11222645** (4.4%)	7483** (0.7%)	18.0** (0.3%)	189.7** (1.9%)	0.02** (9.5%)	139824** (47.0%)
Error	120	137478	3.6	1216210	1904	4.8	11.5	0.001	705.57

[a] Sum of squares and result of F test. [b] Proportion of variance explained by the source of variation relative to the total sum of squares. ** Significant at the probability level of $p<0.01$.

season interaction and species was less pronounced. Grain yield ranged from 6,544 kg/ha to 8,711 kg/ha, in response to different environmental conditions in 2011/12 and 2010/11, respectively (Table 3). Triticale tended to yield more than wheat and barley, but there was only significant difference between triticale and six-rowed barley. The cultivar with highest GY overall was 'Pobeda' (8,557 kg/ha), followed by 'NS Tritikale', 'Odisej', and 'Nonius'. The medium early cultivars ('Pobeda', 'NS tritikale', 'Nonius', and 'NS 565') were the highest yielding genotypes within each species or spike type, while the late cultivars ('Diplomat', 'NS 150', 'Monaco', and 'Garne') had lower GY on average. GY was significantly related ($p<0.01$) to GN in triticale, wheat, two-rowed, and six-rowed barley (Fig. 2). There was no relationship between GY and GW in six- and two-rowed barley (Fig. 3). However, a weak positive relationship between these two traits was recorded in wheat ($r^2=0.39$, $p<0.05$) and triticale ($r^2=0.38$, $p<0.05$). Results from Fig. 4a showed that species differed in the strategy to generate GY. Similar GY was achieved due to a greater GW in two-rowed barley and triticale, while in wheat and six-rowed barley GY was mainly based on establishment of higher GN (Fig. 4a).

Variations in GW were mostly related to the differences between species (79.3% of total variance explained), followed by growing season, cultivar and species by growing season interaction (Table 2). Across growing seasons, triticale cultivars had higher GW than two-rowed and six-rowed barley and wheat cultivars (Table 3). On average, all two-rowed winter barley cultivars had higher GW compared to six-rowed cultivars. Furthermore, cultivars differed significantly in GW, and the average GW among cultivars ranged from 37.4 mg ('Nonius') to 50.5 mg ('Odisej'). Medium early wheat and two-rowed barley ('Pobeda' and 'NS 565') and early six-rowed barley and triticale cultivars ('Dorat' and 'Odisej') presented the highest GW. There was clear difference in mean GW between growing seasons (45.2 mg, 42.1 mg, 44.0 mg, and 41.5 mg for 2008/09, 2009/10, 2010/11 and 2011/12, respectively). The lowest GW was recorded in the 2011/12 growing season that was characterized by less favourable growing conditions, namely low precipitations and more days with maximum temperatures above 25 °C and 30 °C in May during anthesis and grain filling in June (Fig. 1).

Most of the variation in GN was explained by the growing season and species (Table 2). Averaged across growing seasons, six-rowed barley (20,506) and wheat (19,891) had similar GN, and both were higher than in two-rowed barley (17,354) and triticale (17,221). The mean GN of genotypes ranged from 16,380 ('Odisej') to 22,099 ('Nonius'). However, the highest yielding cultivar ('Pobeda') had neither the highest GN nor the highest GW. Across years, GN ranged between 15,906 (2011/12) and 20,009 (2010/11). The lowest GN was recorded in the 2011/12 growing season, when the lowest GY was also measured. A similar GN among species was reached through different strategies (Fig. 4b). In barley, a high GN was more related to a high number of spikes/m^2, while in the other species it was achieved through a high number of grains/spike and spikes/m^2. Differences among species explained the highest proportion of variance (96.5%) for number of spikes/m^2. Differences among the Y, S, C and Y × S interaction were significant ($p<0.01$) for the number of spikes/m^2 (Table 2). Among species/spike type, the mean number of spikes/m^2 was the highest in two-rowed barley, followed by wheat, six-rowed barley and triticale. No significant differences were observed between wheat

Table 3. Means for the main factors (cultivar, species, and growing season) for grain yield (GY), grain weight (GW), number of grains/m^2 (GN), number of spikes/m^2 (NSSM), number of grains/spike (NGS), number of fertile florets/spike (NFS), grain setting (GS), duration of the phase from emergence to heading (HD) and number of days from emergence to heading (NDEH) of wheat, six-rowed barley, two-rowed barley and triticale cultivars grown in four experimental years.

Species	Cultivar	Maturity group[2]	GY (kg/ha)	GW (mg)	GN (grains/m^2)	NSSM	NGS	NFS	GS (%)	HD (GDD)	NDEH (days)
Wheat	'Prima'	E	8058^{abcd}	38.9^{ef}	20730^{ab}	632^{b}	42.8^{e}	56.1^{d}	77^{ab}	1025de	199
	'Pobeda'	ME	8557^{a}	43.2^{cd}	19768^{bc}	565^{c}	45.5^{cde}	63.6^{bc}	72^{cdef}	1111^{c}	205
	'Diplomat'	L	7382^{e}	38.5^{ef}	19176^{cd}	574^{bc}	43.3^{de}	64.4^{bc}	67^{h}	1291^{a}	217
Six-rowed barley	'Dorat'	E	7999^{bcd}	40.8^{de}	19646^{bc}	554^{c}	46.2^{bcd}	60.7^{cd}	76^{abc}	991^{ef}	197
	'Nonius'	ME	8273^{abc}	37.4^{f}	22099^{a}	599^{bc}	48.2^{abc}	63.5^{bc}	76^{abcd}	1044^{d}	199
	'NS 150'	L	7429^{e}	37.6^{f}	19772^{bc}	563^{c}	45.8^{cde}	66.1^{b}	69^{fgh}	1132^{c}	203
Two-rowed barley	'NS 525'	E	8243^{abc}	46.0^{b}	17939^{def}	865^{a}	24.7^{f}	31.9^{e}	78^{ab}	969^{f}	195
	'NS 565'	ME	8258^{abc}	47.1^{b}	17532^{efg}	834^{a}	26.0^{f}	35.3^{e}	74^{bcde}	1033^{ef}	198
	'Monaco'	L	7652de	46.1^{b}	16591^{fg}	866^{a}	23.9^{f}	33.5^{e}	72^{defg}	1105^{d}	203
Triticale	'Odisej'	E	8298^{ab}	50.5^{a}	16380^{g}	435^{d}	49.3^{a}	62.8^{bc}	78^{a}	963^{f}	195
	'NS triti-kale'	ME	8533^{a}	47.1^{b}	18097de	461^{d}	51.1^{a}	72.7^{a}	71^{efgh}	1101^{c}	205
	'Garne'	L	7775^{cde}	45.3^{bc}	17156^{efg}	462^{d}	49.1^{ab}	72.5^{a}	68^{gh}	1236^{b}	212
	Species/spike type[1]										
	Wheat		7999^{ab}	40.2^{c}	19891^{a}	591^{b}	43.9^{c}	61.4^{c}	72^{b}	1142^{a}	207
	6R		7900^{b}	38.6^{d}	20506^{a}	572^{b}	46.7^{b}	63.5^{b}	74^{ab}	1056^{c}	200
	2R		8051^{ab}	46.4^{b}	17354^{b}	855^{a}	24.9^{d}	33.5^{d}	75^{a}	1036^{d}	199
	Triticale		8202^{a}	47.6^{a}	17211^{b}	454^{c}	49.8^{a}	69.3^{a}	72^{b}	1100^{b}	204
	Year										
	2008/09		8868^{a}	45.2^{a}	19791^{ab}	610^{ab}	45.7^{a}	61.1^{a}	76^{a}	1077^{b}	191
	2009/10		8030^{b}	42.1^{b}	19255^{b}	631^{a}	42.0^{b}	57.0^{b}	74^{b}	1061^{bc}	200
	2010/11		8711^{a}	44.0^{a}	20009^{a}	635^{a}	41.5^{b}	56.8^{b}	74^{b}	1047^{c}	206
	2011/12		6544^{c}	41.5^{b}	15906^{c}	595^{b}	36.2^{c}	52.8^{c}	69^{c}	1149^{a}	213

[1] 2R: two-rowed barley; 6R: six-rowed barley. [2] E: early; ME: medium early; L: late. Different letters represent significant difference between cultivars ($p<0.05$; Tukey test).

and six-rowed barley for this trait. Among cultivars, the highest number of spikes/m^2 was reported in 'NS 525' (865) and 'Monaco' (866), with almost half the value for 'Odisej' (435). The lowest number of number of spikes/m^2 was measured in 2011/12, while the highest mean number of spikes/m^2 was recorded in 2010/11.

The variation in the number of grains/spike was under significant effect of S, C, Y and Y × S interaction, with the highest contribution of species (87.4% of total variance explained). Triticale had higher number of grains/spike than wheat, six-rowed and two-rowed barley. However, there were no significant differences in the number of grains/spike among cultivars within each species. Two-rowed barley cultivars ('NS 525', 'NS 565' and 'Monaco') had lower number of grains/spike than other cultivars, while the highest number of grains/spike was recorded in triticale cultivars. Among species, the medium early cultivars ('Pobeda', 'Nonius', 'NS 565', and 'NS tritikale') had the highest number of grains/spike. The lowest mean number of grains/spike was recorded in 2011/12 (36.2) and the highest in 2008/09 (45.7). There were no significant differences between 2009/10 and 2010/11 for number of grains/spike.

The main factor explaining 92.3% of the total variation of the number of fertile florets/spike was species, while the effect of other factors was less pronounced. On average, triticale had the highest number of fertile florets/spike, while the lowest number was recorded in two-rowed barley cultivars. Among cultivars, 'NS tritikale', and 'Garne' produced the highest number of fertile florets/spike compared to other cultivars. On the other hand, two-rowed winter barley cultivars ('NS 525', 'NS 565', and 'Monaco') had the lowest number of fertile florets/spike. Within each species or spike type, early cultivars had the lowest number of fertile

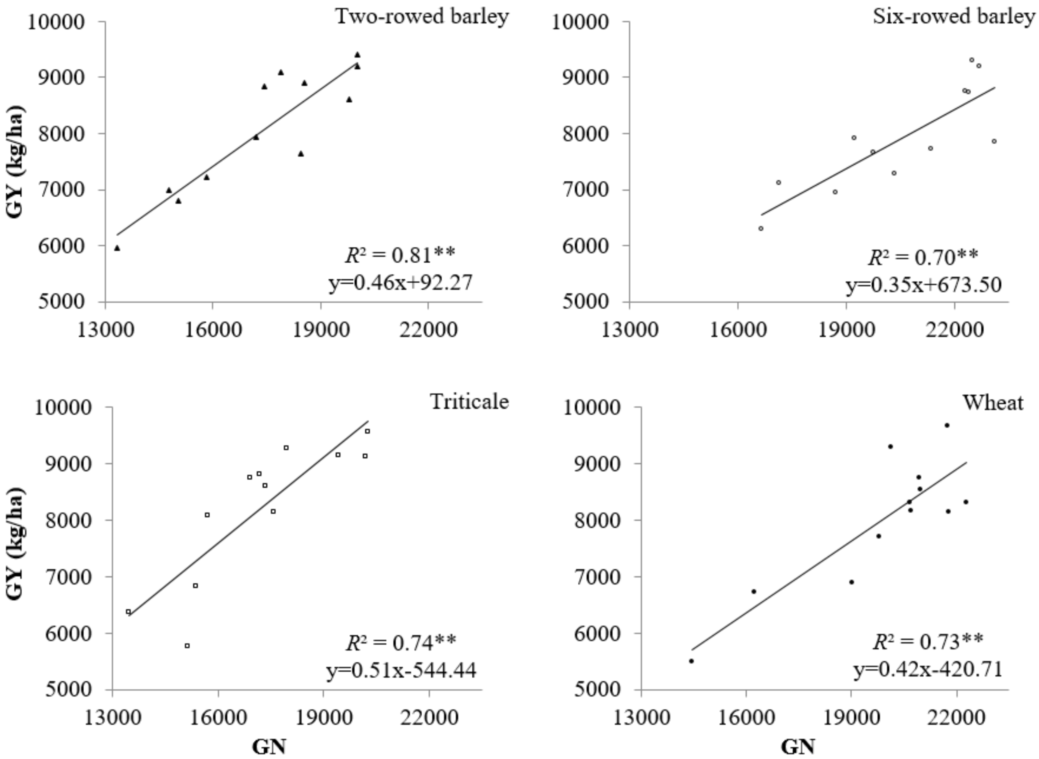

Figure 2. Relationship between grain yield (GY, kg/ha) and number of grains/m^2 (GN) in two-rowed barley, six-rowed barley, triticale and wheat cultivars grown during four growing seasons. Each symbol represents the mean value of each cultivar in each season.

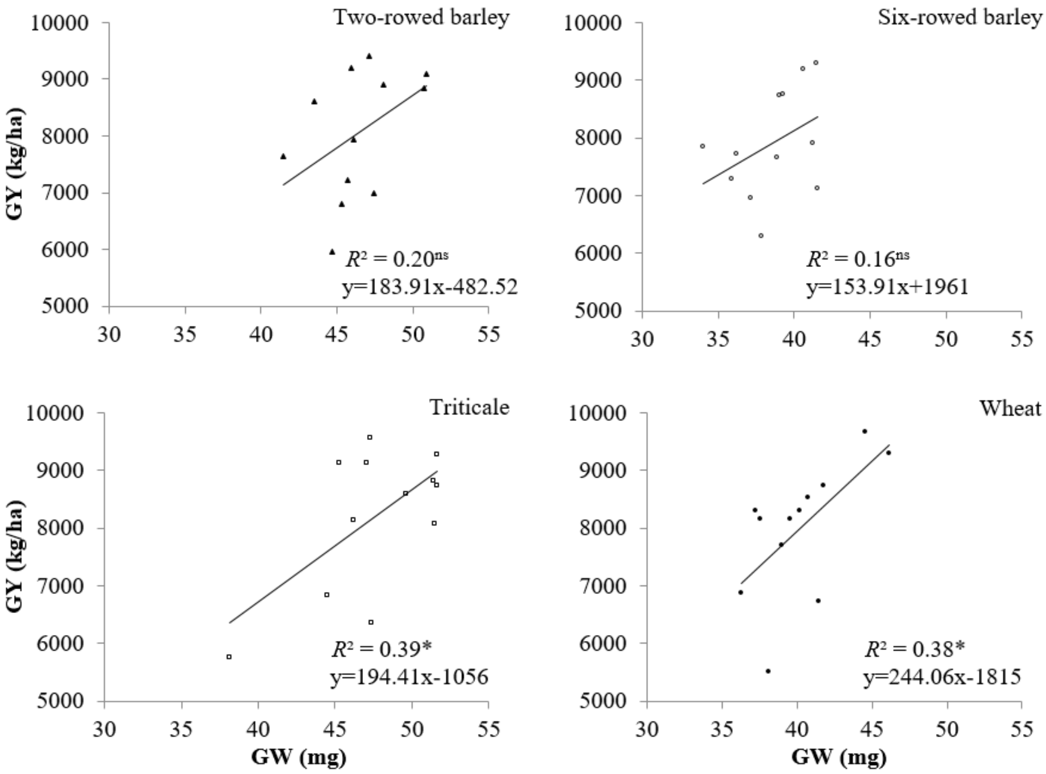

Figure 3. Relationship between grain yield (GY) and mean individual grain weight (GW) in two-rowed barley, six-rowed barley, triticale and wheat cultivars grown during four growing seasons. Each symbol represents the mean value of each cultivar in each season.

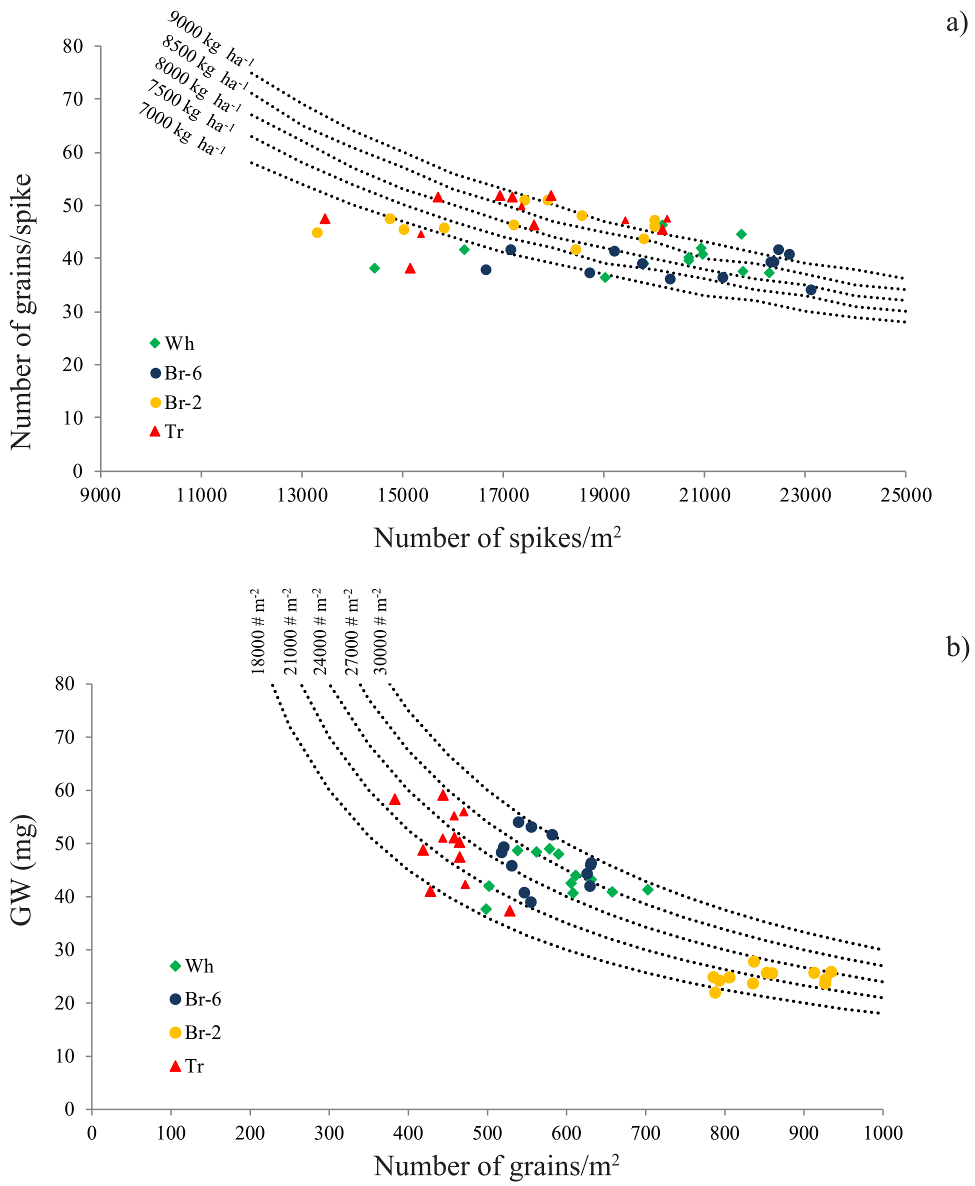

Figure 4. Relationship between mean individual grain weight and number of grains/m^2 (a), and between number of grains/spike and number of spikes/m^2 (b), in wheat (Wh), six-rowed barley (Br-6), two-rowed barley (Br-2), and triticale (Tr) cultivars grown in four growing seasons. The dotted lines represent lines for iso-grain yield in (a), and for iso-number of grains/m^2 in (b).

florets/spike. In wheat and six-rowed winter barley, the highest number of fertile florets/spike was reported in late cultivars, while in two-rowed barley and triticale the highest number of fertile florets/spike was recorded in medium early cultivars. The lowest number of fertile florets/spike was observed in 2011/12 (52.8) while the highest number of fertile florets/spike was recorded in 2008/09 (61.1).

The highest percentage of variation in grain setting was explained by the effect of growing season (80.6%), followed by species, Y × S interaction and cultivar (Table 2). Two-rowed barley presented the highest value of grain setting, while between six-rowed barley, wheat and triticale there were no significant differences (Table 3). Among cultivars, grain setting varied between 67% and 78%, the highest values being recorded in early and/or medium early cultivars within each species. Changes in mean temperature ± 7 days around anthesis explained 0.48, 0.65, 0.86 and 0.70 of the observed variation in grain setting in wheat, triticale, two-rowed and six-rowed barley, respectively (Fig. 5). According to Fig. 5, the increase of the average temperature around anthesis resulted in the decline in grain setting. However, the slope of the relationship between grain setting and mean temperature varied between species, the

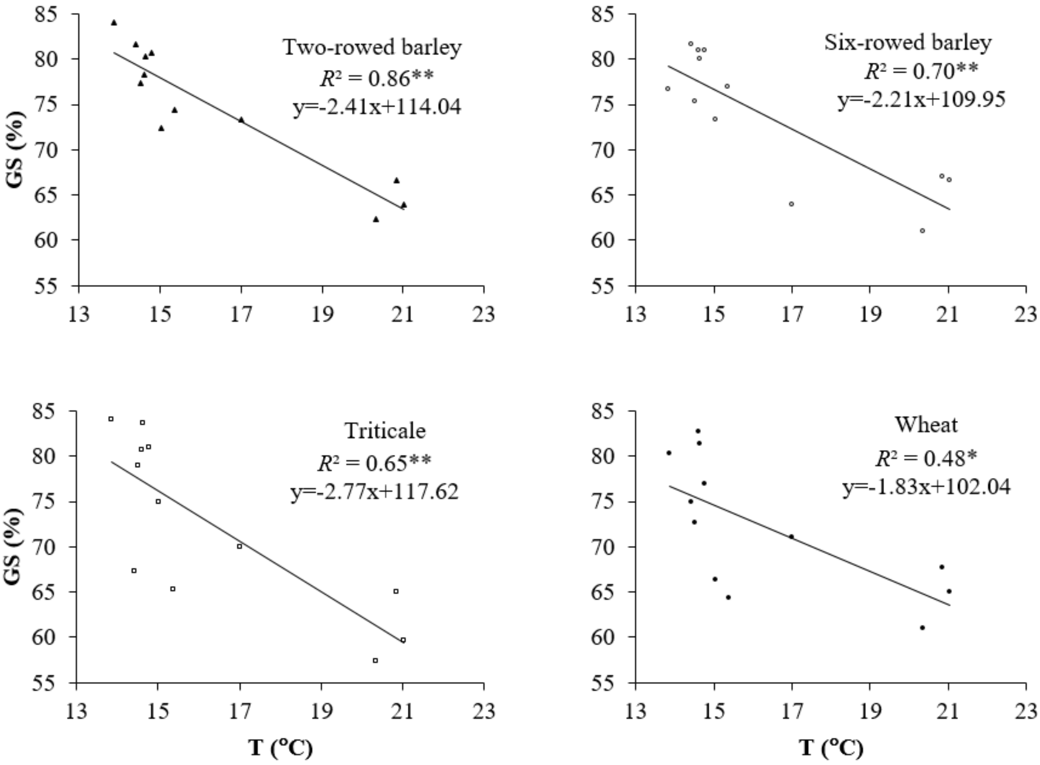

Figure 5. Relationships between grain setting percentage (GS) and mean temperature during the period from 7 days previous to anthesis to 7 days after anthesis (T) in two-rowed barley, six-rowed barley, triticale and wheat cultivars grown during three growing seasons. Each symbol represents the mean value of each cultivar in each season.

highest reduction in grain setting due to temperature increases was recorded in triticale, while wheat was the least sensitive. There was significant difference in grain setting among growing seasons. The lowest grain setting was recorded in 2011/12 (69%) when the lowest number of fertile florets and grains/spike were also observed (Table 3).

Almost half of the variation in the duration of the period between emergence and heading was under effect of cultivars (47.0%), while 27.3% and 24.7% was accounted for by species and growing season (Table 2). On average, the shortest period from emergence to heading was recorded in two-rowed barley cultivars and it was significantly lower than in other species (Table 3). On the other hand, winter wheat cultivars had the longest mean pre-heading duration. Among cultivars, there was no significant difference between early two-rowed ('NS 525'), six-rowed barley ('Dorat') and triticale ('Odisej') cultivars. The late maturity wheat cultivar 'Diplomat' had higher duration of the phase from emergence to heading ($p<0.05$) compared to other cultivars. Among growing seasons, the highest period to heading was recorded in 2011/12 (1149 GDD) and the shortest in 2010/11 (1047 GDD).

Discussion

Variability in GY of two-rowed and six-rowed barley, wheat and triticale cultivars across growing seasons (Tables 1 and 2) was the result of annual differences in total precipitation and its distribution, and temperature during the pre-heading and post-heading phase (Fig. 1). Additionally, many studies reported high year-to-year GY variation in environmental conditions of the Pannonian plain (Pržulj & Momčilović, 2012; Mirosavljević *et al.*, 2014) and a close relationship between GY and the level of precipitation during the pre-heading and post-heading period (Dodig *et al.*, 2012; Pržulj *et al.*, 2015). On average, triticale had higher average GY than barley and wheat, but it was only significantly higher than six-rowed barley. Nevertheless, when comparing only medium early cultivars, there were no significant differences among species (Table 3), suggesting that appropriate selection of cultivars could minimize differences between species/or spike type.

Grain yield was mainly determined by GN in wheat, triticale, six-rowed and two-rowed barley cultivars. This result supports findings of many authors (Fischer, 2008; Francia *et al.*, 2013), who indicated that GN was more important than GW in final GY determination. Yield improvement in wheat cultivars in the Pannonian plain in the previous fifty years was mainly associated with an increase in GN (Mladenov *et al.*, 2011). Furthermore, results from our study showed lack of a significant relationship between GY and GW in two-rowed and six-rowed barley. In wheat and triticale this relationship was significant but lower compared to the relationship between GN and GY. Our results showed that in two-rowed barley, GN variation was more associated with the establishment of high number of spikes/m^2 than in other studied species due to high tillering capacity (Slafer *et al.*, 2014). In triticale, wheat and six-rowed barley, GN was mainly related to the combination of both grain number/spike and number of spikes/m^2. Although six-rowed barley, wheat and triticale produced less spikes/m^2 than two-rowed barley, all studied species had similar GN due to the lower ability of two-rowed barley to increase the number of grains/spike (Alvarez-Prado *et al.*, 2017). Slight GW increase in barley (Mirosavljević *et al.*, 2016) and no yield increase in wheat (Mladenov *et al.*, 2011) were reported for cultivars grown in the Pannonian plain. The difference in genetic improvement of GW between barley and wheat could be the result of strict quality requirements of the malting industry for malting barley cultivars with increased GW. Griffiths *et al.* (2015) reported the possibility of developing new high yielding wheat cultivars with optimal GN and GW. In general, in our study medium early cultivars achieved the highest GY due to high GN, but also high GW, since the grain filling period of these cultivars escaped from terminal drought. Therefore, further improvement of cereal production in the Pannonian environment could be achieved by selecting and growing medium early cultivars with high GN and the same or even higher GW.

Unfavorable environmental conditions (lack of precipitation and high temperatures) during stem elongation, anthesis and grain filling period significantly reduce GN and GW in different cereal crops (Ugarte *et al.*, 2007; Kaur & Behl, 2010). In 2011/12, GW decreased by 8% compared to the maximum recorded GW of 45.2 mg (2008/09), while GN declined by 21% in relation to the season with the maximum values of this trait (20009 grains/m^2 in 2010/11). These results confirm findings of different authors (Sadras, 2007; Sadras & Slafer, 2012) that GN is more plastic to the influence of environmental conditions than GW. On the other hand, the highest GN and GW were recorded in 2008/09 and 2010/11, when high precipitation in March and June and lower temperature in May and June were reported. Although GN was the main component that explained variations in GY among species, GW also showed remarkable differences among studied species. Triticale and two-rowed barley had significantly higher GW than six-rowed barley and wheat.

The lowest number of fertile florets was reported in early cultivars within each species/spike type ('NS 525', 'Odisej', 'Prima', and 'Dorat') characterized by short duration of the period between emergence and heading. There is a close relationship between the duration of the phase from emergence to heading and duration of stem elongation phase (Borràs *et al.*, 2009; Pržulj & Momčilović, 2011). Duration of stem elongation phase is important for determination of the final GN, since during this period the number of fertile florets is formed (Fischer, 2007; Gonzales *et al.*, 2011). Consequently, the lower GY potential of early cultivars in relation to medium early cultivars could be due to shorter duration of the pre-anthesis period and lower number of fertile florets. On the other hand, late maturity varieties had equal or even higher number of fertile florets than medium early and early cultivars. However, they were characterized by reduced grain setting. As a result of late heading, anthesis occured during the period of higher temperature that negatively influenced grain setting (Fig. 5). Therefore, medium early cultivars achieved the highest grain number/spike by simultaneously combining both high percentage of grain setting and increased number of fertile florets/spike. Isidro *et al.* (2011) indicated a negative relationship between temperature around anthesis and grain setting, since increase in temperature was followed by decline in grain setting. Numerous studies recognized the anthesis time as a key adaptive trait (Reynolds *et al.*, 2009; Fischer, 2011). Also, late anthesis increases the risk of terminal stress (high temperature and/or water deficit) in Pannonian and drought prone environments (Francia *et al.*, 2013), which negatively influences final GW (Dias & Lindon, 2009). Therefore, simultaneous increase of the duration of the stem elongation phase (Fischer, 2008) and optimization of anthesis time (Reynolds *et al.*, 2009) could increase number of fertile florets and GN and, ultimately, GY potential in small grain cereals.

In general, results of this study indicate that growing season, species, cultivar, and species by growing season interaction significantly influenced GY and its determinants. Grain yield in the studied cereal crops was more limited by GN than GW, however the species differed in the composition of GN. In two-rowed barley GN depended on the establishment of high number of spikes/m^2, while in other studied species GN was mainly related to the combination of both grain number/spike and number of spikes/m^2. In spite of the fact that GN was the main component that explained variations in GY between species, GW showed remarkable differences between species. Moreover, triticale and two-rowed barley were characterized by higher GW than the other two species. Heading date was recognized as an important adaptive trait in crop development: short duration of the pre-anthesis phase in early cultivars and delayed anthesis in late cultivars had a significant influence on grain number/spike in different species/spike type, reducing the final GY. Medium early cultivars had the highest number of grains/spike due to optimal duration of the pre-anthesis period and heading date. Therefore, further improvement of cereal production in a Pannonian environment could be achieved by selecting and growing medium early cultivars characterized by higher GN.

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