Evaluation of inbred lines as sources of new alleles for improving elite maize hybrid

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Summary

Choice of an appropriate donor of alleles for use in reselection programs of existing inbred lines of maize (*Zea mays* L.) is crucial to the success of such programs. Well-adapted local inbred lines might be used as donors to improve a target genotype. The objectives of this study were to: (i) evaluate Serbian maize inbred lines as donors of favorable alleles for improvement of a single cross hybrid and (ii) estimate Dudley's relationship values to determine which inbred parent should be improved.

Evaluation of four donor lines as sources of new favorable alleles for the yield of grain yield not present in the elite hybrid parent line was conducted, (Dudley, 1987a; 1987b). Each of the potential donors had significant values of the parameter μG, so they can be used as the sources of new alleles in the improvement of elite hybrid A654 x Fu4 yield. The greatest number of favorable new alleles for the improvement of grain yield of hybrid A654 x Fu4 was recorded in inbred line ZPLB368. The improvement of yield in hybrid A654 x Fu4 would be conducted by improving inbred parent Fu4, since all donor lines showed higher genetic parentage with this parent than with A654. The best way for developing initial population is self-fertilization of F_1 generation (P_w x Fu4), which would allow greatest probability for obtaining new lines (improved Fu4).

Introduction

Grain yield of maize is a complex trait. Grain yield includes a number of components that are inherited in a quantitative manner. Phenotypical variability of quantitative characteristics is continuous and conditioned by genotypic variability, variability due to the influence of environmental factors, and their interaction. The analysis of quantitatively inherited traits cannot be based on isolation and measuring of individual genes. The polygenic effects must be measured simultaneously to obtain basic information on the genetic nature of quantitative traits based on complex biometrical methods. A theoretical foundation of genetic analysis of quantitative traits was established by Fisher (1918).

The main task of maize selection is obtaining new hybrids, which with their positive features exceed the existing commercial hybrids. Inbred lines, hybrids, synthetic populations, open-pollinating varieties, etc. may serve for the improvement of elite two-line hybrid, as the donors of favorable alleles. One of the methods used for obtaining single-cross hybrids is the improvement of the best commercial single-cross hybrids by use of inbred lines as the donors of favorable alleles.

The utilization period of maize hybrids is limited. They are replaced with newer hybrids with better agronomic traits and properties required by the market. Reselection in inbred parents of existing hybrids, by the pedigree method of selection (Bernardo, 1990a) is the common method used in commercial maize breeding programs. In this breeding system, an appropriate donor of desirable traits should be identified. Selection of donor parents is crucial to the success of such breeding programs (Hallauer and Miranda, 1988).

The largest number of favorable alleles is accumulated in the best hybrid, grown in a certain area (Dudley, 1984a; 1987a). The identification of additional favorable alleles for

quantitative traits not present in that hybrid is one of the most important tasks facing a breeder. Dudley (1984a, 1984b) developed procedures for identifying donor parents containing alleles not present in parental inbreds. At a later time, Dudley (1987a, 1987b) modified the theory to revise the assumption that the average frequency of favorable alleles (Pj) at the class j loci was equal to the average frequency of favorable alleles (Pk) at the class k loci. This assumption could lead to erroneous estimates of $Lpl\mu$ (Gerloff, 1985). Pfarr and Lamkey (1992) and Zanoni and Dudley (1989) compared the original and the modified method and found the modified procedure to be superior.

Fabrizius and Openshaw (1994) studied 20 donor maize populations. They contained 0, 25, 50, 75 and 100% of new germplasm in relation to the target elite hybrid under improvement. Five population estimators were applied: relative number of favorable alleles ($Lpl\mu$) lacking in inbreds of the elite hybrid (Dudley, 1987b), minimum upper bound (UBND) (Gerloff and Smith, 1988), net improvement (NI) (Bernardo, 1990a; 1990b) predicted three way cross (PTC) (Hallauer and Miranda, 1988) and testcross of the population to the single cross hybrids (TCSC) (Stuber, 1978). Populations with high percentages of new germplasm were better donors of favorable alleles. On the basis of rank correlations, all statistics except NI ranked populations similarly. The NI statistic was unable to distinguish populations from one another and had a large standard error (SE).

Dudley et al. (1996) studied 20 improved populations as sources of favorable alleles for three elite single-cross hybrids. For grain yield, 15 of these 20 populations had significantly higher relative estimates of favorable alleles, while none of the populations proved potential for reducing ear height. $Lpl\mu$ values for grain yield increased as the yield of the target hybrids decreased. This was expected because the lower the yield of the target hybrid, the larger the number of loci lacking favorable alleles.

$Lpl\mu$, UBND, PTC, and NI are all biased estimates of the relative number of favorable alleles at the class l loci. A bias exists because there is a difference between the expectations of these statistics and the true parameter value. Empirical results fail to confirm the expectation due to sampling error, epistasis, or unequal genetic effects among loci. This bias will change with the choice of estimator and the genetic populations being evaluated (Fabrizius and Openshaw, 1994). While $Lpl\mu$, UBND, and PTC estimate potential likely to be achieved, the net improvement statistic (NI) was proposed to identify populations that could provide an immediate contribution to a reference hybrid. Hogan and Dudley (1991) and Fabrizius and Openshaw (1994) have shown the effectiveness of Dudley's method, compared with the UBND, PTC, and NI estimators. Dudley's method has a smaller SE than the other estimators (Fabrizius and Openshaw , 1994; Bernardo, 1990b). Dudley's theory also provides more useful information than the other three methods.

It is assumed that the well adapted local populations, or populations resulting from some type of family-based recurrent selection, have a satisfactory level of favorable alleles and can be used as donors for improving target genotypes. Heterotic patterns among U.S. Corn Belt and Serbian maize populations studied by Mišević (1989a) suggested the possibility of using Yugoslav local varieties as an alternative heterotic pattern to BSSS (Iowa Stiff Stalk Synthetic) or ''Lancaster Sure-Crop''.

The questions arising in these cases are the following:

1. Which selection material can be selected as the donor (P_w) of favorable alleles if we know the parental components (P_1 and P_2) of elite single-cross hybrid?

2. When inbred donor line is identified (P_w), should it be crossed with (P_1) or (P_2) of elite hybrid?

3.   If inbred donor line (P_w) is crossed with (P_2), for instance, should self-fertilization start in F_2 generation, or should F_1 generation previously be crossed with P_2 or with P_w (reversible crossings) (Dudley, 1982)?

The review and elaboration of the method of identification of inbred lines containing favorable alleles bearing impact on the expression of quantitative characteristics, and which are absent from the elite hybrid, is given by Dudley (1984a, 1984b, 1984c, 1987a, 1987b). If the dominant alleles are favorable, which is the case in grain yield, and then G class loci are the most interesting, because the donor line (P_w) has plus (favorable) alleles, while P_1 and P_2 have minus (unfavorable) alleles for yield. For ear height and lodging, it is desirable that the donor line has recessive unfavorable alleles which are absent from parents (P_1 and P_2) of elite hybrid (Dudley, 1987a; 1987b, 1988). The parentage of donor line with one of the parental lines is determined by formulas $(P_2 \times P_w) - (P_1 \times P_w) = (P_1 - P_2)/2$. Positive value suggests greater genetic parentage of donor line (P_w) with parent P_1 and negative value suggests greater genetic parentage of donor line (P_w) with parent P_2 (Dudley, 1987a; 1987b and 1988).

The potential donor inbred lines may have favorable alleles at loci where elite hybrid inbred parent lines (A654 x Fu4) have fixed unfavorable alleles. The purpose of the study is to determine which inbred line is the best donor for improvement elite hybrid A654 x Fu4.

Material and methods

Six inbred lines (A654, Fu4, ZPLB554dr, ZPLB176dr, ZPLB380 and ZPLB368) were selected for the study. A654 line originates from the USA, and Fu4 from Romania. Other four lines were selected at the Maize Institute Zemun Polje in Serbia and Monte Negro. Diallelic crossings of six inbred lines without reciprocal combinations were conducted in 2000, for the purpose of producing F_1 generation seed. A comparative experiment of lines and hybrids was evaluated in a randomized complete block design with five repetitions in 2001 and 2002 in Zemun Polje.

The area of the experimental lot was 5.6 m^2, and the crop density was 71500 plants/ha. Yield was measured in the experimental lot and presented in t/ha with 14% humidity. The soil type at the location is calcareous chernozem. Fertilizer was applied at the rate of 400 $kgha^{-1}$ of 10:30:20 (N:P:K) preplowing and 200 $kgha^{-1}$ of urea (46% of N) at seed bed preparation. Planting and harvesting were done by hand. Plots were over-planted and thinned to desired density. Apart from average values, the study presents two-factorial variance analysis, coefficient of variation, heterosis of F1 in comparison with the value of the better parent, and evaluation of relative value of loci in inbred lines. Evaluation of relative values of loci in inbred lines was conducted according to the modified model Dudley (1987a). Hybrid A654 x Fu4 was selected for the improvement, and other lines served as a potential source of favorable alleles (donor lines). For two homozygous lines (P_1 and P_2) at the elite hybrid and donor line (P_w) there are eight locus classes.

The most significant class for improving characteristics that are inherited is locus class «G» where lines (P_1 and P_2) of elite hybrid have unfavorable (recessive) alleles, while donor line (P_w) has favorable (dominant) alleles (Table 1). It enables the donor line with favorable, dominant alleles to be selected on the loci where hybrid (P_1 x P_2) has unfavorable, recessive alleles. Genotypic value of three possible genotypes (++, +-, --) on one locus are μ, $a\mu$ and $-\mu$ according to Comstock and Robinson (1948) where the degree of dominance, $\mu = \frac{1}{2}$ of the difference of genotypic value ++ and - - genotypes. Dudley model (1987a; and 1987b) assumes with the following: μ = constant for all loci, $a = 1$, full dominance, and absence of epistasis, $\mu A = \mu H$.

Table 1. Genotypes for classes of loci possible for an elite hybrid (P_1xP_2) and a potential donor line P_w (modified from Dudley, 1984a)

Class of loci	Line 1. (P_1)	Line 2. (P_2)	line donor (P_w)
A	+	+	+
B	+	+	-
C	+	-	+
D	+	-	-
E	-	+	+
F	-	+	-
G	-	-	+
H	-	-	-

+ = loci homozygous for favorable alleles; - = loci homozygous for favorable alleles;

A positive value μG shows that line (P_w) has favorable alleles on loci where parental lines (P_1 and P_2) have unfavorable alleles. Value μB gives relative number of loci where P_1 and P_1 have favorable alleles, μC gives relative number of loci where P_1 and P_w have favorable alleles and P_2 does not, and μE gives to the relative number of loci where P_2 and P_w have favorable alleles and P_1 does not. Values μD and μF show that P_1 and P_2 have favorable alleles at the loci where other two lines do not have favorable alleles. In case of $a \neq 1$, (i.e., when there is no full dominance), which is one of the conditions for the use of Dudley model (1987a), the obtained values μG are not very precise. In case of $a > 1$ (overdominance) then μG value is more precise; i.e., if $a < 1$ (partial dominance) then μG value is underestimated. The sum of μC and μF gives relative number of loci where P_1 and P_w have the same (+ or -) alleles, while $\mu D + \mu E$ give relative number of loci where P_2 and P_w have the same (+ or -) alleles. If:

1) $\mu C + \mu F > \mu D + \mu E$ – line P_w is more closely related to P_1 and is used for the improvement of parent P_1

2) $\mu C + \mu F < \mu D + \mu E$ – donor line P_w is more closely related to P_2 and is used for the improvement of parent P_2

Evaluation of parentage of donor (P_w) with elite hybrid parents (P_1 and P_2) can be performed by using the following formulas $[(P_2 x P_w) - (P_1 x P_w) + (P_1 - P_2)/2]$. Positive value points to the parentage between P_1 and P_w, while negative value points to the parentage between P_2 and P_w (Dudley, 1987a).

Depending on which parent is being improved, P_1 or P_2, the founding initial population for selection is determined by comparing values μD or μF with value μG. If parent P_1 is improved, there are three possibilities:

1. $\mu D = \mu G$; The probability that the new line will have more loci with favorable alleles in class D and G than either P_1 or P_w is maximum. Then the approach will be hybrid self-fertilization ($P_1 x P_w$)

2. $\mu D > \mu G$; points to the back crossing of hybrids ($P_1 x P_w$) with parent P_1.

3. $\mu D < \mu G$; back crossing of hybrids with ($P_1 x P_w$) with donor P_w is recommended (Dudley, 1987a, 1987b; Živanović et al, 2001).

Results and Discussion

Based on two-factorial variance analysis experiments with inbred lines *per se* and single-cross hybrids, highly significant means of square of genotypes, years and interactions genotypes x year on the grain yield were determined (Table 2).

Table 2. Analysis of variance for yield of 15 single-cross hybrids and 6 inbreds evaluated in 5 replications for 2 years

Source of variation	d.f.	Mean squares
Replication	8	0.77
Year (Y)	1	317.48**
Genotype (G)	20	110.15**
G x Y	20	12.74**
Error	160	0.54

** = significant at 0.01 level using F-test;

In both study years hybrids had greater grain yield than inbred lines, which was to be expected (Table 3). The greatest yield among the lines for both years was line Fu4 (6.21 t/ha in 2001 and 6.45 t/ha in 2002). The lowest yield was recorded for line ZPLB380 in both years (3.95 t/ha and 5.43 t/ha). The highest average grain yield was recorded in hybrid A654 x ZPLB176dr (16.28 t/ha in 2001.), and hybrid A654 x Fu4 in 2002. (11.65 t/ha). Mean yield of hybrids varied from 9.29 to 16.28 t/ha. These differences were expected, because certain inbred lines were assumed to be more related to one parental inbred than another on the basis of pedigree of lines.

Table 3. Grain yield (t ha^{-1}) and variability of lines and single crosses and heterosis single crosses

Genotype	Yield (t ha^{-1})		CV (%)		Heterosis (%)	
	2001	2002	2001	2002	2001	2002
A654	4.80	6.03	6.16	10.45		
Fu4	6.21	6.45	5.74	7.71		
ZPLB554dr	5.59	5.54	6.88	3.81		
ZPLB176dr	6.00	5.82	8.79	6.44		
ZPLB380	3.95	5.43	8.70	9.76		
ZPLB368	5.22	6.33	15.00	14.23		
$\bar{x}$ inbreds	5.30	5.93				
A654xFu4	15.30	11.65	7.20	7.11	146.44**	80.71**
A654xZPLB554dr	15.01	10.59	4.83	6.46	168,29**	75.72**
A654xZPLB176dr	16.28	11.39	4.62	8.22	171.42**	89.01**
A654xZPLB380	14.35	11.10	6.97	10.58	198.94**	84.17**
A654xZPLB368	15.75	11.25	4.99	7.87	201.53**	77.61**
Fu4xZPLB554dr	14.53	10.54	3.81	10.39	134.07**	63.41**
Fu4xZPLB176dr	9.29	8.66	10.54	6.33	49.58*	34.33*
Fu4xZPLB380	12.35	9.11	4.31	8.33	98.90**	41.22**
Fu4xZPLB368	14.57	10.08	8.18	15.14	134.63**	56.40**
ZPLB554drx ZPLB176dr	14.75	11.38	3.00	4.79	145.93**	95.53**
ZPLB554drx ZPLB380	12.75	11.00	5.62	6.26	127.90**	98.52**
ZPLB554drx ZPLB368	15.32	10.76	2.31	5.44	173.76**	69.91**
ZPLB176drx ZPLB380	13.94	10.10	6.37	5.02	132.46**	73.58**
ZPLB176drx ZPLB368	15.15	10.84	3.27	6.51	152.55**	71.16**
ZPLB380x ZPLB368	14.54	9.98	6.06	5.97	178.49**	57.61**
$\bar{x}$ F$_1$	14.26	10.56				

* = significant at 0.05 level using t-test; ** = significant at 0.01 level using t-test;

Grain yield monitored by means of variation coefficient was consistent between years and ranged from 3.00% to 15.14%. The obtained values of variation coefficient for yield were significantly lower than those obtained by Šatarić (1978) in his study. On the basis of the above we may conclude that these two years were favorable for growing maize.

Grain yield is mainly controlled by dominant gene effects in pure line hybrid combinations (Moreno-Gonzales and Dudley, 1981 and Trifunović et al., 1998), and dominants alleles were considered favorable for improvement of this trait in observed hybrids. High values of heterosis were obtained for grain yield for all tested hybrids in both years. Maximum heterosis value (201.5%) was recorded in 2001. in hybrid combination A654 x ZPLB368 (Table 3). Greater heterosis values in 2001 were the consequence of a relatively higher average grain yield of all tested hybrid combinations with respect to lines.

Inbred line Fu4 had average grain yield 6.33 t/ha and was more productive than inbred line A654 which had average grain yield of 5.42 t/ha (Table 4). The mean comparison of parental inbred x donor lines P_w (A654 x P_w and Fu4 x P_w) crosses indicates significant differences in grain yield. Mean grain yield varied from 8.79 to 13.83 t ha^{-1}. On the average, yields of A654 x P_w crosses were higher yielding than Fu4 x P_w crosses. The greatest average yield in both years was recorded for hybrid A654 x ZPLB176dr (13.83 t/ha), while hybrid A654 x ZPLB368 and elite hybrid A654 x Fu4 had average yield 13.40 t/ha and 13.50 t/ha respectively. Other hybrids between donor lines and one of the parents of elite hybrid had significantly lower average grain yields in comparison with the elite hybrid (Table 4).

Table 4. Grain yield (t ha^{-1}) of elite hybrid and parents of elite hybrid and their hybrids with donor lines

A654	Fu4	A654 x Fu4	Donors	A654 x P_w	Fu4 x P_w
5.42	6.33	13.47	ZPLB554dr	12.80**	12.35**
			ZPLB176dr	13.83**	8.79**
			ZPLB380	12.72**	10.73**
			ZPLB368	13.50**	12.33**

* = significant at 0.05 level using t-test; ** = significant at 0.01 level using t-test;

For grain yield it is desirable that the donor lines (P_w) have dominant alleles for locus class G where the parents of elite hybrid have recessive alleles. The choice of best donor line is based on the greatest positive values of μG (Dudley, 1984a and 1987a). All four lines, potential donors of favorable alleles, had significant positive values of parameter μG. The greatest value of parameter μG was in line ZPLB368 and would be the best donor of favorable alleles for the grain yield (Table 5). The second place was line ZPLB554dr, while lines ZPLB380 and line ZPLB176dr had lower values of parameter μG in comparison with ZPLB368 and ZPLB554dr. Based on the relationship $[(P_2 \times P_w) - (P_1 \times P_w) + (P_1 - P_2)/2]$ relative parentage of donor lines with elite hybrid parents was determined (Dudley, 1987a). Dudley's relationship value parameter indicates the relationship between the donor and the inbred line P_1 or P_2. This relationship is one of the most important factors in applied breeding programs because it influences the improvement procedure of a target hybrid. The inbred to be improved should be the one most closely related to the donor of favorable alleles. Grain yield is the trait for which evaluation of relationship is the most important because the calculation of relationship values is based on estimates of heterosis (Stojšin and Kannenberg, 1995, Todorović et al., 2004). If the value $[(P_2 \times P_w) - (P_1 \times P_w) + (P_1 - P_2)/2]$ is positive, the inbred line is more related to P_1 and if it is negative, the inbred line is more related to P_2. All

four lines had significant negative values which suggest greather genetic parentage with line Fu4 (Table 5). Improvement of elite hybrid A654 x Fu4 for grain yield should be conducted by improving line Fu4.

Table 5. The best way for improvement of hybrid (A654 x Fu4) and for founding initial population

Inbred donors P_w	μG	Relation Relationship $(+P_1; -P_2)$	μD or μF	P_wxP_x cross with:
ZPLB554dr	1.38*	-0.72*	1.72	Self-fertilisation
ZPLB176dr	0.75*	-5.32*	0.57	Self-fertilisation
ZPLB380	0.91*	-2.45*	1.29	Self-fertilisation
ZPLB368	1.50*	-1.63*	1.49	Self-fertilisation

* = larger than 2 x standard error

To determine the method of developing initial populations which will serve for the selection of potentially better lines than line Fu4 for grain yield, the relationship between μG and μF is important. In all instances, the value of parameter μF did not statistically differ significantly from parameter μG (Table 5). This shows that the best way for developing initial population is self-fertilization of F_1 generation (P_w x Fu4), which would allow for greatest probability for obtaining new lines (improved Fu4), which will have greater number of favorable alleles for grain yield on F and G locus classes than line Fu4 or donor line. Similar results and discussion with different selection materials (lines, hybrids, synthetical populations) are given by different authors (Mišević, 1989a, 1989b, 1990; Petrović and Jelovac, 1989; Petrović, 1990; Petrović et al. 1992 and Delić, 1993) and by comparing different statistical tests (Mišević, 1989b). Since in this study we have different genetical material, different conditions of growing and production year it is hard to make direct comparisons with our results.

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