Variability of Spike Productivity in F_2 Hybrids Obtained by Crossing Common Wheat Varieties Novosibirskaya 67, Saratovskaya 29, and Puza-4 with the Skle 123-09 Multifloret Line

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Abstract—Parameters of spike productivity indices were evaluated in plants of F_2 populations obtained by crossing the Novosibirskaya 67, Saratovskaya 29, and Puza-4 varieties with the Skle 123-09 line, characterized by "multifloret". It is shown that the line Skle 123-09 differed significantly from the studied cultivars in spike density, but no significant differences were found in spike length or the number of spikelets. Two-way analysis of variance in F_2 hybrids showed that the variability of the spike length was contributed mainly by the genotypic environment and the interaction of the factors "genotype × environment". The variability of the number of spikelet in spike was determined mainly by environmental conditions. This was particularly true for cultivars Saratovskaya 29 and Puza-4, which were created for the cultivation in arid regions. The variability of the resulting character "spike density" was affected by environmental conditions, genotype, and the "genotype × environment" interaction. Examination of the F_2 populations revealed plants with fan-shaped spikelets; high grain content, as in Skle 123-09; and the best performance of other spike characters. The selected plants will be used to fix the multifloret character in the parental varieties.

Keywords: common wheat, multifloret line, spike productivity characters, genetic analysis of F_2 hybrids, variance analysis

Common wheat (*Triticum aestivum* L.) is the most important cereal. It plays a key role in food supply security, independence, and the well-being country (Vavilov, 1935; Zhuchenko, 2004). Therefore, the increase of wheat performance is a top priority for many branches of genetics and breeding (Zhuchenko, 2004; Godfray et al., 2010; Reynolds et al., 2011). In this regard, the most urgent objectives are the search for and development of new sources of diverse material combining high productivity and adapted to local environment, as well as the investigation of the genetic potential and employment of new approaches for the detection of varieties promising for breeding. Such studies invoke local wheat accessions and relatives with the high spike productivity (Vavilov, 1935; Martinek and Bednar, 1988, 2001; Jiang et al., 1994; Martinek, 1994; Merezhko, 1994; Li and Zhao, 2000; Dobrovolskaya et al., 2009).

Spike productivity, or spike grain weight, is among the main components of the yield formula. However, this component is a generalized index, which depends on other characters: spike length, spike density, number of spikelets, number of grains per spike, and the mean weight of one grain (Vavilov, 1935; Filipchenko,

1934; Hucl and Fowler, 1992; Ma et al., 2007). Therefore, comprehensive analysis of particular spike productivity elements is needed for targeted control of yield formula formation under variable soil, agricultural, and climatic conditions (Lelli, 1980; Börner et al., 2002; Zheng et al., 2010; Morgounov et al., 2013). In addition, wheat yield is affected by the development of spike inflorescences, the number of florets per inflorescence, spike meristem growth, and spike fertility (Kuperman, 1953; Lutova et al., 2010; Sreenivasulu, Schurbusch, 2012).

Common wheat has multifloret spikelets with three to five florets. Up to 8–9 floral primordia are generated in a spikelet at early steps of spike formation, but the upper florets terminate their growth after the development of the first two to four spikes (Kuperman, 1953; Dorofeev, 1979; Lutova et al., 2010). However, there are common wheat lines and cultivars having 5–6 fertile florets per spikelet (Martinek and Bednar, 1988, 2001; Martinek, 1994). A unique form among members of genus *Triticum* L. possesses the elevated multifloret habit: each floret has four glumes, two on the each of the right and left. Under appropriate con-

ditions, such a spikelet can form up to 26 fertile florets (Ostreiko, 1959).

As a rule, the maximum number of grains, up to four, form in spikelets of the middle portion of a spike, whereas spikelets of the top and bottom portions have two. It is assumed that 25—35 grains per spike can provide a grain yield as large as 3000—5000 kg/ha (Nosatovskii, 1965; Zhuchenko, 2004). It is possible to double the productivity of plants by increasing 70 grains in one spike. Some scientists believe that the use of unique forms with a great number of spikelets, florets, and grains in breeding programs can be one of the approaches for increasing wheat yield (Martinek and Bednar, 1988, 2001; Hucl and Fowler, 1992; Martinek, 1994; Li and Zhao, 2000; Aliyeva and Aminov, 2011; Sreenivasulu and Schnurbusch, 2012). The multifloret habit trait has been little investigated in this regard, and there is no data on the effect of the multifloret habit on spike productivity and their inheritance. Therefore, investigation of new sources of the multifloret habit and their genetics is a relevant task.

The goal of the present work is to evaluate parameters of spike productivity (spike length, spike density, and number of spikelets) in plants of common wheat F$_2$ populations raised with the use of the multifloret Skle 123-09 line in order to obtain promising lines with high grain contents.

MATERIALS AND METHODS

The recipients were common wheat cultivars Saratovskaya 29 (S29), Novosibirskaya 67 (N67), and the Indian variety Puza-4 (P-4). Generally, one spikelet of S29 or N67 has three or four grains. Cultivar P-4 has a large thousand kernel weight (up to 44 g), but it is poorly fertile. Its spikelets have generally two grains each. The multifloret Skle 123-09 line was taken as the donor. Its spikelets are fan-like, and they have five or, less often, six fertile florets. The line was obtained by Dr. Martinek (Agrotest Fyto Ltd., Kroměříž, Czech Republic) by self-pollination and selection of multifloret plants. It was submitted to Agrotest Fyto Ltd. by Dr. Wang Tao without a detailed description of its origin.

Recipient varieties (N67, S29, and P-4) were crossed to Skle 123-09 to obtain F$_2$ hybrid populations, in which parameters of spike productivity were assessed. Both experimental F$_2$ and control populations were derived from seeds obtained from one reproduction in two-year experiments. Seeds were sown manually in the experimental field of the Institute of Cytology and Genetics in triplicate on May 24, 2010 and on May 19, 2011. The backgrounds were fallow in 2010 and pea in 2011. Populations of F$_2$ hybrids, recipient varieties, and Skle 123-09 were planted in 1-m wide plots, 20 grains per row. No less than 160 hybrid grains from each population and 60 grains of each parental accession were sown. The crop was harvested

manually. To determine the spike productivity, the 25 best spikes of parental cultivars and 50 randomly chosen spikes of each experimental F$_2$ population were cut separately.

The following parameters were analyzed: spike length (SL), number of spikelets (NS), and spike density (D). Spike density was calculated as $D = (A - 1) \times 10/B$, where $(A - 1)$ is the number of spikelets minus the topmost one and B is rachis length (Yakubtsiner, 1976).

The differences between the mean values for two selection samples were assessed by Student's test (Rokitskii, 1974). Two-way analysis of variance was carry out with the SNEDECOR 5.61 software (www.odssoft. narod.ru).

The weather conditions of the vegetation seasons in 2010 and 2011 and the timing of developmental steps are shown in Fig. 1. The average temperatures of both vegetations showed little difference from the mean annual values. In 2011, June was 3° warmer and July, 2° cooler. As for precipitation, 2010 was dry in June and August. In 2010, water was scarce throughout the vegetation season: 8.5 mm in May, up to 17.9 mm in August, and the worst water scarcity was recorded in the 2nd ten days of June (no precipitation) and the 2nd ten days of July (13 mm) (Fig. 1). This fact directly affected the formation of the traits under study.

RESULTS AND DISCUSSION

Earlier studies showed that yield increased with the number of grains per spike (Vavilov, 1935; Pisarev, 1964; Luk'yanenko, 1973; Feil, 1992; Wang et al., 2002; Tsil'ke, 2003; Green et al., 2012). In addition, there is evidence for the dependence of crop yield on the number of grains per spike (Vavilov, 1935; Arbuzova and Maystrenko, 1986; Feil, 1992; Tsil'ke, 2003) and grain weight per spike (McNeal et al., 1978; Dorofeev, 1987; Wang et al., 2002; Tsil'ke, 2003). These data indicate that the multifloret habit may be of interest for wheat breeders, because it directly affects the number of grains per spikelet. The multifloret line Skle 123-09 displays high characters of the yield formula: the grain number per spike, spike density, seed set, and spike grain weight (Arbuzova, unpublished results).

Table 1 presents indices of the parental varieties averaged over two years. The multifloret line Skle 123-09 significantly differed in SL only from N67. It showed practically no differences in NS from the recipient varieties except for P-4 in 2010. In spike density, Skle 123-09 significantly overpowered other accessions in 2010.

The range of SL variation is shown in Table 2. The distributions of SL in F$_2$ hybrids were generally within the ranges of the parental forms. Plants with SL = 13.4 cm were found in F$_2$ populations (N67, P-4 × Skle 123-09) under severe drought conditions. In both vegetations,
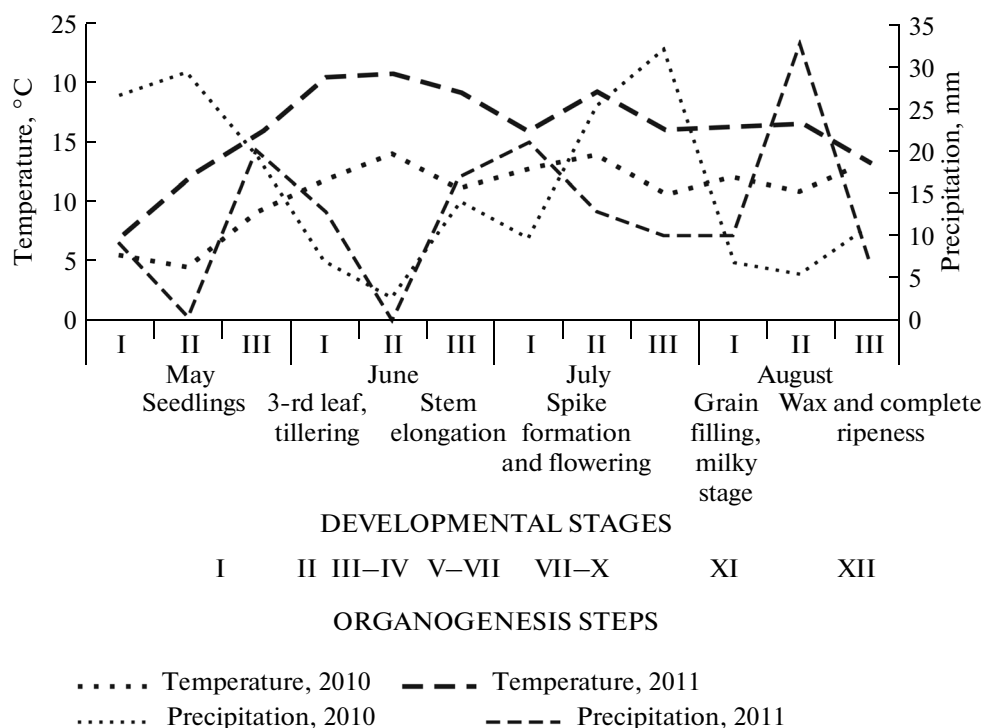
Fig. 1. Weather conditions in 2010 and 2011 and timing of wheat developmental stages and organogenesis.

the medium values of the characteristic were either predominant, or they were biased towards greater values. These results point to the emergence of transgressive phenotypes, e.g., in the F_2 populations (P-4 × Skle 123-09, 2010) (Fig. 2a).

Two-way analysis of the variance of F_2 hybrids showed that SL variation in the (P-4 × Skle 123-09) cross was equally contributed by the genotype and the "genotype × year" factor interaction (43.5%). It should be mentioned that weather conditions in a particular year exerted no effect on the characteristic expressiveness in any of the three combinations. The main portion of SL variation depended on genotype in the F_2 populations (S29 × Skle 123-09) (45.7%) and (N67 × Skle 123-09) (47.1%). The contributions of the "genotype × year" factor interaction constituted 39.5 and 36%, respectively (Table 3).

The SL characteristic is known to be controlled by many genes distributed over nearly all wheat chromosomes (Sears, 1954; Rigin, 1971; Lelli, 1976; Arbuzova and Maystrenko, 1986; Tsil'ke, 2003; Pestsova et al., 2006). The study of monosomic series of wheat cultivars S29 and Diamant 1 has shown that almost all chromosomes are involved in the determination of SL in the monosomic state and effects of monosomy are considerably modulated by environmental conditions (Arbuzova and Maystrenko, 1986). As reported by Morris (1974), genes controlling SL have been found on chromosomes 2A, 3A, 4A, 1B, 2B, 3B, 4B, and 5B. Other scientists identify nine chromosomes controlling

the character: 3A, 3B, 3D, 4B, 4D, 5A, 5B, 5D, and 6D (Auzemus et al., 1970; Tsil'ke R.A. and Tsil'ke I.A., 1973, 1974, 1976).

Currently, molecular approaches are commonly used in agricultural and commercial analysis. They include mapping of quantitative trait loci (QTLs). It has been reported that the major loci determining SL in common wheat are located on chromosomes 1B, 4A, 5A, and 5D (Kato et al., 2000; Börner et al., 2002; Sourdille et al., 2003; Marza et al., 2006; Pestsova et al., 2006). Nine major QTLs have been identified for SL, eight being located on chromosome 4A and one, on 5A (Chesnokov et al., 2012).

The number of spikelets is the key character of spike productivity, because it is among the first components of the yield formula to form, and it is directly correlated to SL. The parental accessions differed little in NS. Analysis of F_2 hybrids revealed several regularities in NS inheritance. Large NS values dominated in F_2 hybrids from crosses of samples equaling in the manifestation of the characteristic. Its distribution curves in hybrids were biased to larger values, pointing to the emergence of new transgressive forms, e.g., in F_2 hybrids (S29 × Skle 123-09, 2010) (Fig. 2b). Thus, it is reasonable to utilize Skle 123-09 in breeding programs aimed at increasing NS. In our experiments of 2010, plants with 24 spikelets in a spike were found in F_2 (S29 × Skle 123-09) and with 22, in F_2 (N67, P-4 × Skle 123-09) (Table 2). A different pattern was observed in the dry year 2011. Forms with 20 spikelets

Table 1. Indices recorded in parental varieties

Character	Year	N67	S29	P-4	Skle 123-09
SL, cm	2010	9.38 ± 0.81*	8.35 ± 0.52	7.43 ± 0.60	7.54 ± 0.66
	2011	8.67 ± 0.57**	6.92 ± 0.64	6.73 ± 0.52	6.79 ± 0.48
NS	2010	14.92 ± 1.19	13.80 ± 1.12	11.63 ± 0.92***	15.28 ± 0.99
	2011	14.78 ± 1.35	12.26 ± 0.93	14.35 ± 1.35	13.40 ± 1.17
Spike density (D)	2010	15.93 ± 1.13**	16.54 ± 1.18*	15.69 ± 1.24**	20.23 ± 1.36
	2011	16.88 ± 1.17*	17.80 ± 1.45	21.32 ± 1.19	21.10 ± 1.90

* $P \le 0.05$; ** $0.05 \le P \le 0.01$; *** $0.01 \le P \le 0.001$.

Table 2. Mean values of spike productivity and variation range in F$_2$ hybrid populations (S29, N67, P-4 × Skle 123-09) in comparison with Skle 123-09. Novosibirsk, 2010 and 2011

Character	Year	Skle 123-09		F$_2$ (S29 × Skle 123-09)		F$_2$ (N67 × Skle 123-09)		F$_2$ (P-4 × Skle 123-09)	
		$M \pm m$	min−max	$M \pm m$	min−max	$M \pm m$	min−max	$M \pm m$	min−max
SL, cm	2010	7.5 ± 0.6	6.2−8.4	7.6 ± 1.2	4.5−10.4	7.5 ± 1.1	4.5−11.4	7.6 ± 1.3	5.5−11.4
	2011	6.8 ± 0.5	5.7−8.0	8.3 ± 1.3	4.5−11.4	8.8 ± 1.1*	4.5−13.4	8.3 ± 1.5	5.5−13.4
NS	2010	15.3 ± 1.0	13.7−16.4	15.2 ± 2.6	10.5−24.4	15.2 ± 2.0	10.5−22.4	14.7 ± 2.7	8.5−22.4
	2011	13.4 ± 1.2	12.5−16.5	14.2 ± 2.6	6.5−20.4	15.4 ± 2.3	8.5−24.4	11.1 ± 2.6	8.5−24.4
D	2010	20.2 ± 1.3	19.3−24.0	20.2 ± 2.2	15.5−27.4	20.6 ± 2.4	15.5−29.4	19.5 ± 2.8	11.5−27.4
	2011	21.1 ± 1.9	19.5−25.0	17.0 ± 2.0	11.5−21.4	17.4 ± 2.3	11.5−25.5	17.2 ± 2.3	11.5−25.5

* $P \le 0.05$.

were found in F$_2$ hybrids (S29 × Skle 123-09), and with 24 spikelets, in F$_2$ (N67, P-4 × Skle 123-09). Two-way analysis of F$_2$ hybrids showed that the NS variability depended considerably on growth conditions in all combinations: by 82.2% in F$_2$ (S29 × Skle 123-09); 74.9%, in F$_2$ (P-4 × Skle 123-09); and 25.6%, in F$_2$ (N67 × Skle 123-09). In the first case, the genotype and "genotype × year" interaction exerted no significant influence on NS. The genotype also did not influence significantly F$_2$ (P-4 × Skle 123-09), but it interacted with the environment by 20.4% (Table 3). Probably, this observation is related to the fact that cvs. S29 and P-4 were created for arid regions.

It has been reported that NS depends, more or less, on almost all chromosomes. Monosomic analysis shows that genes determining NS are located on chromosomes 5A, 6A, 1B, 4B, 6B, 7B, and 7D (Morris,

1974). Other authors indicate that NS is controlled by genes located on all chromosomes except for 4A, 2B, and 6D (Auzemus et al., 1970; Tsil'ke R.A. and Tsil'ke I.A., 1973, 1974, 1976). It has been reported that the major QTLs for NS are located on chromosomes 4A and 5A, and minor QTLs, on 2A, 3B, and 7A (Araki et al., 1999; Pestsova et al., 2006; Chesnokov et al., 2012).

As formerly mentioned, D is a resultant trait, which depends on SL and NS. In our study, the multifloret line Skle 123-09, whose spike density index was 20 or 21 in both years of the study, is prominent with regard to this trait (Table 1). The greatest manifestation of the trait was observed in 2010, when some Skle 123-09 plants had D = 25 (Table 2). Several plants with D values larger than in Skle 123-09 occurred in F$_2$ hybrid populations. In F$_2$ populations of 2010 (S29, N67, P-4 × Skle 123-09), there were plants with D = 27
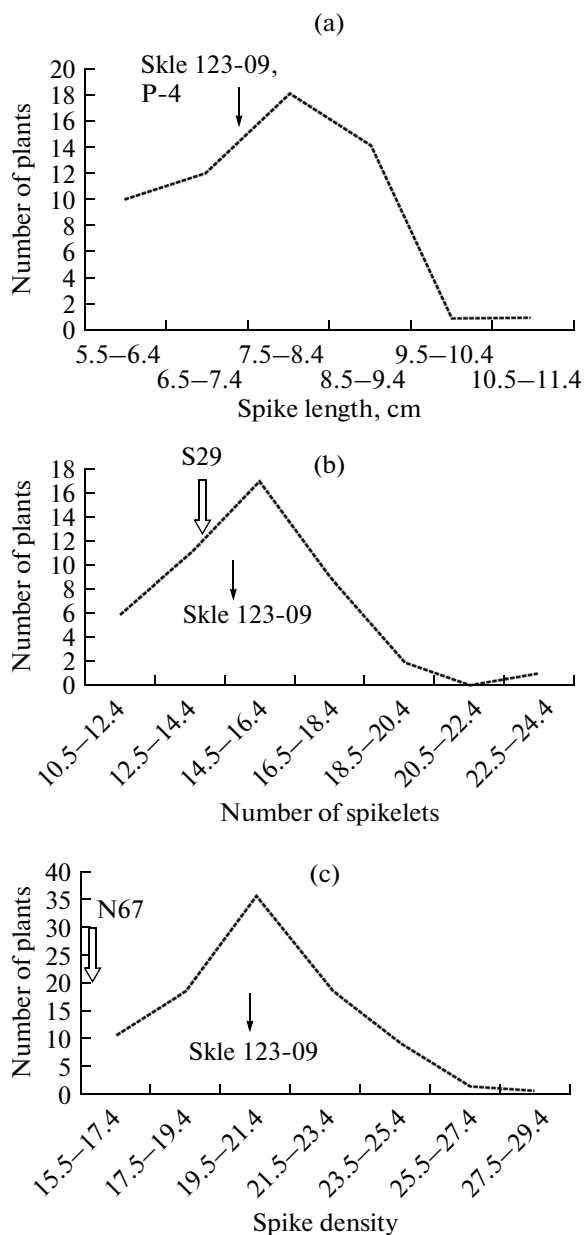
Fig. 2. Spike productivity in plants of F_2 hybrid populations.
(a) P-4 × Skle 123-09, (b) S29 × Skle 123-09, (c) N67 × Skle 123-09. Arrows indicate mean values of parental accessions, Novosibirsk, 2010.

or 29 (Table 2). The distributions of the characteristic in F_2 populations were within the range of variation of the parents, being biased toward larger values; hence, larger values were dominant, e.g., in the F_2 hybrid population (N67 × Skle 123-09, 2010) (Fig. 2c). In our opinion, plants with higher D values than in Skle 123-09 can be donors for breeding for large D values. Evaluation of the contributions of factors showed that environmental conditions exerted the least but still significant action on D variation (12.8, 15.7, and 5%), whereas the genetic background and the "genotype × year" interaction had the greatest effects (Table 3).

Thus, transgressive forms for the characteristics under study were found in the progeny of crosses of cvs. N67, S29, and P-4 with multifloret line Skle 123-09. It may indicate that genes with not only additive effects make significant contributions to the determination of SL, NS, and D. The variability of NS and D is determined mainly by genotype and the environment, and SL, by the genotype and "genotype × year" interaction. Evaluation of F_2 hybrids revealed hybrid combinations with a set of characteristics beneficial for crop performance. The multifloret line Skle 123-09 can be used in breeding to increase D and NS.

Table 3. Two-way analysis of variance of spike productivity in common wheat F_2 hybrids

S29 × Skle 123-09

Variability	Sum of squares, S	Degrees of freedom, df	Mean square, mS	Percentage of variation, V, %	F test	Probability
spike length						
Overall	3.198	7	0.457	100		
Factor A (year)	0.004	1	0.004	0.13	0.0346	0.86149
Factor B (genotype)	1.462	1	1.462	45.71	12.491	0.02414*
A × B interaction	1.264	1	1.264	39.52	10.799	0.03032*
Chance factors	0.468	4	0.117	14.64		
number of spikelets						
Overall	5.115	7	0.731	100		
Factor A (year)	4.205	1	4.205	82.21	64.692	0.00130*
Factor B (genotype)	0.245	1	0.245	4.79	3.7692	0.12417
A × B interaction	0.405	1	0.405	7.92	6.2308	0.06704
Chance factors	0.260	4	0.065	5.08		
spike density						
Overall	18.880	7	2.697	100		
Factor A (year)	2.420	1	2.420	12.82	21.044	0.01013*
Factor B (genotype)	8.000	1	8.000	42.37	69.565	0.00113*
A × B interaction	8.000	1	8.000	42.37	69.565	0.00113*
Chance factors	0.460	4	0.115	2.44		

N67 × Skle 123-09

Variability	Sum of squares, S	Degrees of freedom, df	Mean square, mS	Percentage of variation, V, %	F test	Probability
spike length						
Overall	4.600	7	0.657	100		
Factor A (year)	0.180	1	0.180	3.91	1.7143	0.26057
Factor B (genotype)	2.000	1	2.000	43.48	19.048	0.01202*
A × B interaction	2.000	1	2.000	43.48	19.048	0.01202*
Chance factors	0.420	4	0.105	9.13		
number of spikelets						
Overall	5.655	7	0.657	100		
Factor A (year)	1.445	1	1.445	25.55	28.900	0.00578*
Factor B (genotype)	1.805	1	1.805	31.92	36.100	0.00386*
A × B interaction	2.205	1	2.205	39.99	44.100	0.00267*
Chance factors	0.200	4	0.105	3.54		
spike density						
Overall	16.855	7	2.408	100		
Factor A (year)	2.645	1	2.645	15.69	29.389	0.00561*
Factor B (genotype)	5.445	1	5.445	32.30	60.500	0.00147*
A × B interaction	8.405	1	8.405	49.87	93.389	0.00064*
Chance factors	0.360	4	0.090	2.14		

P-4 × Skle 123-09

Variability	Sum of squares, S	Degrees of freedom, df	Mean square, mS	Percentage of variation, V, %	F test	Probability
spike length						
Overall	2.720	7	0.389	100		
Factor A (year)	0.000	1	0.000	0.00	0.0000	1.00000
Factor B (genotype)	1.280	1	1.280	47.06	11.130	0.02894*
A × B interaction	0.980	1	0.980	36.03	8.5217	0.04328*
Chance factors	0.460	4	0.115	16.91		
number of spikelets						
Overall	4.175	7	0.596	100		
Factor A (year)	3.125	1	3.125	74.85	62.500	0.00138*
Factor B (genotype)	0.005	1	0.005	0.12	0.1000	0.76765
A × B interaction	0.845	1	0.845	20.24	16.900	0.01472*
Chance factors	0.460	4	0.050	4.79		
spike density						
Overall	17.055	7	2.436	100		
Factor A (year)	0.845	1	0.845	4.95	9.3889	0.03751*
Factor B (genotype)	11.045	1	11.045	64.76	122.72	0.00038*
A × B interaction	4.805	1	4.805	28.17	53.389	0.00187*
Chance factors	0.360	4	0.090	2.11		

* Significant at $P < 0.05$.

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