VARIABILITY AND INHERITANCE OF TILLERING IN BARLEY HYBRIDS

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Productive tillering is a very important trait which influences the degree of barley lodging resistance. Five divergent genotypes of two-rowed winter barley (Vada, Djerdap, NS-293, Jagodinac and Sladoran) have been selected for diallel crossing in order to study the mode of inheritance, the gene effect and the components genetic variance for the productive tillering in F_1 and F_2 generation.

The test of the significance of the generations' mean values related to the parental average was used for inheritance mode determinations (KRALJEVIC-BALALIC et al., 1991) and the genetic variance components and regression VrWr analysis from diallel crossings were made using the method of MATHER and JINKS (1971). The variability of the investigated trait differed. The cross combination Djerdap x Jagodinac had the highest coefficient of variance (39.78%). Different modes of inheritance (partial dominance, dominance and overdominance) and partial dominance were found in the F_1 and F_2 generation, respectively. The genetic variance components, average

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degree of dominance and regression line indicated partial dominance in the inheritance of tillering. The range of the obtained values of heritability for the tillering was found to be very wide (0.02-0.47). The cross combinations Djerdap x Jagodinac and Vada x Djerdap were selected for future breeding.

Key words: barley, tillering, variability, gene effect, genetic variance components

INTRODUCTION

Tillering is an important yield component occurring as the process of underground stalk branching and plant shooting at early ontogenesis stages and also as a foundation in terms of the crop uniformity and plant density, directly affecting the crop structure (BOROJEVIC, 1972, KRALJEVIC-BALALIC and PETROVIC, 1991).

Familiarity with the genetic base and mode of inheritance of productive tillering contributes to a more successful breeding of high-yielding barley cultivars. Studies have shown that this trait is affected not only by genetic factors but also, to a great extent, by ecological ones and mineral, primarily nitrogen nutrition (PAVLOVIC, 1997).

In order to perform breeding for tillering in generations after hybridization with more certainty, it is necessary to have information on the mode of inheritance of the trait.

The aim of this paper was to examine the mode of inheritance, gene effect and genetic variance components for productive tillering in F_1 and F_2 generations.

MATERIALS AND METHODS

The genotypes Vada, Djerdap, NS-293, Jagodinac and Sladoran were chosen for the examination of the mode of inheritance and components of the genetic variance of productive tillering.

Diallel crossings, excluding reciprocal ones, were carried out in 1999 when six hybrid combinations of F_1 and F_2 generation were obtained. The same year, the hybrid material and parents were planted at the Experimental Field of the Small Grains Centre in Kragujevac according to the randomized block design with three replications. The seeding was carried out following the sparse seeding principle in 1 m long rows with 20 cm inter–row distance and 10 cm inter-plant spacing in a row. Equal growing conditions for all plants in the generations studied were thus.

The test of the significance of the generations' mean values related to the parental average was used for inheritance mode determinations (KRALJEVIC-BALALIC et al., 1991) and the genetic variance components and regression VrWr analysis from diallel crossings were made using the method of MATER and JINKS (1971).

RESULTS AND DISCUSSION

Mean values and inheritance of productive tillering. – There were significant differences in productive tillering between the parental cultivars used in this programme. The smallest and the largest number of tillers were registered with the cultivar Sladoran (7.8) and Jagodinac (11.8), respectively, table 1.

In the F_1 generation, the number of tillers ranged from 8.03 in the NS-293 x Sladoran combination to 11.43 in the Djerdap x Jagodinac combination. The mean values for the number of tillers in the F_2 generation in most combinations were a bit lower than the mean values of the F_1 generation and ranged from 6.20 in the Djerdap x Sladoran to 9.40 in the Djerdap x Jagodinac combination. In the F_1 generation, a high variability in productive tillering was expressed and it was in certain combinations even higher than the variability of the F_2 generation. The high variability indicated the high environmental factor effect in the expression of the trait (PAUNOVIC, 2002).

The highest variability in the F_2 generation was recorded in the Djerdap x Jagodinac combination and it amounted to 39.78% (Table 1).

The investigated cultivars and their hybrids expressed high variability values for productive tillering. The results were in accordance with the results obtained by other authors (PAVLOVIC et al., 1994; ZECEVIC, 1996; DIMITRIJEVIC et al., 1996) who determined a high variability (30%) in the shoot number per plant for some wheat cultivars. The high values of the coefficient of variation (80%) in the F_1 and F_2 generation were indicated by PAVLOVIC (1997), too.

A different manner of productive tillering inheritance was present in the F_1 generation.

Intermediary inheritance was determined in the Jagodinac x Sladoran combination, overdominance in the Djerdap x NS-293 combination, whereas in other crossing combinations partially dominant or dominant type of inheritance was present (Table 1).

The inheritance of productive tillering in the F_2 generation was in most combinations partially dominant or there was dominance of parents with a smaller number of tillers. Partial dominance was expressed also in the crossing combination where the parents significantly differed in the trait (Jagodinac x Sladoran). The obtained results were in accordance with the results obtained by PAVLOVIC et al. (1994), ZECEVIC et al. (1995), MADIC and DJUROVIC (1996). Productive tillering as generally a high heritability trait was in certain combinations registered as low heritability (0.02). These results were due to the variability of certain parents with high variation coefficients.

Table 1. Statistical parameters and productive tillering inheritance in barley

Combination	Generation	No. of plants	$\overline{X} \pm s_{\overline{x}}$	S	V (%)	h^2
K-1	P_1	30	8.67 ± 0.30	2.20	23.8	
Vada	F_1	30	8.20 ± 0.29	1.60	21.3	
x	F_2	90	8.73 ± 0.26	2.48	32.2	0.37
Ðerdap	P_2	30	9.40 ± 0.39	2.78	22.9	
K-2	P_1	30	8.67 ± 0.30	2.20	25.3	
Vada	F_1	30	8.93 ± 0.48*pd*	2.99	33.4	
x	F_2	90	7.70 ± 0.25 *-d*	2.34	32.5	0.02
NS-293	P_3	30	9.20 ± 0.41	2.23	24.2	
K-3	P_1	30	8.67 ± 0.30	2.20	23.7	
Vada	F_1	30	8.50 ± 0.50 *-d*	3.12	32.2	
X	F_2	90	9.45 ± 0.23 *pd*	2.18	23.0	-
Jagodinac	P_4	30	11.70 ± 0.52	3.72	24.3	
K-4	P_1	30	8.67 ± 0.30	2.74	23.7	-
Vada	F_1	30	8.20 ± 0.57 *pd*	3.10	37.8	
X	F_2	90	8.30 ± 0.24 *pd*	2.23	26.8	
Sladoran	P_5	30	7.80 ± 0.54	1.70	21.7	
K-5	P_2	30	9.40 ± 0.39	2.78	22.9	
Ðerdap	F_1	30	11.06 ± 0.53 *od*	3.54	26.3	
x	F_2	90	8.26 ± 0.25 *od*	2.35	28.4	-
NS-293	P_3	30	9.20 ± 0.41	2.23	24.2	
K-6	P_2	30	9.40 ± 0.39	2.78	22.9	
Ðerdap	F_1	30	11.43 ± 0.97 *d*	3.08	26.9	
x	F_2	90	9.40 ± 0.39 *-d*	3.74	39.7	0.47
Jagodinac	P_4	30	11.70 ± 0.52	3.72	24.3	
K-7	P_2	30	9.20 ± 0.39	2.78	24.2	
Ðerdap	F_1	30	8.90 ± 0.67 *pd*	3.71	41.6	
x	F_2	90	6.20 ± 0.43 *-d*	2.40	38.7	-
Sladoran	P_5	30	7.80 ± 0.54	1.70	21.7	
K-8	P_3	30	9.20 ± 0.41	2.23	24.2	
NS-293	F_1	30	10.10 ± 0.70 *pd*	3.07	30.3	
x	F_2	90	9.03 ± 0.35 *-d*	3.36	37.2	0.34
Jagodinac	P_4	30	11.70 ± 0.52	3.72	24.3	
K-9	P_3	30	9.20 ± 0.41	2.23	24.2	
NS-293	F_1	30	8.03 ± 0.48 *d*	2.48	30.8	
x	F_2	90	7.13 ± 0.23 *d*	2.41	29.0	0.20
Sladoran	P_5	30	7.80 ± 0.54	1.70	21.7	
K-10	P_4	30	11.70 ± 52	3.72	24.3	
Jagodinac	F_1	30	9.40 ± 0.48	2.63	28.9	
x	F_2	90	8.00 ± 0.28 *pd*	2.72	29.1	0.21
Sladoran	P_5	30	7.80 ± 0.30	1.70	21.7	

F_1	LSD	0.05	1.36		F_2	LSD	0.05	1.02
		0.01	1.84				0.01	1.38

od-overdominance   *d*-dominance   *pd*-partial dominance

Genetic variance components and graphical analysis. – The analysis of the genetic variance components showed that genetic variability in the F_1 generation was to a greater extent the result of the dominant gene effect (because the H_1 and H_2 value was higher than value D). The positive value F showed that the dominant alleles predominated over the recessive ones in the phenotypic tillering expression in the F_1 generation. Based on the $H_2/4H_1$ value it can be concluded that dominant and recessive alleles were not evenly distributed in the parents. The average degree of dominance was higher than 1, meaning that overdominance was expressed in the inheritance of productive tillering in the F_1 generation. As K_D/K_R was higher than 1 it can be concluded that the dominant alleles predominated over the recessive ones, considering all the parents (Table 2).

The additive genetic variance component in the F_2 generation was higher than the dominant component $D>H_1$ and H_2, meaning that the additive gene effect played the main role in the inheritance of productive tillering in the F_2 generation. The negative value of interaction F indicated the greater role of the recessive genes in the phenotypic expression of this trait. The average dominance degree was lower than 1, meaning that partial dominance was expressed in the inheritance of productive tillering, considering all the crossing combinations. The value K_D/K_R was lower than 1, so the recessive alleles predominated, considering all the parents.

Table 2. Genetic variance components for productive tillering

Variance components	Values	
	F_1	F_2
D	2.331	1.517
H_1	3.167	0.488
H_2	2.556	0.364
F	0.190	-0.015
E	0.221	0.124
$H_2/4H_1$	0.202	0.187
$\sqrt{H_1/D}$	1.165	0.567
K_D/K_R	1.073	0.983
Heritability		0.78

The analysis of genetic variance components also showed that the additive gene effect played the major role in the inheritance of productive tillering and that partial dominance was expressed. The regression VrWr-analysis in the F_1 generation did not significantly differ from 1, with the regression line a little distant from the limiting parabola indicating that the genetic system for the stalk height inheritance was an additive one. This was confirmed by the calculated average degree of dominance as well as by the positive value a showing that the

intersection of the expected regression line with the Wr axis was above the coordinate start.

The arrangements of points in the dispersion diagram along the regression line shows the divergence of parents. Since the majority of the parents are in the top part of the regression line, it can be concluded that the recessive genes dominated over the dominant ones in the phenotypic expression of the stalk height in the F_1 and F_2 generation which is in accordance with the negative F value (Table 2).

The cultivar Sladoran had the greatest share of the dominance genes for the trait because it was the nearest to the coordinate start. The greatest share of the recessive genes was recorded with the cultivar Jagodinac, because it was the most distant from the coordinate start (Fig. 1).
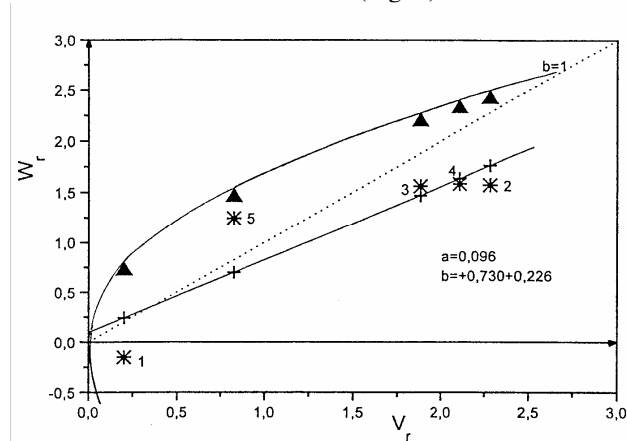
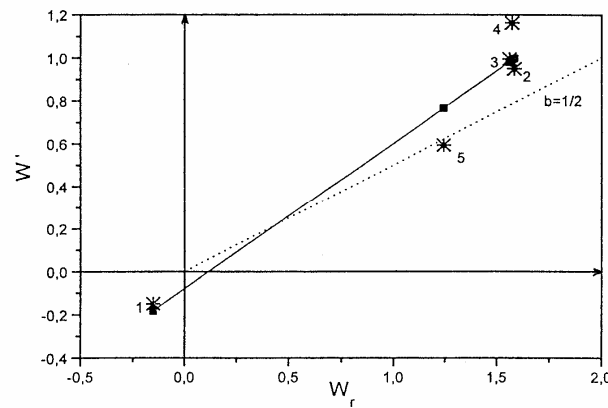Fig. 1. Regression VrWr analysis for productive tillering (P and F_1)

Fig. 2. Regression WrW' analysis for productive tillering (P and F_1)

On the WrW' graph it could be seen that the dispersion diagram points are along the regression line or immediately around it (Fig. 2). The arrangements of points in the dispersion diagram are equal to that in the VrWr graph. The distribution of points in the dispersion diagram from both Figs 1 and 2 shows the absence of inter-allelic interaction in the inheritance of the trait in this diallel.

The regression analysis of the F_2 generation only confirmed the conclusions on the mode of inheritance of the trait (Figs. 3 and 4)
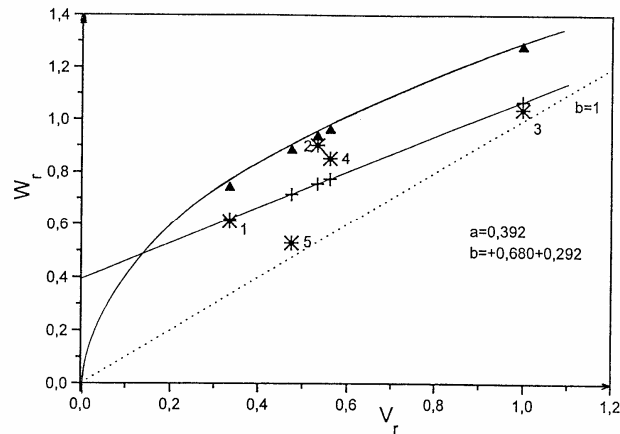

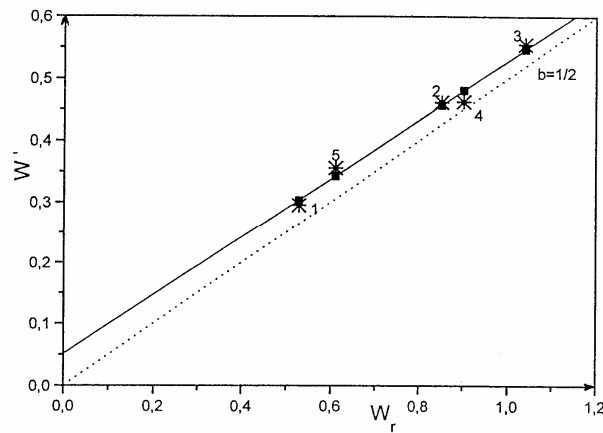Fig. 3. Regression VrWr analysis for productive tillering (P and F_1)

Fig. 4. Regression WrW' analysis for productive tillering (P and F_1)

The analysis the components of genetic variance also showed that the additive gene effect played the main part in the inheritance of productive tillering,

so partial dominance was expressed. The regression VrWr-analysis of productive tillering confirmed the partial dominance in the inheritance of the trait in the phenotypic expression of productive tilllering. Dominant genes predominated in most parents. The results were in accordance with the results obtained by MADIC and DJUROVIC (1996), whereas TSENOV (1990), PRODANOVIC (1992), ZECEVIC et al. (1995), in their analyses of the inheritance of productive tillering in wheat, indicated that the dominant genetic effects were more important than the additive ones and that the average degree of dominance and the regression analysis indicated the overdominance of inheritance of the trait.

In their analyses of the inheritance of productive tillering in wheat, PRZULJ et al. (1999) concluded that dominant gene effects were more important than the additive ones and that they mostly acted towards decreasing the number of productive spikes per plant.

Productive tillering heritability ranged from 0.02 to 0.47, which was in accordance with the results by PAVLOVIC (1997) and PRZULJ et al. (1999), who indicated the values of heritability of productive tillering of wheat ranging from 0.35 to 0.36. A high value of productive tillering heritability was obtained by PRODANOVIC (1992), where the heritability value was about 0.56.

CONCLUSION

Productive tillering is a very important trait affecting the degree of barley tolerance to lodging. Diallel crossings of five divergent genotypes of two-rowed winter barley were made in order to determine the mode of inheritance, the gene effect and genetic variance components for productive tillering in the F_1 and F_2 generation.

The inheritance of barley tillering in the F_1 generation was expressed as partial dominance, dominance or overdominance and in the F_2 generation as partial dominance in most crossing combinations. The genetic variance components, average dominance degree and regression line indicated partial dominance in the inheritance of this trait. The obtained productive tillering heritability values widely ranged (0.02 – 0.47). Combinations Djerdap x Jagodinac and Vada x Djerdap were selected for further breeding process.

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VARIJABILNOST I NASLEĐIVANJE BOKORENJA KOD HIBRIDA JEČMA

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Produktivno bokorenje je veoma značajna osobina od koje zavisi stepen otpornosti ječma prema poleganju. Pet divergentnih genotipova ozimog dvoredog ječma (Vada, Đerdap, NS-293, Jagodinac i Sladoran) je odabrano za dialelna ukrštanja da bi se ocenio način nasleđivanja, efekat gena i komponente genetičke varijanse za produktivno bokorenje u F_1 i F_2 generaciji.

Varijabilnost ispitivanog svojstva je bila različita pri čemu je najveći koeficijent varijabilnosti bio u kombinaciji Đerdap x Jagodinac (39.78%). Nasleđivanje bokorenja ječma u F_1 generaciji ispoljilo se po tipu parcijalne dominacije, dominacije, superdominacije, a u F_2 generaciji ispoljena je uglavnom parcijalna dominacija. Komponente genetičke varijanse, prosečan stepen dominacije i linija regresije ukazali su na parcijalnu dominaciju kod nasleđivanja ove osobine. Dobijene vrednosti heritabilnosti za produktivno bokorenje su bile u veoma širokom dijapazonu (0.02-0.47). Za dalji selekcioni proces odabrane su kombinacije Đerdap x Jagodinac i Vada x Đerdap.