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ABSTRACT

The following maize populations were encompassed by the study: a population with 25% of exotic germplasm (1601/5xZPL913)F_2R_0 and populations developed after three (1601/5xZPL913)F_2R_3, that is, five (1601/5 x ZPL913)F_2R_5 gene recombination cycles. The S_1 progeny trial was set up according to the nested design in two replications and two locations during two years (2001 and 2002). The average values for all traits except moisture at harvest increased. The changes of mean values of yields and other traits can be very important from the aspect of long-term breeding programmes. Different agroecological conditions, genotyp0e, family x location interaction and family x location interaction within the set significantly affected all observed traits of populations. Genetic and phenotypic variances for all traits except the 1000-kernel weight decreased under the effects of the number of recombination cycles, which was confirmed by the coefficients of heritability. A significant decrease was not detected in yields and ear lengths, which is particularly important for practical breeding. Three cycles of gene recombination are sufficient for this population prior to the application by various breeding methods.

Introduction

The common aim of all breeding programmes is to develop genotypes that will be able to express their high yielding potential under different production conditions. In order to accomplish this aim, it is necessary to pay special attention to the development and the utilisation method of the initial material as a source for deriving maize inbred lines (14). In each breeding programme, the initial material also determined the utmost range and success of the maize selection method (17, 19). Gained experience and obtained results point to a conclusion that a further increase of grain yield is possible only under conditions of the permanent improvement of the initial populations (8, 20) and of the increase of desirable genes frequency with the maintenance of genetic variability within the initial populations (10, 20).

The selection process inevitably led to narrowing of the genetic base of the breeding material. Longing for higher yields resulted in narrowing of genetic sources that remained in the competition. In the process of "selection within selection", total variability had been decreasing in favour of the frequency increase of favourable genes that selection was done for. All this indicates that the inductive procedure of genetic variability increasing is the most real. New sources of genetic variability should be introduced to breeding programmes together with their combination with the material adapted by a long-term selection (11). Exotic germplasm has a special role in this.

Exotic maize from the aspect of a genetic constitution of the breeding material and the genotype x environment interaction is considered a genetic material with a lower degree of adaptability than local populations under the given environmental conditions. It is usually thought that genotypes from the tropic and subtropic zones are exotic genotypes in the temperate belt (11). The populations lose their exotic character if the level of their adaptive value is equalized to local populations. Such an observation cannot be attributed to homozygous inbreds *per se*, as they are not subjected to changes in gene frequencies (except for mutations) and cannot change their adaptive value (11). When exotic germplasm is incorporated into the adapted material, a special attention should be paid to the linkage, then to the optimum proportion of exotic to adapted plasma and to the determination of favourable genes that are carried by the exotic sources and that are lacking in the adapted material (20). The linkage with a positive and a negative effect (16) can be alleviated with several cycles of gene recombination in the initial population. The principal aim of the supplementary recombination cycles is to break blocks of linked favourable and unfavourable genes. The number of supplementary recombinations is as a rule higher by a greater proportion of exotic plasma (11, 19). The majority of researches favours the aspect that 25% (or less) of exotic sources in relation to adapted ones are sufficient (11). However, it often happens that the exotic plasma combined with the adapted one does not result in the combinations superior than hybrids developed

from crosses of adapted to adapted plasma (8). Additional selection and recombination provide the integration of favourable gene blocks and the selection of transgression (8). The elementary disadvantage of supplementary recombinations is breakage of linked favourable gene blocks. This would be even more pronounced if these blocks express epistatic effects, which would result in the reduction of combining abilities of progenies (15).

The objective of the present study was to observe the effect of gene recombination cycles on genetic and phenotypic variability and heritability of some traits of maize populations with exotic germplasm. These studies can help maize breeders to make a selection of the most optimum number of supplementary gene recombinations and to gain experience in the use of similar maize populations.

Materials and Methods

A synthetic maize population (1601/5 x ZPL$_{913}$)F$_2$ with 25% of exotic germplasm and narrow genetic base was observed in this study. The inbred ZPL$_{913}$ encompasses both plasmas, exotic and adapted, in the same ratio. The other inbred (1601/5) has been adapted to the conditions of Serbia. The F$_2$ generation (Sin(1601/5 x ZPL$_{913}$)F$_2$R$_0$) was developed. With the aim to study the effect of different recombination cycles on the genetic variability, the following was observed: changes in grain yields (14% moisture, t ha^{-1}), yield components [ear length (cm), the number of kernel rows per ear, 1000-kernel weight (g) and moisture at harvest (%)] and morphological traits [plant height up to the tassel tip (cm) - plant height, plant height up to the base of the upper ear (cm) - ear height and the number of lodged and broken plants (%)] of the initial population (Sin(1601/5 x ZPL$_{913}$)F$_2$R$_0$ = R$_0$) and populations derived after three years (Sin(1601/5 x ZPL$_{913}$)F$_2$R$_3$ = R$_3$), i.e. five years of gene recombinations (Sin(1601/5 x ZPL$_{913}$)F$_2$R$_5$ = R$_5$). This was monitored via self-pollination of 120 to 140 maize plants of the initial population and populations derived after gene recombinations. A total of 96 ears were selected from

the populations (R$_0$, R$_3$ and R$_5$), and their seeds were arranged into four sets with 24 genotypes per a set. The two-replicate plots with 16 plants were set up according to the nested random design (1) in two locations (Zemun Polje, Velika Plana, Serbia) during two years (2001 and 2002). The sowing density was 57.000 plants per hectare. Biometric processing of data was based on means and the analysis of variance. The following parameters were calculated after Falconer (4): genetic and phenotypic variances

$(\sigma^2_g = (MS_5 - MS_6)/rl; \sigma^2_f = \sigma^2_g + \sigma^2_{gl}/l + \sigma^2_e/rl = (MS_5 - MS_6)/rl + (MS_6 - MS_7)/rl + MS_7/rl)$,

their standard errors

$(SE_{\sigma^2_g} = \sqrt{2/r^2l^2\left[(MS_5^2/(s(g-1)+2)) + (MS_6^2/(s(g-1)(l-1)+2))\right]};$

$SE\sigma^2_f = \sqrt{2/r^2l^2\left[(MS_5)^2/(df+2) + 2(MS_6)^2/(df+2) + 2(MS_7)^2/(df+2)\right]})$

and coefficients of variations (CV_g; CV_f;

$CV_{g(f)} = (\sqrt{\sigma^2_{g(f)}}/\overline{X})x100)$.

Where MS_5, MS_6, MS_7 are values from ANOVA. (**Table 1**)

The comparison of genetic, i.e. phenotypic variances among plots was done by the application of the Hartley-test (9), where: $F = \sigma^2_{g(f)}(higher)/\sigma^2_{g(f)}(lower)$ for degree of freedom $n_1(n_2) = gs$. Broad-sense heritability ($h^2 = \sigma^2_g/\sigma^2_f$) and standard error of heritability ($SEh^2 = SE\sigma^2_g/\sigma^2_f$) were calculated after Hadživuković (6). Upper and lower limits for heritability were estimated after method of Knapp et al. (12) $h^2 = 1 - 1/[(MS_5/MS_6)xF_n]$, where are: F_n is value from F distribution ($F_{0,95}$ – lower limit, $F_{0,05}$ – upper limit), n_1 number degrees of freedom for MS_5 and n_2 number degrees of freedom for MS_6.

TABLE 1

ANOVA - *Neseted* design (*Random Model*)

Source of variation	Degrees of freedom	Mean squares	Expected mean squares	F - relation
Locations (L)	l-1	MS$_1$	$\sigma^2_e + r\sigma^2_{gl/s} + g\sigma^2_{r/s/l} + rg\sigma^2_{ls} + rgs\sigma^2_l$	MS$_1$/MS$_3$
Sets (S)	s-1	MS$_2$	$\sigma^2_e + r\sigma^2_{gl/s} + g\sigma^2_{r/s/l} + rl\sigma^2_{f/s} + rg\sigma^2_{ls} + rgl\sigma^2_s$	MS$_2$+MS$_5$/MS$_3$+MS$_6$
L x S	(l-1)(s-1)	MS$_3$	$\sigma^2_e + r\sigma^2_{gl/s} + g\sigma^2_{r/s/l} + rg\sigma^2_{ls}$	MS$_3$/MS$_6$
Replicates/S/L	ls(r-1)	MS$_4$	$\sigma^2_e + g\sigma^2_{r/s/l}$	MS$_4$/MS$_7$
Genotype (G)/S	s(g-1)	MS$_5$	$\sigma^2_e + r\sigma^2_{gl/s} + rl\sigma^2_{g/s}$	MS$_5$/MS$_6$
G x L /S	s(g-1)(l-1)	MS$_6$	$\sigma^2_e + r\sigma^2_{fl/s}$	MS$_6$/MS$_7$
Error	ls(g-1)(r-1)	MS$_7$	σ^2_e	
Total	rlsg-1			

r-number of replicates, g-number of genotypes, l-number of location and s-number of sets

TABLE 2

Means, standard errors and significance of differences of studied traits in the initial (R_0) and recombined (R_3 and R_5) populations of maize

Population ⇒ Traits⇓	R_0	R_3	R_5	Significant differences (Δx)		
				$R_0 : R_3$	$R_0 : R_3$	$R_0 : R_3$
Yield t ha⁻¹	2.88 ±0.06	3.81 ±0.03	3.70 ±0.06	**	**	ns
Moisture content (%)	32.46 ±0.29	27.30 ±0.22	27.85 ±0.21	**	**	ns
1000-kernel weight (g)	234.97 ±1.56	241.16 ±1.92	236.08 ±1.37	ns	ns	ns
Ear length (cm)	12.17 ±0.08	12.88 ±0.08	13.15 ±0.23	ns	**	**
Kernel row number	15.72 ±0.09	16.01 ±0.07	15.68 ±0.06	ns	*	ns
Lodged and broken (%)	16.36 ±0.90	25.40 ±0.76	25.72 ±0.74	**	**	ns
Plant height (cm)	190.60 ±0.61	195.56 ±0.66	197.96 ±0.71	**	**	ns
Ear height (cm)	72.01 ±0.42	77.39 ±0.48	79.53 ±0.45	**	**	ns

( ) Statistical significance of differences of means; P<0.05 = *; P<0.01=**; P>0.05 = ns;

Results and Discussion

Supplementary recombination cycles led to the increase of means of all traits, except of the moisture content at harvest, whose mean was significantly reduced. The increase of means was statistically very significant in the populations R_3 and R_5 in comparison to the initial population, while there was no statistical significance between R_3 and R_5 except for the 1000-kernel weight and the kernel row number (**Table 2**). These results deviate from results obtained by Covarrubias-Prieto et al. (2). These authors, observing effects of recombinations in F_2 populations of related (B73xB84) and unrelated (B73xMo17) inbreds concluded that the supplementary gene recombination cycles did not cause significant changes in average values of grain yields after five recombination cycles. The average values for plant and ear heights decreased in both populations, while the ear length and the kernel row number reduced only in the population of the unrelated single cross hybrid.

TABLE 3

Mean squares (MS) ANOVA of traits of maize populations (R_0, R_3 and R_5)

Sources of variation	df	MS	Popul.	Grain yield	Ear length	Row number	1000-k weight	Moisture %	Plant height	Ear height	Lodged and broken (%)
Locations (L)	2	MS_1	R_0	468.99**	470.74**	624.00**	331783.25**	6110.62**	453879.41**	131334.44**	47024.34**
			R_3	510.39**	433.78**	439.29**	508729.16**	3252.36**	443953.84**	151620.84**	110172.50**
			R_5	397.87**	294.44**	477.06**	482513.69**	2798.30**	510400.84**	172327.70**	99806.09**
Sets (S)	3	MS_2	R_0	15.19 ns	31.98 ns	31.93*	4083.51 ns	260.60 ns	3608.71 ns	1510.26**	474.71 ns
			R_3	11.28 ns	26.49 ns	11.01 ns	3006.37 ns	46.82*	2310.07 ns	253.25 ns	279.87*
			R_5	14.89 ns	4.28 ns	3.02 ns	1016.86 ns	51.28 ns	1173.12 ns	1843.39 ns	560.22 ns
L ∗ S	6	MS_3	R_0	5.99**	15.60**	8.30**	1905.91*	126.71**	1514.82**	123.20*	196.62 ns
			R_3	7.37**	9.08**	6.86**	1543.35*	33.68*	2104.10**	88514**	112.52 ns
			R_5	8.19**	35.29*	8.04**	2152.61**	114.72**	2692.60**	568.10**	312.68 ns
Repl. /S/L	12	MS_4	R_0	0.02 ns	1.23**	0.73	69.76 ns	0.78 ns	498.66**	166.96**	41.24 ns
			R_3	0.03 ns	0.22 ns	0.74 ns	194.33 ns	0.42 ns	330.36**	97.59**	19.33 ns
			R_5	0.05 ns	16.23s	2.97**	54.33 ns	0.30 ns	207.93**	76.48*	79.64**
Families /S	92	MS_5	R_0	3.63**	8.49**	15.34**	1925.77**	130.07**	955.34**	541.78**	423.66**
			R_3	3.25**	7.56**	7.53**	2685.89**	68.91**	643.54**	291.60**	299.45**
			R_5	3.67**	22.83 ns	7.72**	1977.10**	60.94**	911.74**	453.89**	261.47*
Family ∗L/S	184	MS_6	R_0	0.94**	2.02**	2.57	707.24**	24.30**	107.38 ns	51.45 ns	234.42**
			R_3	0.82**	1.88**	1.53**	555.41**	14.66**	126.11**	67.15**	168.21**
			R_5	1.21**	16.47	1.27**	545.61**	13.72**	148.71**	60.51**	157.54**
Error	276	MS_7	R_0	0.02	0.48	0.52	88.05	0.58	75.88	40.37	26.41
			R_3	0.03	0.53	0.54	112.72	0.39	69.97	33.18	17.89
			R_5	0.03	16.00	0.47	80.71	0.36	61.09	34.13	28.92

P<0.05 = *; P<0.01 = **; P>0.05 = ns;

Lamkey et al. (15) recorded the grain yield reduction after eight recombination cycles in the hybrid population (B73 x B84)F_2. The authors explained this as a result of a recombination of blocks of genes with a fixed epistatic effect that probably existed in the parents of the studied population. Deviations of these results from ours can be explained by the differences in the initial material, unrelatedness of parental inbreds, number of gene recombinations and absence of favourable blocks of loci with the fixed epistatic effect. The increase of average values of recombined populations is probably a result of the increased frequency of favourable genes, i.e. the increased frequency of genotypes with a greater expression of traits characteristic for a given population. Significant interactions with environments and the significance for observed traits present among families show the limited success of applied breeding methods in a gradual alteration in favourable gene frequencies within the population.

Different agroecological conditions, genotypes (families) and mutual interactions affected the variation of traits of the initial and recombined populations. Mean squares for families within sets for the yield of the studied populations were several times greater than the family x location interaction within the set, which is a good prerequisite for the estimation of genetic variability and heritability of traits of these populations (**Table 3**).

The estimated values of genetic and phenotypic variances of the studied population traits can be considered reliable and significant, as they are at least two-fold higher than the corresponding values of the standard error (4). Genetic variance decreased over the increased number of recombinations for all studied traits except for the 1000-kernel weight in which it significantly increased after the third recombination cycle (**Table 4**). The reduction of genetic variance was not significant only for the grain yield and the ear length, while it was significant for remaining traits. Genetic variability

TABLE 4

Components of variance, heritability and coefficients of variation for grain yields of maize populations (R_0, R_3 and R_5)

Parameters	Populations	Grain yield	Ear length	Row number	1000-k weight	Moisture %	Plant height	Ear height	Lodged and broken (%)
σ_g^2	R_0	0.45±0.09	1.07±0.20	2.12±0.37	203.08±48.38	17.62±3.19	141.32±23.29	66.72±11.01	31.54±11.06
	R_3	0.41±0.08	0.94±0.18	1.00±0.18	355.07±65.07	9.04±1.69	86.23±15.79	37.40±7.18	21.87±7.83
	R_5	0.41±0.09	1.06±0.62	1.07±0.18	238.58±48.98	7.86±1.50	127.17±22.31	65.56±11.08	17.32±6.91
σ_f^2	R_0	0.60±0.09	1.41±0.21	2.55±0.37	320.96±49.93	21.67±3.21	159.22±23.42	75.29±11.08	70.61±11.81
	R_3	0.54±0.08	1.26±0.19	1.25±0.18	447.64±66.73	11.48±1.71	107.25±16.01	48.60±7.30	49.90±8.37
	R_5	0.61±0.09	3.80±0.75	1.28±0.19	329.5±49.90	10.15±1.51	151.95±22.49	75.64±11.15	43.57±7.45
CV_g (%)	R_0	23.22	8.53	9.55	6.06	12.19	6.23	11.34	31.32
	R_3	16.71	7.55	6.24	7.81	9.61	4.74	7.90	18.94
	R_5	17.28	7.82	6.60	6.54	8.85	5.69	10.18	16.59
CV_f (%)	R_0	26.96	9.76	10.47	7.62	13.52	6.62	12.04	46.87
	R_3	19.31	8.71	6.99	8.77	9.00	5.29	9.00	28.61
	R_5	21.11	14.82	7.23	7.68	10.93	6.22	10.93	26.31
h^2 (%)	R_0	74.19±0.14	76.26±0.14	83.22±0.14	63.27±0.15	81.32±0.14	88.76±0.14	88.61±0.14	44.66±0.14
	R_3	74.94±0.14	75.16±0.14	79.66±0.14	79.32±0.14	78.72±0.14	80.40±0.14	76.97±0.14	43.82±0.15
	R_5	66.96±0.15	27.85±0.16	83.56±0.14	72.40±0.14	77.47±0.14	83.68±0.14	86.66±0.14	39.74±0.15
LLh^2	R_0	64.54	67.30	76.98	49.53	74.33	84.55	84.35	23.97
	R_3	65.56	65.83	72.08	71.58	70.76	73.07	68.35	22.81
	R_5	54.60	0.87	77.39	62.08	69.06	77.58	81.68	17.21
ULh^2	R_0	81.03	82.51	87.68	73.00	86.26	91.73	91.62	59.32
	R_3	81.57	81.72	85.06	84.79	84.36	85.59	83.03	58.70
	R_5	75.71	46.97	87.90	79.71	90.20	88.01	90.20	55.63
Significance									
$\Delta\sigma_g$	(R_0:R_3)	ns	Ns	**	**	**	*	**	**
	(R_0:R_5)	ns	ns	**	ns	**	ns	ns	**
	(R_3:R_5)	ns	ns	ns	**	ns	**	**	ns
$\Delta\sigma_f$	(R_0:R_3)	ns	Ns	**	*	**	**	**	**
	(R_0:R_5)	ns	**	**	ns	**	ns	ns	**
	(R_3:R_5)	ns	**	ns	*	ns	**	**	ns

$P<0.05 = *$; $P<0.01 = **$; $P>0.05 =$ ns; LLh^2 - lower limit of heritability; ULh^2 - upper limit of heritability; $\Delta\sigma_g$, $\Delta\sigma_f$ are statistical significance of differences for genetic and phenotypic variances, respectively

decreased for the majority of traits in the course of five recombination cycles, while phenotypic variability increased for grain yield, ear length and 1000-kernel weight. Such values of this parameter indicate that the participation of the ecological variance increased with the increase of the number of recombination cycles, which is an undesirable phenomenon from the aspects of practical selection.

Coefficients of phenotypic variation (CV_f) were higher in all cases than the corresponding coefficients of genetic variation (CV_g), which is logical considering that the phenotypic variance includes the genetic variance (Table 3). These parameters were changing similarly to corresponding genetic and phenotypic variations. It means that lower coefficients of genetic and phenotypic variations mean the reduction of variability. The decrease of the correlation coefficient for the grain yield was not significant, which is another proof that the genetic composition of the population was not significantly changed with the pronounced increase of the ecological variance in the total variation. Higher coefficients of genetic variability can be explained by a wider genetic background (19), which is achieved by the effect of exotic germplasm (20).

Heritability after three, that is five, recombination cycles changed similarly to the values of the genetic variance. It increased with the number of gene recombinations only in the 1000-kernel weight, while it decreased in all other traits (Table 3). The highest values of heritability for these traits were estimated in the plant and ear height, the kernel row number and grain yield and they varied from 66.96% in R_5 to 74.94% in R_3 maize population, as it was a broad-sense heritability, which is also in accordance with results obtained by other authors (8). Based on the gained results it can be concluded that all these traits were, to the highest extent, determined by the additive gene effects (8). This can be explained by the fact that genetic variability is conditioned by the three-fold higher value of additive than dominant variance in S_1 progeny (), as stated by Nawar (18). Heritability increased insignificantly up to the third recombination cycle, and then decreased by 7.23%. It points out to a greater participation of the ecological variance in the phenotypic variance on one hand, and to a reduction of the genetic variance, on the other hand. Positive values for the lower limits of heritability indicate that the estimated heritability values for all traits of studied populations are reliable as they differ from zero (13). Contrary to the increase of the average grain yield, values of genetic and phenotypic variances and their coefficients of variability decreased in these populations. Such a sequence was not recorded in heritability, since the participation of the ecological variance in the total phenotypic variation changed; hence the highest, i.e. lowest heritability occurred after the third, i.e. the fifth gene recombination cycle, respectively. The estimations of genetic variability in F_2 and populations derived

after five generations of gene recombination point to a fact that a higher number of supplementary gene recombinations is not sufficiently effective in the genetic variance increase. Hence, the number of recombinations in this case should be three cycles. Crossa and Gardner (3) indicate 0.57 for grain yield in the populations with 50% of exotic plasma, 0.45 in the populations with 25% of exotic plasma (it ranged from 0.41 to 0.45 in our studies) and 0.49 in the adapted population. The differences in the values of genetic and selection parameters for these traits, can be contributed to the specificity of the genetic material and its different respond to the growing conditions, type of the experiment, as well as to the estimation method for certain parameters (4, 9, 5, 14)

Many authors (5, 10, 15), studying the effect of supplementary gene recombination cycles, did not determine significant changes in values of genetic variation in populations under selection, while variability was still high enough to provide successful breeding. Populations with high genetic variability could be a good initial material for the systemic improvement of populations. Based on theoretical research, Hallauer (7) suggests that a lower selection intensity (20-30%) should have priority in maintenance of genetic variability for a longer period of time.

Sallah and Geadelmann (1984), cit. Ivanović and Rosić (11), showed that the incorporation of exotic plasma did not lead to significant changes in the genetic variance and heritability for the grain yield in relation to a population with the adapted plasma, while the genotype x environment interaction increased with a higher percent of exotic plasma in the population. From the aspect of practical selection, authors give priority to a population with 25% of exotic plasma.

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