Performance and Inbreeding Depression of an Exotic Maize Population under Selfed Progeny Recurrent Selection

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Leistung und Inzuchtdepression von einer exotischen Maispopulation unter S-Rekurrenter Selektion

1. Introduction

The use of inbred-hybrid concept in maize breeding has emphasised the pedigree method of selection for inbred lines development from genetically narrow-base populations. Consequently, the germplasm base of the hybrids grown for commercial production has been reduced (ZUBER, 1975; ZUBER and DARRAH, 1980; SMITH, 1988). Introgression of exotic germplasm into adapted breeding populations of maize has been suggested as a mean for increasing genetic variability (STUBER, 1978; GOODMAN, 1985; TALLURY and GOODMAN, 1999; GOODMAN et al., 2000; CARENA and HALLAUER, 2001). In Europe, local populations are of special interest to breeders as a source of favourable alleles for improvement of adapted germplasm (LENG et al., 1962; BRANDOLINI, 1969; MISEVIC, 1989; SINOBAS and MONTEAGUDO, 1996; GARAY et al., 1996; DUBREUIL and CHARCOSSET, 1999).

Recurrent selection methods were developed to gradually improve the mean performance of genetically broad-base populations and their incorporation into current breeding programs could favour the use of exotic germplasm (HALLAUER, 1990). Among several methods of recurrent selection proposed, selfed progeny selection is of particular interest to breeders, because it is theoretically expected to be more effective than selection among full-sib and half-sib families (HALLAUER, 1992). Although in several studies selfed progeny selection was not as effective as expected in improving grain yield in random-mated generations (TANNER and SMITH, 1987; HALLAUER, 1992; LAMKEY, 1992), it has proven to be superior to other methods in reducing inbreeding depression for grain yield (TANNER and SMITH, 1987; HORNER et al., 1989; ODHIAMBO and COMPTON, 1989; WALTERS et al., 1991). Thus, selfed progeny selection is suitable for improvement of exotic germplasm with substantial genetic load and above-average expression of inbreeding depression.

Zusammenfassung

In einer M3S Maispopulation, die aus Rekombinationen zwischen 12 heimischen Inzuchtlinien aus exotischem Zuchtmaterial entstanden, wurden zwei Zyklen Rekurrenter Selektion von Selbstungen selektierter Nachkommenschaften durchgeführt. Diese Selektionen hatten das Ziel, den Kornertrag und die Standfestigkeit dieser Population zu verbessern. In einem ersten Zyklus wurde die S_1–S_2 Selektion benützt, um auf Standfestigkeit der S_1 Linien und auf Kornertrag der S_2 Linien auszulesen. Im zweiten Zyklus selektierte man auf höheren Kornertrag zwischen den S_1 Linien und 20 oder 30 der leistungsfähigen S_1 Linien wurden erneut wieder verkreuzt, um C2(+20) und C2(+30) Populationen zu erstellen. Der Ertrag in der S_1 Generation war um 21% (C2(+20)) und um 24.7% (C2+(30)) höher als in der C0, während in der S_0 Generation die Ertragssteigerung nur 3.8% für C2(+20) und 4.8% für C2(+30) war. Durch diesen Rekurrenten Selektionszyklus wurde die Standfestigkeit nicht verbessert, jedoch die Reifezeit verändert und die Pflanzenhöhe sowie die Höhe des Kolbenansatzes erhöht. Die Inzuchtdepression für den Kornertrag war 40.8 % in der C0 und nahm danach zu 31.4 % und 29.7 % in der C2(+20) und C2(+30) ab. Die C2(+30) Population, die aus einer geringeren Selektionsintensität entstand, erhöhte ihren Kornertrag und ihre Standfestigkeit gegenüber der C2(+20) Population.

Schlagworte: Mais, exotisches Zuchtmaterial, Rekurrente Selektionsmethodik, Inzuchtdepression.

Summary

The M3S maize population obtained by intercrossing of 12 domestic inbreds (exotic germplasm) was subjected to two cycles of selfed progeny recurrent selection to improve grain yield and lodging resistance. In the first cycle S_1–S_2 selection was used with emphasis on standability among S_1 progenies and on grain yield among S_2 progenies. In the second cycle, selection for better grain yield was conducted among S_1 progenies and, 20 and 30 best yielding S_1 progenies were intermated to form the C2(+20) and C2(+30) population, respectively. The S_1 generation grain yield increased 21 % and 24.7 % whereas, the S_0 generation grain yield increased 3.8 % and 4.8 % from C0 to C2(+20) and C2(+30), respectively. The standability was not improved, but, maturity was delayed and plant and ear height increased. The inbreeding depression for grain yield decreased from 40.8 % in C0 to 31.4 % and 29.7 % in C2(+20) and C2(+30), respectively. The lower selection intensity in the population C2(+30) in comparison to the C2(+20) population resulted in higher grain yield and slightly higher stalk lodging resistance.

Key words: maize, exotic germplasm, recurrent selection, inbreeding depression.

A number of Croatian domestic inbred lines showed equally good combining ability with both the BSSS and the Lancaster testers (PEJIĆ and KOZUMPLIK, 1990) and the same level of isoenzymatic differences to both testers (PEJIĆ, 1992). Twelve of these lines were used to form the Maksimr 3 Synthetic population (M3S) in 1990. The population underwent two cycles of selfed progeny recurrent selection. The objectives of this study were: (i) to evaluate the response of the population per se and population per se selfed, to two cycles of selection, (ii) to compare estimates of inbreeding depression in different cycles of selection, and (iii) to compare effectiveness of two effective population sizes used in the second cycle of selection.

2. Materials and Methods

2.1 Development of the M3S population and selection trials

The M3S population used in this study was developed by intermating 12 inbred lines at the Faculty of Agriculture, University of Zagreb. The origin of inbreds traces back to several open-pollinated varieties and local populations from different regions of the former Yugoslavia (Table 1). In 1990 the 12 inbreds were crossed to form six single crosses, which were crossed to each other to form 15 double crosses in 1991. Equal amount of seed of each double cross was mixed to form C0 of the M3S population. The population was then subjected to two cycles of selfed progeny recurrent selection (Table 2).

The first cycle of selection was started by selfing 750 S_0 plants in C0 in 1992. The derived S_1 progenies were grown

Table 1: Germplasm sources included in formation of the M3S maize population

Tabelle 1: Herkunft von zur Synthese der M3S Maispopulation benutztem Germplasm

Inbred line	Germplasm source	Country
Bc10	Beljski žuti zuban (Belie's Yellow Dent)	Croatia
Bc14Ht	Beljski žuti zuban (Belie's Yellow Dent)	Croatia
Bc30965	Maksimirski zuban (Maksimir's Dent)	Croatia
L1-26	Maksimirski zuban (Maksimir's Dent)	Croatia
L81-ŠL	Populacija iz Istre (Population from Istria)	Croatia
L80	Populacija iz Bujštine (Population from Buistina)	Croatia
L86	Populacija iz Savudrija (Population from Savudria)	Croatia
L219	Populacija iz Istre "Šišan" (Population from Istria "Shisan")	Croatia
Bc12	Populacija iz Banje Luke (Population from Banja Luka)	Bosnia and Hercegovina
L131F-d	Populacija iz Metohije (Population from Metohia)	Serbia and Montenegro
L131F-e	Populacija iz Metohije (Population from Metohia)	Serbia and Montenegro
LFA	Šidski zuban (Shid's Dent)	Serbia and Montenegro

ear to row in 1993. The rows were artificially inoculated with *Helminthosporium turcicum* Pass. and *Colletotrichum graminicola* (Ces.) G.W. Wils. fungi. In each row five healthy plants were selfed. At harvest, the best performing 225 S_1 progenies with good root and stalk strength were selected. Their S_2 progenies were evaluated in a 15x15 lattice design with two replications at two locations in 1994. The primary trait under selection was grain yield, with selection pressure to increase resistance to root and stalk lodging. Forty best performing S_2 progenies were intermated in 1995 using bulk-entry method (HALLAUER, 1985) to

Table 2: Selection protocols for the two cycles of selection conducted in the M3S maize population
Tabelle 2: Selektionsverfahren für zwei Zyklen von Selektion in der M3S Maispopulation

Cycle of selection[1]	Year of progeny testing	Type of progeny		No. of progeny		Selection intensity %	Expected level of inbreeding
		Evaluated	Intermated	Evaluated	Intermated		
C1	1993	S_1		750			
	1994	S_2	S_2	225	40	5	0.019
C2(+20)	1997	S_1	S_1	225	20	9	0.045
C2(+30)	1997	S_1	S_1	225	30	13	0.036

[1] Cycle population formed by intermating selected progenies

form the C1 population. In 1996 225 S_0 plants in C1 were selfed. The derived 225 S_1 progenies were also evaluated in the 15x15 lattice design in 1997. The best yielding 20 S_1 progenies were intermated to form the C2(+20) population and the best yielding 30 S_1 progenies (including the former 20 progenies) were intermated to form the C2(+30) population in a winter nursery.

2.1 Evaluation trials

In 1998 seed of the populations per se (S_0 generations) was produced for the C0, C1, C2(+20), and C2(+30) by random mating 200 plants in the isolation. In 1999 seed of the populations per se selfed (S_1 generations) was produced for the same four cycle populations by selfing 60 plants. Equal quantities of seed from each ear were bulked to form each population. The four S_0 and four S_1 entries were evaluated in separate experiments set up as a randomised complete-block design with three replications. The S_0-experiment was conducted at three locations (Zagreb, Rugvica, and Osijek) in 1999 and 2000. The S_1-experiment was conducted at the same locations adjacent to the S_0 experiment in 2000 only. Each experimental plot consisted of eight rows 10 m long and spaced 0.70 m apart. Plots were over-planted and later thinned to 57,200 plants/ha. Fertilisation and weed control practices were as recommended for optimum maize production at each location. All plots were hand-planted and harvested with gleaning of dropped ears.

Data were collected on all replications for root lodging (percentage of plants leaning more than 30° from vertical), stalk lodging (percentage of plants broken at or bellow the primary ear node), grain moisture (%) at harvest, yield of shelled grain (t/ha) adjusted to 14 % grain moisture, and ear traits. Grain yield was determined from the field ear weight of the middle four rows. Grain moisture and shelling

percentage were determined on a 15-ear sample. The ear traits included ear length (cm), kernel-row number, and ear diameter (mm). Data for the ear traits were recorded as the average of measurements on 50 random ears from the middle four rows, regardless of being first or second ear. Plant and ear height were measured in each environment except at Osijek in 1999 for the S_0-experiment. Plant and ear height were recorded as the average of measurements on 80 competitive plants per plot and were measured as the distance from the soil surface to the collar of the flag leaf and the primary ear node, respectively. Days to anthesis and days to silking were recorded only at Zagreb in 1999 and 2000 for the S_0-experiment and in 2000 for the S_1 experiment.

2.2 Statistical analysis

Analyses of variance were conducted separately for the S_0- and the S_1-experiment for data combined over environments. Each location by year combination was treated as a different environment for a total of six environments in the S_0-experiment and three environments in the S_1-experiment. The model assumed was mixed, where environments were random and entries were fixed. To compare S_0 and S_1 means, an LSD was calculated by using the S_0 error mean square (or GxE if significant) and the S_1 error mean square (or GxE if significant), respectively. Inbreeding depression in absolute units was calculated by using cycle means from the three environments where both the S_0 and S_1 entries were evaluated. Inbreeding depression in absolute units was calculated as the S_0 minus S_1 cycle mean. Percentage inbreeding depression was calculated by dividing inbreeding depression in absolute units by the noninbred mean and multiplying by 100. The significance of inbreeding depression was tested by a t-test (STEEL and TORRIE, 1980).

3. Results

The combined analysis of variance across environments (Table 3) revealed significant (P<0.05) differences among S_0 entries for all traits except root lodging, kernel row number, and ear diameter and among S_1 entries for all traits except root lodging, stalk lodging, ear length, kernel row number, and ear diameter.

Significant differences among environments were found for all traits except kernel row number in the S_1 generation. The genotype by environment interaction was significant for root lodging and ear height in the S_0 generation and for kernel row number and ear diameter in both S_0 and S_1 generations.

Grain yield in the S_0 generation increased 0.26 t/ha (3.8 %) and 0.33 t/ha (4.8 %) from C0 to C2(+20) and C2(+30), respectively (Table 4). The difference was significant only for the C2(+30). Selection was more effective in the S_1 generation, resulting in a significant increase in grain yield of 0.75 t/ha (21 %) and 0.88 t/ha (24.7 %) from C0 to C2(+20) and C2(+30), respectively. In the S_0 generation the yield increase occurred essentially during the second cycle of selection, whereas in the S_1 generation both cycles of selection contributed equally to the yield increase. Of the three ear traits significant differences among cycles of selections was observed only for ear length in the S_0 generation although, a positive trend toward higher values in later cycles of selection was observed for all three ear traits in both S_0 and S_1 generation. Ear length in the S_0 generation was significantly higher for C2(+30) as compared to C2(+20), C1 and C0.

Significant improvement in stalk lodging resistance in the S_0 generation was observed after the first cycle of selection. However, this gain was lost during the second cycle of selection, bringing the incidence of stalk lodging for both C2(+20) and C2(+30) back to the level observed for C0. No significant difference was found in root lodging among the S_0 and in root and stalk lodging among both S_0 and S_1 entries. Slightly lower incidence of stalk lodging was found in the S_1 generation for the C2(+30) than for the C2(+20) population.

Grain moisture in the S_0 generation was significantly higher for both C2 populations compared to C0 and C1 with a more positive response for C2(+30) than for C2(+20). In the S_1 generation grain moisture increased significantly after the first cycle of selection and did not change after the additional cycle of selection. Days to anthesis and days to silking increased by approximately 2 days after two cycles of selection in both the S_0 and the S_1 generation.

Ear and plant height in the S_0 generation increased significantly with the cycles of selection with a more positive response for C2(+30) than for C2(+20). In the S_1 generation ear height increased significantly after the first as well as after the second cycle of selection for both C2 populations, whereas plant height increased significantly only for C2(+30).

Significant inbreeding depression was found for grain yield, ear length, ear diameter, ear height and plant height in all cycle populations, and for kernel row number only in C0 (Table 5). For grain moisture, root and stalk lodging inbreeding depression was not significant for any of the cycle populations (data not shown). Inbreeding depression for grain yield was 40.8 % in C0 and decreased by approx-

Table 3:   Analysis of variance across environments for 11 traits in S_0 and S_1 generations of the M3S maize population
Tabelle 3: Varianzanalyse für die Umgebungen für 11 Merkmale in den S_0 und S_1 Generationen der M3S Maispopulation

Source of variation	df	Grain yield t/ha	Grain moisture %	Root lodging %	Stalk lodging %	Ear length cm	Kernel row number	Ear diameter mm	Ear height cm	Plant height cm	df	Days to anthesis	Days to silking
					S_0 generation mean squares								
E[1]	5 (4)[3]	25.1**	96.2**	8.0*	3170.3**	8.3**	1.2**	49.1**	1132.7**	6789.0**	1[4]	12.0*	88.2**
C[2]	3 (3)	0.6*	6.4**	0.6	111.4**	1.4**	1.1	4.1	122.6**	105.6**	3	7.4**	6.8**
C x E	15 (12)	0.2	0.7	2.4**	25.0	0.3	0.5**	1.6	16.5**	21.6	3	0.9	0.6
Error	36 (30)	0.2	0.5	0.8	13.6	0.3	0.1	0.7	4.0	11.9	12	0.5	0.6
					S_1 generation mean squares								
E	2	16.4**	161.1**	2.5**	2999.6**	7.5*	0.75	40.4*	86.6**	1349.6**			
C	3	1.4**	11.3**	0.3	10.4	1.2	1.2	2.6	183.2**	219.9**	3	1.6*	4.1**
C x E	6	0.2	1.4	0.2	12.1	1.1	0.4*	2.0*	3.6	4.2			
Error	18	0.2	1.3	0.2	16.0	0.5	0.2	0.8	5.2	20.2	6	0.2	0.4

[1] environment, [2] cycle of selection, [3] the degrees of freedom for ear and plant heights, [4] the degrees of freedom for days to anthesis and silking, * and ** mean square significant at P<0.05 and P<0.01

Table 4: The S_0 and S_1 means for grain yield and other agronomic traits in the M3S maize population
Tabelle 4: Die S_0 and S_1 Mittelwerte für Kornertrag und andere agronomische Merkmale in der M3S Maispopulation

Cycle of selection	Grain yield t/ha	Grain moisture %	Root lodging %	Stalk lodging %	Ear length cm	Kernel row number	Ear diameter mm	Ear height cm	Plant height cm	Days to anthesis	Days to silking
						Trait					
						S_0 generation					
C0	6.88	19.61	1.12	18.22	17.61	14.47	41.09	76.87	171.84	76.00	78.50
C1	6.86	19.67	0.66	12.93	17.70	14.72	41.43	78.12	172.48	76.17	78.83
C2(+20)	7.14	20.29	0.93	17.71	17.87	15.01	41.64	81.70	174.79	78.00	80.50
C2(+30)	7.21	20.75	0.90	17.71	18.25	14.96	42.24	82.88	177.70	78.00	80.50
LSD (0.05)	0.29	0.49	ns[1]	2.50	0.34	ns	ns	3.23	2.57	0.91	0.97
						S_1 generation					
C0	3.56	18.64	0.40	18.38	14.99	13.62	36.97	56.12	130.80	79.00	81.67
C1	3.97	20.90	0.19	18.63	15.39	14.15	38.03	61.96	138.02	79.33	82.33
C2(+20)	4.31	20.82	0.58	20.01	15.53	14.45	37.77	61.52	135.00	79.67	83.33
C2(+30)	4.44	20.94	0.53	17.41	15.89	14.30	38.16	67.17	142.52	80.67	84.33
LSD (0.05)	0.44	1.07	ns	ns	ns	ns	ns	2.27	4.45	0.94	1.29

[1] Not significant at P<0.05

Table 5: Inbreeding depression in actual units and percentages (in parentheses) for grain yield and other agronomic traits in the M3S maize population
Tabelle 5: Inzuchtdepression in absoluten Größen und Prozenten (in Klammern) für Kornertrag und andere agronomische Merkmale in der M3S Maispopulation

Trait	C0			C1			C2(+20)			C2(+30)		
							Cycle of selection					
Grain yield (t/ha)	2.5	(40.8)	**	1.8	(31.7)	**	2.0	(31.4)	**	1.9	(29.7)	*
Ear length (cm)	2.5	(14.1)	**	2.0	(11.5)	**	1.9	(11.0)	**	1.8	(9.8)	**
Kernel row number	1.4	(9.4)	**	0.0	(-0.3)	ns	0.4	(2.5)	ns	0.4	(2.5)	ns
Ear diameter (mm)	4.2	(10.3)	**	2.2	(5.4)	*	2.4	(6.0)	*	2.6	(6.4)	*
Ear height (cm)	16.1	(22.3)	**	9.2	(12.9)	**	13.9	(18.4)	**	8.7	(11.4)	**
Plant height (cm)	26.5	(15.9)	**	11.2	(7.0)	**	20.6	(12.2)	**	13.2	(7.7)	**
Days to anthesis	-2.0	(-2.6)	ns	-3.0	(-3.9)	**	-0.7	(-0.8)	ns	-2.0	(-2.5)	ns
Days to silking	-1.0	(-1.2)	ns	-2.0	(-2.5)	*	-0.7	(-0.8)	ns	-2.0	(-2.4)	*

ns, * and ** Inbreeding depression nonsignificant or significant at P<0.05 and P<0.01

imately 10 % during the first cycle of selection with no further change during the second cycle of selection for any of the two C2 populations. Inbreeding depression for other traits was also lower in the improved cycle populations than in the base population. The observed decrease in the amount of inbreeding depression occurred essentially in the first cycle of selection, except for ear and plant height in C2(+20), where an increase of inbreeding depression compared to C1 was observed.

4. Discussion

The M3S population was formed to exploit favourable alleles of the local germplasm showing similar heterotic complementarity to both the BSSS and the Lancaster testers. Two cycles of selfed progeny selection in the M3S population were successful in improving grain yield in the S_1 generation (direct response to selection), but had little effect in the S_0 generation (indirect response to selection). Several authors also reported that selfed progeny selection was not very effective in improving grain yield in random-mated generations (HALLAUER, 1992; LAMKEY, 1992).

After the first cycle of selection stalk lodging resistance of the S_0 generation was significantly improved with no change in grain yield. However, in the second cycle of selection the increase in grain yield was accompanied by a decrease in stalk lodging resistance. In several earlier studies improvement of stalk quality was accompanied by a decrease in grain yield too (DEVEY and RUSSELL, 1983;

MARTIN and RUSSELL, 1984; NYHUS et al., 1989). However, WEYHRICH et al. (1998b) and CARENA and HALLAUER (2001) demonstrated the possibility of simultaneous improving grain yield and stalk lodging resistance by using selection indices where both traits were included, which in the present study was not done.

After two cycles of selection the M3S population became significantly later with increased plant and ear height. VASAL et al. (1995a; 1995b) and VALES et al. (2001) also reported delayed maturity and increased height due to selfed progeny recurrent selection for grain yield. Grain yield, height and maturity traits were generally positively correlated with each other (HALLAUER and MIRANDA, 1988).

Inbreeding depression for grain yield in C0 of the M3S population was 40.7 %. HALLAUER and MIRANDA (1988) reported an average of 25.5 % inbreeding depression for grain yield in temperate maize germplasm. In our study inbreeding depression for grain yield was reduced 10 % through S_1-S_2 selection in the first cycle of selection but did not change during the S_1 selection in the second cycle of selection. Tolerance to inbreeding depression for ear and plant traits was also improved mainly during the first cycle of selection. It is to be expected that deleterious recessive genes will be more exposed in the S_2 generation than S_1, which might have resulted in the observed pattern of reduction of inbreeding depression in the M3S population. VASAL et al. (1995a; 1995b) reported a 10 % decrease in inbreeding depression for grain yield in several subtropical and tropical maize populations after two cycles of S_3 recurrent selection. The populations improved through selfed progeny selection generally showed lower inbreeding depression as compared to other recurrent selection procedures (TANNER and SMITH, 1987; HORNER et al., 1989; ODHIAMO and COMPTON, 1989; WALTERS et al., 1991).

There were no significant differences for grain yield between the two C2 populations. Still, C2(+20) had significantly lower ear length in the S_0 generation and slightly higher stalk lodging incidence than C2(+30) and showed higher inbreeding depression for ear and plant height compared to the C2(+30) and C1. The negative effect of random genetic drift due to the reduced effective population size in developing the C2(+20) population might have been more pronounced than the expected positive effect of the higher selection intensity. HALLAUER (1990) concluded that effective population sizes of 20 to 25 were too small to permit long-term response to selfed progeny selection in several populations including exotic germplasm. However, WEYHRICH et al. (1998a) did not find an advantage of inter-

mating more than 10 S_1 lines per cycle of selection in the BS11 population. Our results from the second cycle of selection might suggest using larger effective population size than 20 in future selection in the M3S population, which could improve the M3S population in terms of both grain yield and stalk lodging resistance. To maintain the independent heterotic pattern of the M3S population, the selfed progeny selection needs to be complemented with the testcross selection using testers from both the BSSS and the Lancaster source.

Acknowledgement

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