

Research Article

Turk J Agric For 35 (2011) 469-480 © TÜBİTAK doi:10.3906/tar-1011-1474

Soybean breeding: comparison of the efficiency of different selection methods

Jegor MILADINOVIĆ^{1,}*, Joe W. BURTON², Svetlana BALEŠEVIĆ TUBIĆ¹, Dragana MILADINOVIĆ¹, Vuk DJORDJEVIĆ¹, Vojin DJUKIĆ¹

¹Institute of Field and Vegetable Crops, M. Gorkog 30, 21000 Novi Sad - SERBIA
²US Department of Agriculture, USDA Plant Science Building, 3127 Ligon Street, Raleigh, NC, 27607 - USA

Received: 18.11.2010

Abstract: The following study was conducted in order to compare the modified single-seed descent method of selection used in soybean breeding at the Institute of Field and Vegetable Crops in Novi Sad, Serbia, with the standard bulk method and the pedigree method. The source materials for the development of hybrid populations were 15 genotypes, and a total of 10 cross combinations were made. Comparison of the lines developed by the different breeding methods was done in the F6 generation. Genetic gain from selection was taken as the main indicator of efficiency of the tested methods. The modified single-seed descent method produced the best results. In most cases, the mean values for seed yield of the populations developed by that method were significantly higher than the values shown in the populations developed by the other 2 methods. The advantages of using genetic gain as the indicator of breeding efficiency were clearly demonstrated when interpreting the results for seed yield and yield components. Populations possessing desirable traits were easier to perceive, which is exceedingly useful when breeding for a complex trait such as yield.

Key words: Breeding, genetic gain, soybean

Introduction

Soybean (*Glycine max* (L.) Merr.) breeding, like the breeding of other crops, is a process involving the development of variability for desired traits, identification of superior genotypes, and multiplication of seed for commercial production. Variability is obtained by crossing parents that possess specific traits intended for transfer into new or improved varieties. Progenies of these crosses segregate genetically in the course of successive generations of selfing, and new genotypes are thus formed. Various selection methods are used for identification of those progenies that possess the

most useful combinations of the desired traits. These most often include: pedigree selection, which involves visual selection of the best-appearing families in each generation, followed by withinfamily selection of one or more plants to advance to the next generation; single-seed descent, which involves advancing one seed or pod from each plant to the next generation to develop nearly homozygous lines that still preserve most of the original genetic variation in a population; and bulk breeding, in which the population is advanced in bulk with no artificial selection until later generations, when nearly homozygous lines are selected for yield testing

^{*} E-mail: jegor.miladinovic@ifvcns.ns.ac.rs

(Orf et al. 2004). Other procedures used in soybean cultivar development include mass selection (Burton and Brim 1981; Tinius et al. 1991), selection among half-sib families (Burton and Carver 1993), selection within half-sib families (Burton et al. 1983; Carver et al. 1986), and the selection from S1 (or S2) families (Brim and Burton 1979; Kenworthy and Brim 1979; Sumarno and Fehr 1982; Rose et al. 1992). Still, the traditional pedigree method and the single-seed descent method (SSD) have been used successfully and most often in soybean breeding (Goulden 1939; Hayes et al. 1955; Grafus 1965; Brim 1966; Cooper 1990; Orf 2008).

The choice of method depends on the breeding objective as well as on other important factors such as the available variability, availability of agricultural machines and greenhouses, and size and skill of breeding team. Breeding objectives depend on the local agroecological conditions, available acreage, intensity of production, market demand, and the economy of production. At the Institute of Field and Vegetable Crops in Novi Sad, Serbia, the SSD method of selection has been used successfully for more than 20 years and has resulted in 103 varieties registered in the home country and 43 in other European countries. However, the SSD method is used with an important modification: a lack of winter nurseries and greenhouses allows for the development of just one generation each year. This modified SSD method thus denies the main advantage of the original SSD method: production of multiple generations in a single year, or, in other words, faster development of homozygous lines. Preserving most of the original genetic variation in a population is another shortcoming of this model, for there are massive progenies and much plant material to maintain until the production of a generation in which uniform lines are selected for yield testing. On the other hand, visual selection of the best-appearing families in each generation, followed by within-family selection of one or more plants to advance to the next generation, increases the frequency of lines with desirable traits using the pedigree method. This indicates that use of the pedigree method of selection could be even more efficient in soybean breeding.

Researchers who tested and compared the efficiency of various methods of selection failed to

show significant differences among them (Raeber and Weber 1953; Torrie 1958; Luedders et al. 1973; Boerma and Cooper 1975; Degago and Caviness 1987; Byron and Orf 1991; Bravo et al. 1999; Cober and Voldeng 2000). This, however, may be due to the fact that the different methods did not receive equal treatment. Furthermore, the studies were conducted on a relatively small number of populations and in a smaller number of generations. In our study, each method was treated equally, from the number of combinations to the number of evaluated lines. A greater number of populations (10 per method) was used and developed to F₆ generations or lines. The reason for doing so was that we believe that, in the application of pedigree and SSD selection methods, actual selection intensities differ when both methods result in equal numbers of selected progenies, and differences should be evident in the mean values of the selected traits. If this hypothesis is correct, then it should be possible to identify the most efficient method for further advances in soybean breeding.

Materials and methods

The source material for development of hybrid populations were 15 genotypes: 9 varieties or lines developed at the Institute of Field and Vegetable Crops in Novi Sad, 5 genotypes from the United States, and 1 line from Romania.

The Novi Sad genotypes, Gordana, Kolubara, Krajina, Balkan, Afrodita, Vojvodjanka, NS Nada, NS-L-310144, and NS-L-310166, were characterized by exceedingly high genetic potential for seed yield, resistance to pod dehiscence and lodging, satisfactory field resistance to major diseases, and adaptation to the growing conditions in Serbia.

The 5 American genotypes, Gadir, Conrad, Flyer, Sturdy, and 9273, were obtained courtesy of Dr. Randal Nelson, Curator of the US Department of Agriculture (USDA) Germplasm Collection in Urbana, Illinois, USA. These 5 genotypes were part of a larger sample provided by the Germplasm Collection, and they were chosen on the basis of their performance in previously conducted field trials.

The Romanian line, F2186, characterized by an exceptionally high genetic potential for seed yield, had been used previously with much success in the

soybean breeding programs of the Institute of Field and Vegetable Crops in Novi Sad.

The 10 following cross combinations were made from these genotypes.

- 1. Gordana × Kolubara
- 2. Krajina × Gadir
- 3. Balkan \times 9273
- 4. NS-L-310144 × Afrodita
- 5. Gordana × Vojvodjanka
- 6. Balkan × F2186
- 7. NS-L-310166 × Conrad
- 8. NS-L-310166 \times Flyer
- 9. Sturdy × NS Nada
- 10. Gordana × NS Nada

The F1 generations were cultivated in wide rows $(50 \times 50 \text{ cm})$ for full genotypic expression and maximum seed formation. Further selection in the F5 generation proceeded in accordance with the specific requirements of the applied methods, as described below. In the F5 generation, a uniform procedure described under "line evaluation" was used in all 3 methods.

Modified single-seed descent method

Seeds of all F1 hybrid plants from each cross combination were bulked and planted in a single 100-m row in the F2 generation. We obtained about 3000 plants per combination. After all plants in a combination matured, one mid-plant pod was taken from each plant, and one seed per pod was used for planting the F3 generation in order to make sure that progenies of each F2 plant were present in the F3 generation. The same procedure was applied in the F3 and F4 generations. From the F4 generation of each combination, 50 plants were selected visually, and seeds of each plant were planted in a separate row for the F5 generation.

Bulk method

Seeds of all F1 hybrid plants from each combination were bulked and planted. F2 plants from each combination were bulk-harvested. As it was not feasible to plant all seeds in the F3 generation, 3000 seeds from each combination were sampled and bulk planted in 100-m rows. Each combination

was harvested separately, and samples were taken for planting the F4 generation. Visually, 50 F4 plants were selected, and seeds of each were planted in separate rows in the F5 generation.

Pedigree method

Seeds of each F1 plant were planted in separate rows. Visually, 50 F2 plants were selected according to phenotype, giving preference to erect plants that were free of perceptible disease symptoms and dehisced pods and that had large numbers of pods per plant and seeds per pod. Each plant was harvested separately and planted in a separate row in the F3 generation. Selection of plants for the planting in the F4 generation was done in the same way. Visually, 50 F4 plants were selected from each combination, and seeds of each were planted in separate rows in the F5 generation.

Line evaluation

The F5 lines were planted in 3-m rows, 50 cm apart. There were 50 lines from each combination, and, at harvest, 10 lines per combination (20%) were selected based on best appearance. As a result, a total of 1500 lines were reduced to 300 lines in F6. These F6 lines were evaluated in 10 preliminary trials. Each preliminary trial included 30 lines, 10 per method, planted in plots containing 4 rows 5 m long, in 2 replicates using RCBD design. This was the first generation in which yield could be measured, and it was the criterion for the selection of lines for further evaluation. Phenological observations were conducted during the growing seasons. At the end of the season, 10 plants were randomly taken from each plot for morphological analyses. The plots were harvested with a plot combine harvester.

The following traits were measured:

seed yield, expressed in kg ha⁻¹ and calculated on the 14% moisture basis;

mass of 1000 seeds, expressed in g; number of pods per plant; and number of seeds per plant.

Within each combination, the data obtained for individual traits were subjected to analysis of variance (ANOVA) in order to confirm the presence of differences among lines and different levels of interaction. There were 40 ANOVAs in total, 1 for each of the 10 combinations and 4 traits investigated. Based on expected mean squares, total variance was partitioned into components, genotypic variance and phenotypic variance, due to genetic differences among the lines, environmental effect, and error.

Differences between the trait means were evaluated by t-test and by calculating the least significant difference according to the methods of Steel and Torrie (1980).

Genetic gain from selection was calculated by the Allard formula (1960):

$$G_{s} = k \times \sigma_{p} \times H,$$

where k is the value of selection differential, which contains a mean genetic value between q selected and n source lines, phenotypic standard deviation, and intensity of selection, or, in other words, the percentage of plants selected for the establishment of the subsequent generation (q/n). In this trial, the value of k was 1.40 for 20% of the selected plants. σ_p is the phenotypic standard deviation of the mean value of the selected trait, or the square root of phenotypic variance, and H is the heritability coefficient in the wider sense, or the portion of genotypic variance in the total phenotypic variance:.

$$H = \frac{\sigma_g^2}{\sigma_n^2}.$$

Correlation coefficients between investigated traits were calculated according to the method of Falconer (1987):

$$\mathbf{r}_{xy} = \frac{\mathbf{Cov}_{xy}}{\sqrt{\mathbf{\sigma}_x^2}.\mathbf{\sigma}_y^2}$$

Results

The highest average seed yield for all 3 populations, 3743 kg ha⁻¹, was achieved by combination 3 (Balkan \times 9723), which was higher than the already high parental average of 3722 kg ha⁻¹ (Table 1). This combination produced the highest yielding population, at 3858 kg ha⁻¹, which, however, did not yield more than the better parent. Out of 10 combinations, 7 made an average value higher than the parental average, and the mean value was higher than the better parent in only 3 combinations: all of the populations in combinations 2 (Krajina × Gadir) and 7 (NS-L-310166 × Conrad) and the SSD offspring population created by combination 8 (NS-L-310166 × Flyer). The highest seed yield on average for all combinations was achieved by using the SSD method of selection (Figure 1). However, this value was not significantly different than those achieved by the other 2 methods.

Unlike results for seed yield, only 4 combinations achieved a higher pod number per plant than the parental averages (Table 2). The average value was higher than the better parent in only 2 cases: combinations 1 (Gordana × Kolubara) and 7 (NS-L-310166 × Conrad). On average, for all combinations, there were no significant differences among the methods (Figure 2).

Out of 10 combinations, 6 had a higher seed number per plant than the parental averages (Table 3). In 4 cases, the average value was higher than that of the better parent: all populations in combinations 1 (Gordana × Kolubara), 4 (NS-L-310144 × Afrodita),

Table 1. Average see	d yield of each	combination and	l parents (kg ha ⁻¹).
----------------------	-----------------	-----------------	-------------	------------------------

Combination method	1	2	3	4	5	6	7	8	9	10
Bulk	3107	3749	3659	3489	3776	3705	3734	3628	3211	3083
Pedigree	2995	3493	3711	3569	3725	3749	3636	3448	3250	3209
SSD	3118	3849	3858	3646	3724	3649	3751	3838	3216	3188
Н	3073	3697	3743	3568	3742	3701	3707	3638	3226	3160
Parent 1	3137	3361	3240	3668	3064	3393	3403	3066	3568	3092
Parent 2	2659	3327	4204	3710	3901	4320	3265	3752	2707	3367
Н	2898	3344	3722	3689	3482	3856	3334	3409	3138	3230
LSD 0.05	156	128	149	142	166	152	112	158	186	153
0.01	210	165	201	191	224	204	151	214	251	206

H = average value, SSD = single-seed descent.

Combination method	1	2	3	4	5	6	7	8	9	10
Bulk	40.8	37.3	33.9	30.5	31.9	27.4	30.5	40.0	32.6	31.1
Pedigree	42.9	34.2	30.4	29.2	30.7	25.1	35.9	36.8	33.3	25.5
SSD	38.1	34.4	31.7	29.4	29.3	28.6	36.0	36.7	29.3	24.4
Н	40.6	34.5	32.0	29.7	30.6	27.0	34.1	37.8	31.7	27.0
Parent 1	24.9	32.0	34.0	30.2	29.1	30.0	22.0	34.6	33.2	39.4
Parent 2	29.2	37.8	37.6	30.7	35.0	19.2	23.8	48.2	26.8	34.2
Н	27.0	34.9	35.8	30.4	32.0	24.6	22.9	41.4	30.0	36.8
LSD 0.05	2.1	2.1	2.1	1.8	1.9	2.4	1.9	2.0	2.1	1.7
0.01	2.8	2.8	2.8	2.4	2.6	3.2	2.6	2.7	2.8	2.3

Table 2. Average number of pods per plant of each combination and parents.

H = average value, SSD = single-seed descent.

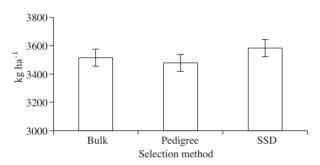


Figure 1. Seed yield (average of all combinations) with different selection methods.

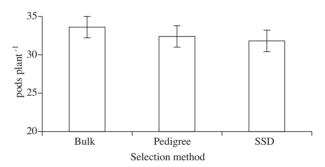


Figure 2. Number of pods per plant (average of all combinations) with different selection methods.

and 7 (NS-L-310166 \times Conrad), as well as populations obtained using the pedigree and bulk methods in combination 9 (Sturdy \times NS Nada). Average values of seed number per plant for all combinations were uniform, with no significant differences among the methods (Figure 3).

The highest average 1000-grain mass, 186.2 g, was achieved by combination 6 (Balkan × F2186) (Table 4). Only 2 other combinations, 4 (NS-L-310144 × Afrodita) and 5 (Gordana × Vojvodjanka), had average values higher than the parental averages. On average, for all combinations, there were no

Table 3. Average number of seeds per plant of each combination and parents.

Combination method	1	2	3	4	5	6	7	8	9	10
Bulk	96.7	85.2	79.1	72.5	79.3	64.0	65.3	88.4	76.7	72.2
Pedigree	103.7	78.8	70.4	70.2	77.2	59.6	79.5	84.1	77.3	60.4
SSD	90.3	79.7	71.2	71.2	74.3	67.4	77.1	79.6	67.8	58.8
Н	96.9	81.2	73.6	71.3	76.9	63.7	74.0	84.0	73.9	63.8
Parent 1	64.2	63.9	79.0	69.5	73.4	68.2	48.6	76.7	76.0	94.4
Parent 2	72.2	87.4	86.1	68.4	88.8	41.6	51.0	104.7	63.8	85.6
Н	68.2	75.6	82.6	69.0	81.1	54.9	49.8	90.7	69.9	90.0
LSD 0.05	5.3	5.9	5.1	4.4	5.1	6.1	4.6	4.4	4.9	3.8
0.01	7.1	8.0	6.9	5.9	6.8	8.3	6.2	5.9	6.6	5.1

H = average value, SSD = single-seed descent.

Combination method	1	2	3	4	5	6	7	8	9	10
Bulk	147.5	167.7	164.5	164.0	156.7	177.5	156.8	143.8	174.4	162.7
Pedigree	141.1	158.0	161.6	170.8	162.9	187.7	149.5	146.0	168.1	132.1
SSD	146.7	162.8	169.9	165.5	162.3	193.5	151.4	146.3	162.8	155.9
Н	145.1	162.8	165.3	166.8	160.6	186.2	152.6	145.4	168.4	150.2
Parent 1	140.0	201.0	192.0	157.0	161.0	192.0	153.0	158.0	197.0	149.0
Parent 2	151.0	132.0	166.0	165.0	148.0	162.0	193.0	154.0	172.0	164.0
Н	145.5	166.5	179.0	161.0	154.5	177.0	173.0	156.0	184.5	156.5
LSD 0.05	2.4	2.1	2.7	2.1	2.6	2.7	1.9	2.7	2.6	2.9
0.01	3.2	2.8	3.6	2.7	3.5	3.7	2.5	3.6	3.5	3.9

Table 4. Average values of 1000-grain mass of each combination and parents (g).

H = average value, SSD = single-seed descent.

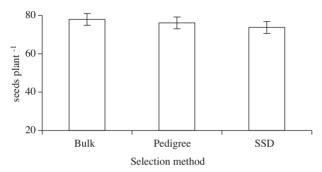


Figure 3. Number of seeds per plant (average of all combinations) with different selection methods.

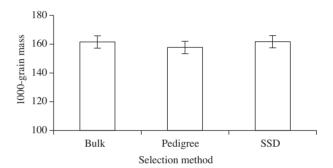


Figure 4. 1000-grain mass (average of all combinations) with different selection methods.

significant differences between the methods (Figure 4).

The pedigree method produced higher genetic gain values for seed yield in 6 combinations, and the SSD method produced this outcome in 4 combinations. However, the highest genetic gain was achieved using the SSD method in combination 2 (Krajina × Gadir) (Table 5). Similar results were obtained for number of pods per plant (Table 6) and number of seeds per plant (Table 7). Furthermore, the SSD method had the highest genetic gain values for 1000-grain mass in 5 out of 10 combinations, the pedigree method in 3 combinations, and the bulk method of selection in 2 combinations (Table 8).

There were no significant interdependences between seed yield and yield components, but the yield components were highly significantly correlated with each other (Table 9). Number of pods per plant and number of seeds per plant were in positive correlation. Both traits were in negative correlation with 1000-grain mass.

Discussion

The results obtained in this study indicated that a change in the mean value of a population frequently did not reflect the actual status of mean values for the studied trait. In other words, a population with the highest mean value for a given trait usually was not the population with the highest gain in relation to the previous generation. It had been expected that the population with the highest genetic gain would also have the highest mean value. However, in the case of the major trait, seed yield, the highest genetic gains from selection were most frequently found in populations developed by the pedigree

Table 5. Components of variance, heritability, and genetic gain from selection for soybean seed yield.

6 1	Selection	2	2	II (0/)	Geneti	ic gain
Comb. no.	method	s_g^2	S_g^2	H (%)	kg ha ⁻¹	% of x
	Bulk	0.015	0.083	18.6	75.2	2.42
1	Pedigree	0.054	0.097	55.9	244.2	8.15
	SSD	0.008	0.079	10.1	39.7	1.27
	Bulk	0.032	0.075	42.7	163.8	4.37
2	Pedigree	0.073	0.109	67.0	309.4	8.86
	SSD	0.134	0.170	78.8	454.5	11.8
	Bulk	0.003	0.040	6.33	17.6	0.48
3	Pedigree	0.062	0.153	40.5	221.7	5.97
	SSD	0.043	0.080	53.8	213.2	5.53
	Bulk	0.053	0.103	51.2	229.4	6.57
4	Pedigree	0.057	0.095	59.8	257.0	7.20
	SSD	-0.006	0.031			
	Bulk	0.009	0.067	13.4	48.6	1.29
5	Pedigree	-0.003	0.067			
	SSD	0.059	0.142	41.5	218.7	5.87
	Bulk	0.007	0.099	7.0	31.2	0.84
6	Pedigree	0.035	0.085	40.8	165.8	4.42
	SSD	0.070	0.094	74.3	318.4	8.73
	Bulk	0.046	0.077	59.5	229.8	6.15
7	Pedigree	0.032	0.069	46.4	170.8	4.70
	SSD	0.060	0.078	76.9	300.5	8.01
	Bulk	0.065	0.095	68.2	293.3	8.08
8	Pedigree	0.103	0.171	60.2	348.3	10.10
	SSD	0.009	0.085	10.1	41.0	1.07
	Bulk	0.009	0.054	15.9	51.4	1.60
9	Pedigree	0.065	0.135	47.9	246.4	7.58
	SSD	-0.011	0.133			
	Bulk	0.086	0.189	45.5	276.5	8.97
10	Pedigree	0.097	0.140	69.3	362.8	11.3
	SSD	0.038	0.062	61.3	213.6	6.70

 $s_g^2=$ genotypic variance, $s_p^2=$ phenotypic variance, H (%) = heritability coefficient, SSD = single-seed descent.

Table 6. Components of variance, heritability, and genetic gain from selection for the number of pods per plant.

Comb. no.	Selection	02	0.2	H (%)	Genetic gain		
Comb. no.	method	S_g^2	s_f^2	П (%)	pods plant ⁻¹	% of x	
	Bulk	18.9	31.1	60.8	4.7	11.6	
1	Pedigree	140.9	146.7	96.0	16.3	37.9	
	SSD	23.9	34.4	69.5	5.7	14.9	
	Bulk	39.5	49.8	79.3	7.8	21.0	
2	Pedigree	11.6	18.4	63.0	3.8	11.1	
	SSD	7.6	23.1	32.9	2.2	6.4	
	Bulk	46.9	52.6	89.1	9.1	26.7	
3	Pedigree	47.1	57.2	82.3	8.7	28.7	
	SSD	15.6	29.0	53.8	4.1	12.8	
	Bulk	29.5	37.7	78.2	6.7	22.0	
4	Pedigree	8.9	15.8	56.3	3.1	10.7	
	SSD	37.2	43.1	86.3	7.9	26.9	
	Bulk	18.3	26.2	69.8	5.0	15.7	
5	Pedigree	0.8	9.9	8.1	0.4	1.2	
	SSD	12.3	17.4	70.7	4.1	14.1	
	Bulk	17.2	38.9	44.2	3.9	14.1	
6	Pedigree	15.8	25.0	63.20	4.4	17.6	
	SSD	6.3	17.8	35.4	2.1	7.3	
	Bulk	31.9	38.9	82.0	7.2	23.5	
7	Pedigree	70.8	81.6	86.8	11.0	30.6	
	SSD	10.1	19.5	51.8	3.2	8.9	
	Bulk	14.2	23.1	61.5	4.1	10.3	
8	Pedigree	71.0	76.5	92.8	11.4	30.9	
	SSD	38.5	55.7	69.1	7.2	19.7	
	Bulk	16.1	23.1	69.7	4.7	14.4	
9	Pedigree	13.5	25.1	53.8	3.8	11.3	
	SSD	23.5	36.5	64.4	5.4	18.6	
	Bulk	30.7	34.3	89.5	7.3	23.6	
10	Pedigree	19.0	23.6	80.5	5.5	21.5	
	SSD	15.0	25.1	59.8	4.2	17.2	

 $s_{\rm g}^2=$ genotypic variance, $s_{\rm p}^2=$ phenotypic variance, H (%) = heritability coefficient, SSD = single-seed descent.

Table 7. Components of variance, heritability, and genetic gain from selection for the number of seeds per plant.

Comb. no.	Selection	22	e.?	II (0/)	Genetic g	ain
Comb. no.	method	S_g^2	s_{f}^2	H (%)	seeds plant-1	% of x
	Bulk	98.8	162.6	60.8	10.8	11.2
1	Pedigree	882.8	925.9	95.3	40.6	39.2
	SSD	155.2	210.6	73.7	15.0	16.6
	Bulk	187.5	306.7	61.1	15.0	17.6
2	Pedigree	41.5	93.0	44.6	6.0	7.6
	SSD	16.6	109.5	15.2	2.2	2.8
	Bulk	255.8	302.9	84.4	20.6	26.0
3	Pedigree	293.2	355.6	82.4	21.8	30.9
	SSD	75.0	144.8	51.8	8.7	12.2
	Bulk	121.9	150.9	80.8	13.9	19.2
4	Pedigree	74.6	118.9	62.7	9.6	13.6
	SSD	225.6	273.9	82.4	19.1	26.8
	Bulk	105.8	164.4	64.3	11.5	14.6
5	Pedigree	51.8	99.0	52.3	7.3	9.4
	SSD	86.5	126.4	68.4	10.8	14.5
	Bulk	63.3	226.6	27.9	5.9	9.2
6	Pedigree	96.2	153.9	62.5	10.8	18.1
	SSD	55.8	113.0	49.4	7.3	10.9
	Bulk	171.0	204.0	83.8	16.8	25.7
7	Pedigree	394.3	453.1	87.0	25.9	32.6
	SSD	44.8	105.1	42.6	6.1	7.9
	Bulk	118.1	161.5	73.1	13.0	14.7
8	Pedigree	379.0	421.7	89.9	25.8	30.7
	SSD	183.8	244.3	75.2	16.5	20.7
	Bulk	107.3	146.4	73.3	12.4	16.2
9	Pedigree	67.3	127.0	53.0	8.4	10.9
	SSD	128.0	202.3	63.3	12.6	18.6
	Bulk	135.2	162.5	83.2	14.8	20.6
10	Pedigree	64.0	85.0	75.3	9.7	16.1
	SSD	110.1	144.2	76.4	12.8	21.8

 $s_{\rm g}^2$ = genotypic variance, $s_{\rm p}^2$ = phenotypic variance, H (%) = heritability coefficient, SSD = single seed descent.

Table 8. Components of variance, heritability, and genetic gain from selection for 1000-grain mass.

Comb. no.	Selection	62	c ²	Ц (0/)	Genetic gain	1
Comb. no.	method	S_g^2	s_{f}^2	H (%)	1000-grain weight	% of x
	Bulk	1.239	1.338	92.5	15.0	10.16
1	Pedigree	0.545	0.696	78.3	9.1	6.5
	SSD	0.827	1.010	81.9	11.5	7.8
	Bulk	3.039	3.101	98.0	24.2	14.4
2	Pedigree	2.732	2.916	93.7	22.4	14.2
	SSD	3.170	3.246	97.6	24.6	15.1
	Bulk	1.728	1.849	93.5	17.8	10.8
3	Pedigree	3.101	3.327	93.2	23.8	14.7
	SSD	2.042	2.202	92.7	19.3	11.3
	Bulk	2.629	2.763	95.1	22.1	13.5
4	Pedigree	1.781	1.873	95.1	18.2	10.7
	SSD	4.007	4.091	97.9	27.7	16.7
	Bulk	0.283	0.455	62.2	5.9	3.7
5	Pedigree	1.149	1.373	83.7	13.7	8.4
	SSD	1.616	1.728	93.5	17.2	10.6
	Bulk	4.509	4.656	96.8	29.2	16.5
6	Pedigree	2.950	3.119	94.6	23.4	12.5
	SSD	1.974	2.237	88.2	18.5	9.5
	Bulk	6.254	6.334	98.7	34.8	22.2
7	Pedigree	3.309	3.418	96.8	25.0	16.7
	SSD	3.590	3.634	98.8	26.4	17.4
	Bulk	0.717	0.873	82.1	10.7	7.5
8	Pedigree	3.593	3.726	96.4	26.1	17.8
	SSD	2.079	2.230	93.2	19.5	13.3
	Bulk	0.942	1.151	81.8	12.3	7.0
9	Pedigree	0.779	0.937	83.1	11.3	6.7
	SSD	3.177	3.314	95.9	24.4	15.0
	Bulk	2.011	2.162	93.0	19.1	11.8
10	Pedigree	3.120	3.368	92.6	23.8	18.0
	SSD	2.724	2.824	96.4	22.7	14.5

 $s_{\rm g}^2$ = genotypic variance, $s_{\rm p}^2$ = phenotypic variance, H (%) = heritability coefficient, SSD = single seed descent.

method, while highest mean values were found in populations developed by the SSD method. A possible explanation for this disagreement could be sought in different levels of variability in the populations from the previous generation. It appeared that an increased intensity of selection tended to reduce the genetic variability in a population, which resulted in lower mean values of the studied trait. This is why heritability, the most important factor in the calculation of genetic gain from selection, turned out to be an unreliable indicator of variability, as previously observed by other authors (Mitchell-Olds and Rutledge 1986).

Theoretically, the highest intensity of selection is achieved by the pedigree method (Borojevic 1986). This method implies that the best individuals, i.e., those possessing the highest phenotypic value, are selected in each generation. In this manner, the highest selection differential is obtained, which, when standardized, expresses the intensity of selection.

In our case, however, the available facilities allowed only the simplest kind of selection to be used, i.e., the selection of individuals on the basis of their phenotypic value. Therefore, we could not state unequivocally that the selected genotypes did possess the highest values for the studied traits. Furthermore, the effects of heterosis and dominance masked the genotypic value of the selected plants, while the degree of homozygosity kept increasing and variability kept decreasing. This explains why we obtained poorer results with the pedigree method than with the SSD method.

There are 2 basic shortcomings of the bulk method: a steady reduction of genetic variability in each generation due to inadequate sample size and the natural selection within the population moving in an undesirable direction. These shortcomings made this method inferior to the other 2 methods. However, when natural selection within the population favored high-yielding genotypes, the population exhibited a higher genetic gain from selection and higher mean values than populations developed by the other 2 methods. Unfortunately, the frequency of such cases was too low to accept the bulk method as practical for soybean breeding.

While selecting for seed yield, the basic advantage of the SSD method, i.e., high variability in each generation, was fully expressed in most of the tested combinations. This method produced the highest selection differential, i.e., the highest intensity of selection, when we selected F4 plants for the establishment of F5 lines. Accordingly, the F5 populations developed by this method exhibited the highest mean values for seed yield, although most of them had low genetic gain from selection. When individuals were selected exclusively on the basis of their phenotypic value, this method was shown to be the most effective for soybean selection for seed vield. In combination 2 (Krajina × Gadir), 2 lines derived from populations obtained by SSD were registered as varieties, 1 in Serbia, and the other in Serbia, Hungary, and Ukraine. In light of the results obtained and space and labor requirements for the selection process, this method could be considered the most optimal for modern soybean breeding when compared with the other 2 methods.

Nonsignificant correlation between yield and yield components indicates the true nature of yield as a set of traits, or as a supertrait of low heritability influenced by a number of other traits. Therefore, it is the most challenging trait to breed for in a genetic improvement program.

Finally, the merit of genetic gain as an indicator of the efficiency of selection for seed yield should not be underestimated in spite of the exhibited disagreement with population mean values. When analyzing yield components, genetic gain was an important indicator of a value of a certain population. Genetic gain simplifies the interpretation of results and singles out populations with desirable traits, which may be useful when selecting for a complex trait such as yield.

Because of the small number of parameters required and the simplicity of calculation, genetic gain from selection may be calculated in each generation in which measurements are taken for seed yield, number of pods per plant, number of seeds per pod, mass of 1000 seeds, plant height, and so on. Calculation of genetic gain may be particularly useful in complex breeding programs, when it is necessary to increase the value of one trait while maintaining the values of other traits at the same level or increasing them as well.

References

- Allard RW (1960) Principles of Plant Breeding. John Wiley and Sons, Inc., New York.
- Boerma HR, Cooper RL (1975) Comparison of three selection procedures for yield in soybeans. Crop Sci 15: 225-229.
- Borojevic K (1986) Genes and Population. Forum, Novi Sad.
- Bravo JJ, Fehr WR, Welke GD, Hammond EG, Cianzio SR (1999) Family and line selection for elevated palmitate of soybean. Crop Sci 39: 679-682.
- Brim CA (1966) A modified pedigree method of selection in soybeans. Crop Sci 6: 220.
- Brim CA, Burton JW (1979) Recurrent selection in soybeans. II. Selection for increased percent protein in seeds. Crop Sci 19: 494-498.
- Burton JW, Brim CA (1981) Recurrent selection in soybeans. III. Selection for increased percent oil in seeds. Crop Sci 21: 31-34.
- Burton JW, Carver BF (1993) Selection among $\rm S_1$ families vs. selfed half-sib or full-sib families in autogamous crops. Crop Sci 33: 21-28.
- Burton JW, Wilson RF, Brim CA (1983) Recurrent selection in soybeans. IV. Selection for increased oleic acid percentage in seed oil. Crop Sci 23:744-747.
- Byron DF, Orf JH (1991) Comparison of three selection procedures for development of early-maturing soybean lines. Crop Sci 31:656-660.
- Carver BF, Burton JW, Carter TE Jr, Wilson RF (1986) Response to environmental variation of soybean lines selected for altered unsaturated fatty acid composition. Crop Sci 26: 1176-1181.
- Cober ER, Voldeng HD (2000) Developing high-protein, high-yield soybean populations and lines. Crop Sci 40: 39-42.
- Cooper RL (1990) Modified early generation testing procedure for yield selection in soybean. Crop Sci 30: 417-419.
- Degago Y, Caviness CE (1987) Seed yield of soybean bulk populations grown for 10 to 18 years in two environments. Crop Sci 27: 207-210.
- Falconer, DS (1987) Introduction to Quantitative Genetics. The Ronald Press Co., New York.

- Goulden CH (1939) Problems in plant selection. In: Proceedings of the 7th International Genetics Congress, Edinburgh, Scotland, pp. 132-133.
- Grafus JE (1965) Shortcuts in plant breeding. Crop Sci 5: 377.
- Hayes HK, Immer FR, Smith DC (1955) Methods of Plant Breeding. McGraw-Hill, New York.
- Kenworthy WJ, Brim CA (1979) Recurrent selection in soybeans. I. Seed yield. Crop Sci 19: 315-318.
- Luedders VD, Duclos LA, Matson AL (1973) Bulk, pedigree, and early generation testing breeding methods compared in soybeans. Crop Sci 13: 363-364.
- Mitchell-Olds T, Rutledge JJ (1986) Quantitative genetics in natural plant populations: a review of a theory. Am Naturalist 127: 379-402.
- Orf JH (2008) Methods of soybean breeding. In: Soybean (Eds. J Miladinovic, M Hrustic, M Vidic). AMB Grafika, Novi Sad, pp. 176-194.
- Orf JH, Diers BW, Boerma HR (2004) Genetic improvement: conventional and molecular-based strategies. In: Soybeans: Improvement, Production, and Uses, 3rd ed. (Eds. HR Boerma, JE Specht). ASSA, CSSA, and SSSA, Madison, WI, pp. 417-450.
- Raeber JG, Weber CR (1953) Effectiveness of selection for yield in soybean crosses by bulk and pedigree systems of breeding. Agron J 45: 362-366.
- Rose JL, Butler DG, Ryley MJ (1992) Yield improvement in soybeans using recurrent selection. Aust J Agric Res 43: 135-144.
- Steel RGD, Torrie JH (1980) Principles and Procedures of Statistics. McGraw Hill Book Co., Inc., New York.
- Sumarno, Fehr WR (1982) Response to recurrent selection for yield in soybeans. Crop Sci 22: 295-299.
- Tinius CN, Burton JW, Carter TE Jr (1991) Recurrent selection for seed size in soybean. I. Response to selection in replicate populations. Crop Sci 31: 1137-1141.
- Torrie JH (1958) A comparison of the pedigree and bulk methods of breeding soybeans. Agron J 50: 198-200.