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HERITABILITY, GENETIC ADVANCE AND CORRELATIONS OF PLANT HEIGHT, SPIKE LENGTH AND PRODUCTIVE TILLERING IN BREAD WHEAT AND DURUM WHEAT

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Summary: The aim of this research was to examine variability, broad-sense heritability, genetic advance of plant height (PH), spike length (SL) and productive tillering (PTC) of 30 genotypes of bread and durum wheat, and correlations between them. Field trials were carried out during 2010-2011 and 2011-2012 growing seasons at the three sites: Rimski Šančevi, Zemun Polje and Padinska Skela. Results of this investigation showed that genotype was the most significant source of variation for SL in bread and durum wheat with 67.1% and 54.4% of explained sum of squares (SS) and for PH in bread wheat with the 66% of SS. Environment represented the most important source of variation for PTC in bread and durum wheat with 68% and 35.9% of SS and also for PH in durum wheat with 51.6% of SS. The ratio of genetic and genotype \times environment interaction ($\sigma_g^2 / \sigma_{ge}^2$) components of variance indicated more stability in bread wheat for PH and SL and less for PTC in both wheat species. Broad-sense heritability (h^2) was very high (>90%) for PH and SL in bread and durum wheat, but smaller for PTC (80.7% and 75.6%, respectively). Considering the high obtained values of h^2 and high expected genetic advance as percent of mean for PH and SL of bread wheat and for PTC of durum wheat the success of selection for desired trait values can be predicted. PH proved to be correlated with PTC at three environments (0.538, 0.532, $P < 0.05$, 0.708, $P < 0.01$).

Key words: wheat, plant height, spike length, productive tillering, genetic advance, correlations.

INTRODUCTION

After a period in wheat breeding known as the "Green Revolution", wheat varieties are short stature and highly responsive to management and fertilizer inputs with greater potential to high grain yield as compared to the long statured varieties (Khush, 2001). Genetic inheritance of plant height is complex, because although plant height is a quantitative trait, major genes are also involved. There are many Rht genes for the reduction of plant height in wheat,

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but only Rht-B1b (Rht1), Rht-D1b (Rht2) and Rht8 are intensively used in wheat breeding (Zhang et al. 2011). In addition, many QTLs for plant height have been identified in wheat (Heidari et al. 2012). In most diallel studies of wheat, which investigated the mode of the inheritance of plant height, partial dominance of additive genetic effects was determined (Yao et al. 2011), while superdominance was also reported (Saleem et al., 2005). Spike length is one of the important grain yield components, and the source of assimilates closest to the caryopsis. The spike structure provides the most beneficial effects in the use of light as compared to the other parts of the wheat plant (Sharma et al. 2003). Together with the awns, spike remains longer green as compared to other parts of the plant. Because of these properties spike contributes with 20-30% to grain dry weight accumulation (Abdoli et al. 2013). The importance of additive genes in the inheritance of spike length in wheat, which can be fixed in the early generations due to high heritability, was determined by Songsri et al. (2008), but also significant bigenic epistatic effects were reported by Nanda et al. (1981). Wei and Wu (1990) reported that the spike length is qualitative trait affected by a major gene with a number of modifying genes. Tillering is an important yield component representing underground stalk branching and plant shooting at an early ontogenesis stages, influencing the crop uniformity and plant density, and directly affecting the crop structure (Madić et al. 2006). The intensity of tillering is affected by nutrition, plant density, planting date and genotype tendency towards the secondary tillers formation (Glamočlija, 2012). Productive tillering is controlled by the effects of dominant genes and superdominance (Zečević et al. 1995). Also, environmental factors affect PTC, and among them especially important are sum of mean temperatures (≥ 0 °C) from sowing to dormant phase (Lv et al. 2013), precipitation or irrigation levels in the spring, and mineral nutrition, primarily nitrogen (Pavlović, 1997). Fischer (2008) reported that, under normal conditions, approximately 30 to 50% of wheat grain yield comes from the main stem, and 50 to 70% from the tillers.

The aim of this study was to explore components of variance, heritability in a broad sense, genetic advance of plant height, spike length and productive tillering in bread and durum wheat, as well as, correlations among them, for the assessment of good breeding practice possibilities.

MATERIAL AND METHODS

Genetic material, experimental design and field trials: The genetic material used for the multi-environment field trials consisted of 15 bread wheat (*Triticum aestivum* L. ssp. *aestivum*) and of 15 durum wheat (*Triticum durum* Desf.) genotypes. Genotypes represented accessions from the GeneBank of Institute of Field and Vegetable Crops in Novi Sad, and from the GeneBank of the Maize Research Institute "Zemun Polje" in Belgrade, Serbia. The field trials were set as randomized complete block design with four replications at the Rimski Šančevi (RS) (45°19'51" N; 19°50'59" E), Zemun Polje (ZP) (44°52' N; 20°19' E) and Padinska Skela (PS) (44°57' N 20°26' E), in Serbia, during two vegetation seasons-2010–2011(11) and 2011–2012(12). The two vegetation seasons were different from meteorology viewpoint across test sites: 2010-2011 year was warmer and with much more precipitation during November-February period, but also with smaller average mean temperatures during March-June in comparison to 2011-2012. The experimental plot consisted of 5 rows of 1 m length with inter-row spacing of 0.2 m. The elementary plot consisted of 3 internal rows of 0.6 m² (3 × 0.2 × 1 m) and plant material within it was used for the analysis. Haplic Chernozem (CHha) is the soil type at the RS and ZP, while Humic Gleysol (GLhu) is at the PS, according to the IUSS Working Group WRB (2014) classification. Standard agricultural practices were applied at all trial sites during both growing seasons. Plant height (PH) and spike length (SL) were measured on 20 representative plants per elementary plot and expressed in cm. Coefficient of the productive tillering (PTC) was determined as the ratio of the number of spikes in the maturation stage and the number of overwintered plants counted in the spring at the elementary plot per each repetition.

Statistical analyses: The two-way fixed analysis of variance (ANOVA) was used for the quantification of the sources of variation effects, based on random complete block design, with the effects of genotype and environment as fixed ones. Environment represented year × test site combination. Testing the difference in trait means between bread and durum wheat was carried out using t-test. ANOVA and Pearson's correlation coefficients were calculated by the use of the STATISTICA 9.0. (Statsoft, 2009). Broad sense heritability (h^2) was calculated as the ratio the genotypic variance to the phenotypic variance according to Falconer and Mackay (1996). Expected genetic advance as part of the mean (GA) for each trait at 5% selection intensity ($k = 2.056$) was computed using the formula described by Johnson et al. (1955). Expected genetic advance as percent of mean (GAM) was calculated to compare the extent of predicted genetic advance of different traits with different measurement units.

RESULTS

PH varied in the interval of 66.5-112.2 cm with the mean value of 88.7 cm in bread wheat and in the interval of 58.8-85.5 cm with the mean value of 71.5 cm in durum wheat (Figure 1). The highest mean PH of 101.0 cm had RS-11 environment, while the lowest mean PH of 80.9 cm was measured for PS-12 for bread wheat. The significant mean ($P < 0.05$) differences for PH were observed between bread and durum wheat based on the t -test at the all three test sites and also for all sites mean values. The RS-11 environment had the highest mean PH of 81.9 cm, while the lowest mean of 63.1 cm was measured in RS-12 environment for durum wheat. Based on the ANOVA the major source of variation for PH expressed as % of sum of squares (SS) was genotype (G) (66%), environment (E) (28%) afterwards, and then $G \times E$ interaction (GEI) (6%) for bread wheat and E (51.6%), G (33%), and GEI (15.4%) in descending order, for durum wheat (Table 1). h^2 , CV_g and CV_p for PH were higher in bread wheat compared to durum wheat, and GA and GAM were higher, up to two times, in bread wheat (Table 1).

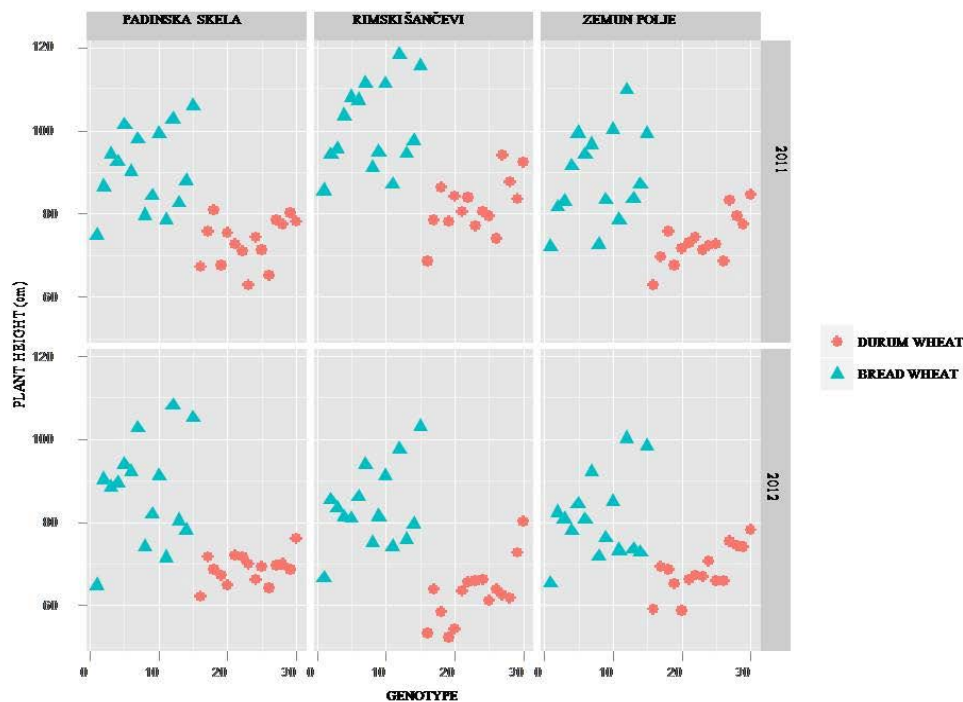


Figure 1. Plant height for bread and durum wheat by test sites in 2010–2011. and 2011–2012 year.

Table 1. Analysis of variance, variance components, heritability, genetic advance and coefficients of variation of PH.

Source of variation	df	SS	SS (%)	MS [†]	σ_g^2	σ_{ge}^2	σ_e^2	$h^2(\%)$	CV_g (%)	CV_p (%)	GA	GAM (%)
<i>Triticum aestivum ssp. aestivum</i>												
Environment (E)	5	14475.8	28.0	2895.2***	99.8	8.5	1.9	98.2	11.3	11.4	20.4	23
Genotype (G)	14	34158.5	66.0	2439.9***	-	-	-	-	-	-	-	-
$G \times E$	70	3106.3	6.0	44.4***	-	-	-	-	-	-	-	-
Error	252	2628.0		10.4	-	-	-	-	-	-	-	-
<i>Triticum durum</i>												
Environment (E)	5	12248.5	51.6	2449.7***	21.2	11.3	2.2	90.7	6.4	6.8	9.0	12.5
Genotype (G)	14	7839.5	33.0	560.0***	-	-	-	-	-	-	-	-
$G \times E$	70	3656.3	15.4	52.2***	-	-	-	-	-	-	-	-
Error	252	1791.5		7.1	-	-	-	-	-	-	-	-

*** $P < 0.001$; [†] tested with error mean square, df-degrees of freedom, SS-sum of squares, MS-mean squares, σ_g^2 -genetic variance, σ_{ge}^2 -variance of GEI, σ_e^2 - environmental variance, h^2 -broad-sense heritability, CV_g -coefficient of genetic variation, CV_p -coefficient of phenotypic variation, GA-expected genetic advance, GAM-expected genetic advance as percent of mean.

Interval of variation for SL was 6.5-11.3 cm with the mean value of 8.8 cm in bread wheat and 6.1-9 cm with the mean value of 7.3 cm in durum wheat (Figure 2). The mean value for SL was by 17.1% higher in bread wheat as compared to durum wheat. PS-11 environment exhibited the highest mean SL of 9.5 cm, while the lowest mean SL of 8.0 cm had ZP-12 environment in bread wheat. In durum wheat, the highest mean SL of 7.8 cm was recorded for the RS-12 environment, while the lowest mean SL of 6.8 cm was measured for the ZP-11 environment. The significant means ($P < 0.05$) differences for SL were observed between bread and durum wheat according to t -test at the all three sites and also for all sites mean values. ANOVA determined the same hierarchy of importance in sources of variation for SL expressed in % of sum of squares in bread and durum wheat, respectively: $G (67.1\% \text{ and } 54.4\%) > E (22.5\% \text{ and } 24.6\%) > GEI (10.4\% \text{ and } 21\%)$ (Table 2). h^2 , CV_g , CV_p and GA for SL were higher in bread wheat comparing with durum wheat, and GAM was higher for 36.3% in bread wheat (Table 2).

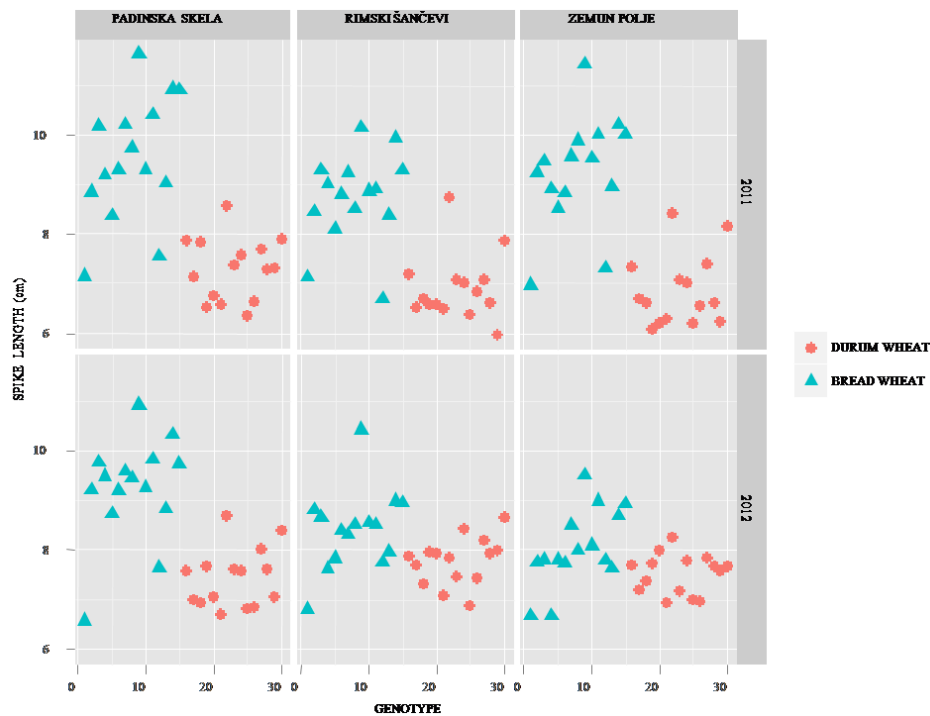


Figure 2. Spike length for bread and durum wheat by test sites in 2010–2011. and 2011–2012 year.

Table 2. Analysis of variance, variance components, heritability, genetic advance and coefficients of variation of SL.

Source of variation	df	SS	SS (%)	MS [†]	σ_g^2	σ_{ge}^2	σ_e^2	$h^2(\%)$	CV_g (%)	CV_p (%)	GA	GAM (%)
<i>Triticum aestivum</i> ssp. <i>aestivum</i>												
Environment (E)	5	98.1	22.5	19.6 ^{***}	0.8	0.1	0.03	96.9	10.4	10.5	1.8	20.4
Genotype (G)	14	291.7	67.1	20.8 ^{***}	-	-	-	-	-	-	-	-
G × E	70	45.3	10.4	0.6 ^{***}	-	-	-	-	-	-	-	-
Error	252	43.0		0.2	-	-	-	-	-	-	-	-
<i>Triticum durum</i>												
Environment (E)	5	38.4	24.6	7.7 ^{***}	0.2	0.1	0.02	92.3	6.6	6.9	1.0	13.0
Genotype (G)	14	85.1	54.4	6.1 ^{***}	-	-	-	-	-	-	-	-
G × E	70	32.8	21.0	0.5 ^{***}	-	-	-	-	-	-	-	-
Error	252	29.4		0.1	-	-	-	-	-	-	-	-

*** $P < 0.001$; [†] tested with error mean square, df-degrees of freedom, SS-sum of squares, MS-mean squares, σ_g^2 -genetic variance, σ_{ge}^2 -variance of GEI, σ_e^2 - environmental variance, h^2 -broad-sense heritability, CV_g -coefficient of genetic variation, CV_p -coefficient of phenotypic variation, GA-expected genetic advance, GAM-expected genetic advance as percent of mean.

PTC varied from 1.3-2.3 in bread wheat with the average value of 1.76, and from 1.0-2.8 with the mean value of 1.67 (Figure 3). Bread wheat had higher PTC mean value by 5.1% compared to durum wheat. The highest mean PTC of 2.3 was recorded for the PS-12 environment, while the lowest average value of 1.3 was measured for the ZP-12 environment in bread wheat. The PS-11 environment had the highest mean PTC of 2.3 and for the RS-12 was observed the lowest mean PTC value of 1.3 in durum wheat. Based on the *t*-test non-significant differences were observed between PTC mean values for bread wheat and durum wheat across all three sites and sites average. ANOVA showed the impact of sources of variation for PTC in the following descending order: E (68%) > G (16.3%) > GEI (15.7%) for bread wheat and E (35.9%) > GEI (35.2%) > G (28.9%) for durum wheat (Table 3). Although h^2 for PTC was higher in bread wheat compared to durum wheat, CV_g , CV_p , GA were higher in durum wheat with GAM being higher up to 43% in durum wheat (Table 3).

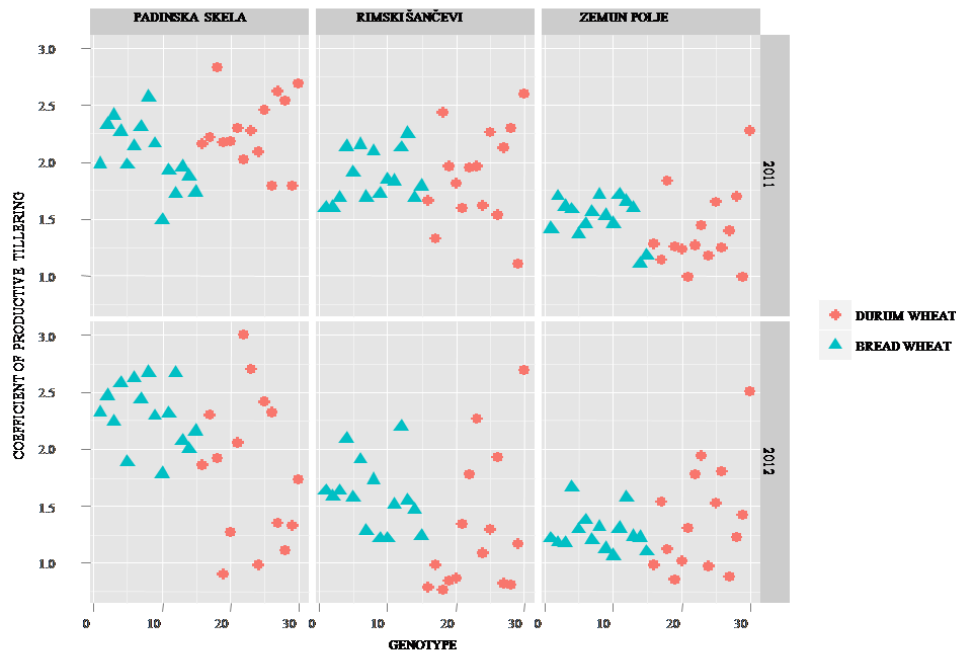


Figure 3. Productive tillering coefficient for bread and durum wheat by test sites in 2010–2011, and 2011–2012 year.

Table 3. Analysis of variance, variance components, heritability, genetic advance and coefficients of variation of PTC.

Source of variation	df	SS	SS (%)	MS [†]	σ_g^2	σ_{ge}^2	σ_e^2	$h^2(\%)$	CV_g (%)	CV_p (%)	GA	GAM (%)
<i>Triticum aestivum ssp. aestivum</i>												
Environment (E)	5	43.6	68.0	8.7 ^{***}	0.02	0.03	0.01	80.7	9.0	10.0	0.3	17
Genotype (G)	14	10.4	16.3	0.7 ^{***}	-	-	-	-	-	-	-	-
G × E	70	10.0	15.7	0.1 ^{***}	-	-	-	-	-	-	-	-
Error	252	2.1		0.0	-	-	-	-	-	-	-	-
<i>Triticum durum</i>												
Environment (E)	5	43.6	35.9	8.7 ^{***}	0.08	0.2	0.03	75.6	16.8	19.3	0.5	29.8
Genotype (G)	14	35.1	28.9	2.5 ^{***}	-	-	-	-	-	-	-	-
G × E	70	42.9	35.2	0.6 ^{***}	-	-	-	-	-	-	-	-
Error	252	2.2		0.0	-	-	-	-	-	-	-	-

*** $P < 0.001$; [†] tested with error mean square, df-degrees of freedom, SS-sum of squares, MS-mean squares, σ_g^2 -genetic variance, σ_{ge}^2 -variance of GEI, σ_e^2 - environmental variance, h^2 -broad-sense heritability, CV_g -coefficient of genetic variation, CV_p -coefficient of phenotypic variation, GA-expected genetic advance, GAM-expected genetic advance as percent of mean.

Significant ($P < 0.05$) medium correlation was shown between PH and PTC at the RS11 and ZP11 environments (0.538 and 0.532, respectively), whereas highly significant ($P < 0.01$) medium high correlation was recorded at the RS12 (0.708) in durum wheat (Table 4).

Table 4. Pearson's correlation coefficients between examined agronomic traits per environment for bread and durum wheat

	RS11		RS12		ZP11		ZP12		PS11		PS12	
	PH	SL	PH	SL	PH	SL	PH	SL	PH	SL	PH	SL
<i>Triticum aestivum</i> ssp. <i>aestivum</i>												
SL	-0.081		0.254		-0.187		0.221		0.025		0.057	
PTC	0.256	-0.286	-0.103	-0.546*	-0.273	-0.097	0.066	-0.503	-0.372	0.152	0.081	-0.152
<i>Triticum durum</i>												
SL	0.182		0.357		0.332		0.076		0.255		0.344	
PTC	0.538*	0.365	0.708**	0.095	0.532*	0.375	0.339	-0.245	0.444	0.180	0.266	0.027

* Significant at $P < 0.05$; ** Significant at $P < 0.01$.

DISCUSSION

Plant height mean value was 19.4% higher in bread wheat than in durum wheat and similar to the findings of Ali and Shakor (2012) (Figure 1). PH is an important trait in regard to achieving high and stable grain yield. Varieties with high stature are prone to lodging when excessive fertilization is applied. Vice versa, very short stature varieties have denser leaves, poor ventilation and poor light transmission from middle canopy parts to bottom what affects adversely grain filling and leads to yield decrease (Zhang et al. 2011). The most important source of PH variation in bread wheat proved to be G ($P < 0.001$) but other authors as predominant source emphasized E (Aydin et al. 2010, Degewione et al. 2013). σ^2_g was higher than σ^2_{ge} by 11 times in bread wheat but in durum wheat only by 1.8 times, indicating PH to be more stable in bread wheat (Table 1). The higher mean PH values but lower of CV_g and CV_p in bread wheat were reported by some authors (Tayyar, 2008, Aydin et al. 2010, Gulnaz et al. 2011). The lower mean PH values, CV_p and CV_g , h^2 and GAM were reported by Degewione et al. (2013) in bread wheat, whereas similar mean value and CV_g and CV_p to our results were reported by Ali et al. (2008). Mohammadi et al. (2011) found higher mean values for PH in durum wheat with higher CV_g and also similar h^2 as in our investigation. Kashif and Khaliq (2004) found smaller CV_p , CV_g , GA and similar h^2 for PH as our values, but Aydin et al. (2010) reported much lower h^2 than in our study. High GA and GAM for PH in bread wheat in our study and altogether with high h^2 indicated presence of additive gene actions and possible success of selection in the early generations. Kahrizi et al. (2010) and showed h^2 estimate for PH to be medium to medium high but GAM was higher than in our investigation, whereas Khalid et al. (2011) and Khan and Naqvi (2011) reported smaller h^2 and smaller GA.

Spike length is contributing toward higher yield because longer spikes can carry more grains. Mohammadi et al. (2011) and Tayyar (2008) also pointed G as the predominant source of variation for SL in durum wheat, whereas Degewione et al. (2013) emphasized environment as most influential. σ^2_g was higher than σ^2_{ge} by 7 times in bread wheat and by 2.6 times in durum wheat making SL more stable trait in bread wheat. Similar values for h^2 , CV_g , CV_p , GA, for SL reported Kashif and Khaliq (2004), whereas smaller values for h^2 for SL were obtained by other authors (Khan and Naqvi, 2011, Ali and Shakor, 2012). Ali et al. (2008) and Ali and Shakor (2008) obtained smaller mean SL values, h^2 , GA and GAM in bread and durum wheat, whereas Eid (2009) showed higher GAM, and Gulnaz et al. (2011) showed higher GA than in our study.

Coefficient of the productive tillering indicates potential for uniformity and crop density influencing canopy and yield. Dodig et al. (2012) showed similar PTC values for regional accessions of bread wheat from south-east Europe. Protić et al. (1999) obtained yield regression in bread wheat, showing that by enlarging PTC as independent variable by 1, grain yield increased for 1174 kg ha⁻¹. Dodig et al. (2012) reported that E was predominant source of variation for PTC of south-east European bread wheat accessions and landraces. Smaller h^2 values than ours for PTC in bread wheat were reported by other authors (Pavlović, 1997, Pržulj et al. 1999). Gulnaz et al. (2011) obtained similar h^2 estimates for PTC in bread wheat as in our study, but their CV_g and CV_p were higher.

The main purpose of estimating heritability and variance components is to compare the expected success from selection based on different selection strategies. PH and SL in bread and durum wheat showed an ample scope for genetic improvement. It means that breeders should pay more attention to select the genotypes with lodging resistance and optimal SL for the sites in which trials were conducted. Heritability, a measure of the phenotypic variance attributable to genetic causes, has predictive function in crop breeding (Songsri et al. 2008). The utility of heritability increases when it is used to calculate GA, which indicates the degree of gain in a character obtained under a particular selection pressure (Shukla et al. 2004). Considering the high obtained values of h^2 and high expected GA as percent of mean for PH and SL in bread wheat and for PTC in durum wheat, additive gene action is assumed for these traits and the success of selection is anticipated.

Correlation among different traits is generally due to the presence of linkage and pleiotropic effects of different genes and is useful in unraveling possibilities for the simultaneous multi-trait breeding. Ali et al. (2008) showed negative correlation between PH and PTC (-0.342, $P < 0.01$) in bread wheat, whereas Gulnaz et al. (2011) reported

positive one (0.132, $P < 0.01$). SL was negatively correlated with PTC at the RS12 (-0.546, $P < 0.05$) in bread wheat (Table 4), what is similar with Kashif and Khaliq (2004) and Mohammadi et al. (2011). Consistent and significant correlations across only one environment for PTC and SL, and across two environments for PH and PTC are not enough for generalizing findings.

CONCLUSION

The results obtained from field trials carried out at three sites during two growing season showed quite considerable range of variability for PH, SL and PTC in bread and durum wheat. The genetic component of variance was dominant for SL in bread and durum wheat and for PH in bread wheat. The ecological variance represented the most important component of variation for PTC in bread and durum wheat and also for PH in durum wheat. The ratio of the genetic and genotype \times environment interaction components of variance indicated more stability in bread wheat for PH and SL and less for PTC in both wheat species. Broad-sense heritability was very high (>90%) for PH and SL in bread and durum wheat, and medium high for PTC. PH proved to be significantly positively medium to medium high correlated with PTC at three environments.

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HERITABILNOST, GENETIČKA DOBIT I KORELACIJE VISINE BILJKE, DUŽINE KLASA I PRODUKTIVNOG BOKORENJA HLEBNE I DURUM PŠENICE

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Izvod: Cilj ovog istraživanja je bio da se prouči varijabilnost, heritabilnost u širem smislu, genetička dobit za visinu biljke (PH), dužinu klasa (SL) i koeficijent produktivnog bokorenja (PTC) 30 genotipova hlebne i durum pšenice, kao i korelacije među njima. Poljski ogledi su bili postavljeni tokom 2010-2011. i 2011-2012 vegetacione sezone na tri lokaliteta: Rimski Šančevi, Zemun Polje i Padinska Skela. Rezultati ovog istraživanja su pokazali da je genotip bio najznačajniji izvor variranja za SL hlebne i durum pšenice sa 67,1% i 54,4% objašnjene sume kvadrata (SS) i za PH hlebne pšenice sa 66% SS. Ekološki faktori su predstavljali najznačajniji izvor variranja za PTC hlebne i durum pšenice sa 68% i 35,9% SS, kao i za PH durum pšenice sa 51,6% SS. Odnos komponenti varijanse-genetičke i interakcije genotip \times sredina ($\sigma_{ge}^2 / \sigma_{ge}^2$) je ukazala na veću stabilnost hlebne pšenice za PH i SL, i manju za PTC, za obe vrste pšenice. Heritabilnost u širem smislu (h^2) je bila veoma visoka (> 90%) za PH i SL hlebne i durum pšenice, dok je za PTC bila niža (80,7% i 75,6%). Uzimajući u obzir dobijene visoke vrednostiza h^2 i očekivanu genetička dobit izraženu u procentima proseka za PH i SL hlebne pšenice i za PTC durum pšenice, može se očekivati uspeh selekcije za očekivane vrednosti proučavanih osobina. PH je bila korelisana sa PTC u tri sredine (0,538 i 0,532, $P < 0,05$, 0,708, $P < 0,01$).

Ključne reči: pšenica, visina biljke, dužina klasa, produktivno bokorenje, genetička dobit, korelacije.

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