

Mode of inheritance and combining ability for seed yield and morphophysiological components of yield in sunflower (*Helianthus annuus* L.)

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ABSTRACT

- Used in this study were 13 new divergent cms inbred lines (A) originating from four interspecies populations originating from three annual (*H. debilis*, *H. praecox runyonii*, *H. deserticola*) and one perennial (*H. resinosus*) wild species, three Rf restorer lines with good GCA were utilized as testers, and 39 F₁ hybrids were developed at the Institute of Field and Vegetable Crops in Novi Sad.
- A two-year trial with three replicates was set up on the Rimski Šančevi experiment field at the Institute of Field and Vegetable Crops using the line x tester method.
- Significant differences were found between the A lines, Rf testers and their F₁ hybrids for plant height (PH), head diameter (HD), total seed number per head (TSN), seed yield per plant (SY). The mode of inheritance for PH, TSN and SY was superdominance of the better parent, for HD it was dominance and superdominance of the better parent. Analysis of variance of the combining abilities revealed highly significant differences for GCA and SCA. Highly significant positive values of GCA for all traits were found in cms inbred line NS-G-4 and restorer line RHA-N-49. Based on GCA value, for lines were chosen with the best GCA for SY per plant (NS-G-7) and PH (NS-G-9) originating from interspecies populations, originating from *H. praecox runyonii*, HD (NS-G-12), TSN per head (NS-G-11) lines originating from interspecies populations, originating from *H. deserticola*. High significant positive SCA values are possessed by NS-G-9xRHA-R-PL-2/1 and NS-G-10xRHA-N-49 hybrids for SY and morphophysiological components PH, HD and TSN per head.
- The non-additive components of genetic variance played the main role in the inheritance of all traits that was confirmed by the relationship GCA/SCA in the F₁ generation which is less than one. The largest average contribution in the expression of PH, HD and SY was that of the female A-line while the average contribution of Rf testers was higher in the TSN expression.
- These researches can be significant for the creation of new high-yielding sunflower hybrids on the basis of interspecies hybridization.

Key words: GCA -*H. annuus* -interspecific hybridization -mode of inheritance -SCA

INTRODUCTION

The main precondition for designing a model of a hybrid is to obtain parental lines possessing desirable genes so as to be able to pair up as parents lines that produce superior F₁ progeny over the existing hybrids for the largest number of agronomic traits. The genus *Helianthus*, besides constituting the basic genetic stock from which cultivated sunflower originated, continues to contribute specific characteristics for cultivated sunflower improvement (Seiler, 2010). Breeding for SY, yield components and the creation of a new sunflower ideotype require an increased use of wild *Helianthus* species in breeding programs (Hladni *et al.*, 2011). Interspecific hybridization was applied in sunflower breeding, this process involves first the discovery of desirable genes in the wild *Helianthus* species and then their incorporation into cultivated sunflower genotypes (Škorić *et al.*, 2007). Farrokhi *et al.* (2008) report that the non-additive component of the genetic variance has a bigger role in the SY inheritance. PH plays a major role in the creation of new SC-hybrids with a different plant model and high genetic potential for SY. The predominant role in the inheritance of the PH was held by the additive component of the genetic variance Marinković (2005), while Parameswari *et al.*, (2004) determine a higher ratio of the non-additive gene effect. HD is a very important trait in the sunflower seed yield structure. The size of the HD influences the number of flowers and seeds per head which directly influence the SY per plant. The result of the research done so far on the inheritance of the HD differs. Ashok *et al.* (2000) determined a higher ratio of the additive component of the genetic variance in the inheritance of the HD, while Gvozdenović *et al.* (2005) determined that the non-additive component had bigger influence than the additive one. TSN represents one of the most important components of sunflower SY. It is conditioned by the number of formed tubular flowers, the degree of self compatibility, attractiveness towards the pollinators and the conditions of the external environment during flowering and pollinization of sunflower Hladni (2010). That the non-additive gene effect has the bigger influence in the inheritance of the TSN per head was stated by Goksoy *et al.* (2004).

The objective of this study was to investigate the mode inheritance, general combining ability (GCA) effects in new divergent inbred lines obtained by interspecies hybridization, specific combining ability (SCA) effects of the F₁ hybrids, gene effects, components of genetic variance, average percentage contributions of the lines, testers and their interactions with the expression of the studied morphophysiological traits.

MATERIALS AND METHODS

Used in the study were 13 new divergent (A) cms inbred lines NS-G-1, NS-G-2, NS-G-3, NS-G-4, NS-G-5, NS-G-6, NS-G-7, NS-G-8, NS-G-9, NS-G-10, NS-G-11, NS-G-12, NS-G-13), 3 Rf-restorer lines, 39 F₁ hybrids developed at the Institute of Field and Vegetable Crops in Novi Sad. Initially the plants were selected from the interspecies population RES-1, DEB-SIL-367-2, PRA-RUN-1321 and DES-1474-2, provided by Dr Gerald Seiler (USDA-ARS, Fargo ND, USA). Plants of four sunflower interspecies populations were subjected to inbreeding and used as male lines (B lines) in the initial crosses with several cytoplasmic male-sterile (cms) inbred lines from the IFVCNS breeding program. Obtained cms F₁ hybrids were backcrossed with B lines. Backcrossing of cms progeny was continued for 6-8 generations, to obtain 13 new cms inbred lines. Rf inbred line (RHA-R-PL-2/1, RHA-N-49, RUS-RF-OL-168) with good combining abilities were used as testers in the form of fertility restorers. The F₁ hybrids had been developed by crossing each tester with each female inbred line. The trial was carried out at the Institute's experiment field at Rimski Šančevi. There were three replications, and the experiment was designed according to the line x tester method. The lines and hybrids were planted manually at an optimum time, during mid April on a well-prepared soil. The plots consisted of four rows with 12 plants in each. The row-to-row spacing was 70 cm and the plants were spaced at 30 cm intervals within the rows. Each trait was analyzed on a sample consisting of 30 plants (10 per replicate) taken from the middle rows in each block. PH (cm) and HD (cm) was measured in the field at the stage of physiological maturity. SY per plant was determined by measuring of the total amount of seeds of the each plant acquired in free pollinization on a technical scale with the accuracy of 0.01 (g). TSN per head was determined by the count of full seeds per head. For the evaluation of the test of significance (t-test) of mean values of hybrids in relation to the parental average (Kraljević-Balalić *et al.*, 1991). The mean values of the inbred lines and F₁ hybrids were used to calculate the values of the combining abilities and assess the gene effects for morphophysiological traits using the line x tester method (Singh and Choudhary, 1976).

RESULTS AND DISCUSSION

The significant differences in PH, HD, TSN, SY per plant between the A lines and Rf testers on one side and their F₁ hybrids on the other indicate the presence of genetic differences among the studied

genotypes. The mode of inheritance for PH, TSN, and SY was super dominance of the better parent, for HD it was dominance and superdominance of the better parent (Tab.1). Superdominance as the mode inheritance for SY was reported by Jocić (2003).

Table 1. Mean values, mode of inheritance of morphophysiological traits in sunflower

	Parents and hybrids	PH	HD	TSN	SY
		cm	cm		
1	NS-G-1 RES	93,5	22,10	844	52,7
2	NS-G-2 RES	99,0	21,79	981	57,5
3	NS-G-3 RES	104,4	21,26	1057	69,1
4	NS-G-4 DEB-SIL	116,4	20,85	1031	71,7
5	NS-G-5 DEB-SIL	114,2	20,18	1093	74,4
6	NS-G-6 DEB-SIL	109,8	21,73	924	56,0
7	NS-G-7 PRA-RUN	111,9	21,83	746	61,2
8	NS-G-8 PRA-RUN	93,0	22,03	872	80,7
9	NS-G-9 PRA-RUN	92,7	22,28	717	63,5
10	NS-G-10 DES	79,3	22,04	761	30,5
11	NS-G-11 DES	89,6	23,05	874	45,1
12	NS-G-12 DES	90,1	21,67	960	49,5
13	NS-G-13 DES	73,1	21,60	625	28,4
14	RHA-R-PL-2/1	116,1	19,13	707	34,1
15	RHA-N-49	99,5	14,28	848	27,0
16	RUS-RF-OL-168	114,0	16,99	903	31,0
17	1x14	139,6 ^h	23,4 ^{d+}	1793 ^h	106,4 ^h
18	1x15	150,8 ^h	23,1 ^{d+}	2080 ^h	115,0 ^h
19	1x16	130,7 ^h	23,7 ^h	1845 ^h	103,7 ^h
20	2x14	143,3 ^h	24,5 ^h	1787 ^h	110,2 ^h
21	2x15	152,2 ^h	24,3 ^h	2190 ^h	119,6 ^h
22	2x16	138,7 ^h	23,9 ^h	1867 ^h	101,6 ^h
23	3x14	143,2 ^h	23,1 ^h	1692 ^h	100,9 ^h
24	3x15	149,2 ^h	23,3 ^h	1968 ^h	108,1 ^h
25	3x16	138,4 ^h	23,8 ^h	1639 ^h	104,0 ^h
26	4x14	158,4 ^h	23,9 ^h	1789 ^h	117,3 ^h
27	4x15	164,9 ^h	23,9 ^h	2249 ^h	124,0 ^h
28	4x16	152,3 ^h	24,2 ^h	1921 ^h	126,4 ^h
29	5x14	160,3 ^h	24,1 ^h	1903 ^h	123,5 ^h
30	5x15	161,2 ^h	23,6 ^h	2155 ^h	135,2 ^h
31	5x16	158,5 ^h	23,6 ^h	1820 ^h	110,1 ^h
32	6x14	151,4 ^h	23,4 ^h	1874 ^h	114,7 ^h
33	6x15	157,5 ^h	26,2 ^h	2315 ^h	132,6 ^h
34	6x16	142,2 ^h	23,7 ^h	1786 ^h	110,1 ^h
35	7x14	167,3 ^h	24,2 ^h	1684 ^h	136,7 ^h
36	7x15	159,4 ^h	25,8 ^h	2102 ^h	143,2 ^h
37	7x16	161,0 ^h	26,1 ^h	1682 ^h	130,3 ^h
38	8x14	159,8 ^h	24,7 ^h	1667 ^h	131,3 ^h
39	8x15	159,9 ^h	24,9 ^h	2069 ^h	137,7 ^h
40	8x16	155,5 ^h	22,9 ^{d+}	1686 ^h	137,8 ^h
41	9x14	167,5 ^h	23,3 ^h	1777 ^h	139,4 ^h
42	9x15	168,3 ^h	24,4 ^h	1875 ^h	127,8 ^h
43	9x16	159,4 ^h	25,2 ^h	1536 ^h	132,7 ^h
44	10x14	136,0 ^h	24,1 ^h	1628 ^h	103,0 ^h
45	10x15	144,6 ^h	25,8 ^h	2062 ^h	119,4 ^h
46	10x16	129,8 ^h	26,1 ^h	1683 ^h	85,8 ^h
47	11x14	141,8 ^h	25,3 ^h	1895 ^h	113,8 ^h
49	11x15	140,7 ^h	28,2 ^h	2379 ^h	111,2 ^h
49	11x16	135,8 ^h	24,3 ^h	1801 ^h	110,5 ^h

50	12x14	140,6 ^h	26,2 ^h	1824 ^h	107,4 ^h
51	12x15	140,3 ^h	28,6 ^h	2024 ^h	109,9 ^h
52	12x16	135,8 ^h	26,6 ^h	1783 ^h	111,3 ^h
53	13x14	138,0 ^h	26,2 ^h	1755 ^h	105,6 ^h
54	13x15	140,9 ^h	27,8 ^h	2161 ^h	116,3 ^h
55	13x16	131,6 ^h	27,7 ^h	1675 ^h	97,6 ^h
	LSD 0.05	2.17	0.300	28.36	5.59
	LSD 0.01	3.26	0.450	42.53	8.39

The analysis of combining ability showed that the A lines and Rf testers differed significantly in GCA values. Highly significant cms line for GCA values for PH, HD and SY per plant was NS-G-7, for PH, TSN per head, SY per plant are NS-G-4 and NS-G-5. Rf tester line RHA-N-49 have highly significant GCA values for PH, HD, TSN per head and SY per plant. Based on the GCA values chosen were cms lines with the best GCA for PH (NS-G-9, NS-G-7) originating from PRA-RUN, HD (NS-G-13, NS-G-12) originating from DES, TSN (NS-G-11, NS-G-6) originating from DES and DEB-SIL and SY (NS-G-7, NS-G-8) originating from PRA-RUN. It is very difficult to combine all positive traits in one combination. By comparing mean values with GCA parent values in the F₁ generation it can be concluded that the parents with higher mean values were in most cases better general combiners while lines with lower mean values were worse combiners. So lines with the best GCA for PH (NS-G-4), TSN per head (NS-G-5) have the highest mean values for that trait while the line with the worst GCA for PH (NS-G-13) has the lowest mean value for that trait. If the aim is the change of sunflower plant architecture, genotypes with shorter plant height (NS-G-10, NS-G-11, NS-G-12, NS-G-13) and negative GCA values, originating from interspecies population DES, are desirable in breeding programs (Tab.2).

Table 2. GCA values and SCA hybrids for height and head diameter in sunflower inbreeds

	Parents and hybrids	PH	HD	TSN	SY
1	NS-G-1 RES	-8,60	-1,428	25,11 ^{**}	-8,88
2	NS-G-2 RES	-4,24	-0,603	66,85 ^{**}	-6,77
3	NS-G-3 RES	-5,35	-1,439	-114,66	-12,88
4	NS-G-4 DEB-SIL	9,62 ^{**}	-0,858	105,27 ^{**}	5,33 ^{**}
5	NS-G-5 DEB-SIL	11,04 ^{**}	-1,044	78,49 ^{**}	5,73 ^{**}
6	NS-G-6 DEB-SIL	1,43	-0,403	110,42 ^{**}	1,87
7	NS-G-7 PRA-RUN	13,65 ^{**}	0,742 ^{**}	-58,15	19,49 ^{**}
8	NS-G-8 PRA-RUN	9,46 ^{**}	-0,675	-74,08	18,38 ^{**}
9	NS-G-9 PRA-RUN	16,79 ^{**}	-0,542	-171,88	16,07 ^{**}
10	NS-G-10 DES	-12,15	0,464 ^{**}	-89,93	-14,50
11	NS-G-11 DES	-9,49	1,086 ^{**}	143,96 ^{**}	-5,42
12	NS-G-12 DES	-10,07	2,292 ^{**}	-4,22	-7,70
13	NS-G-13 DES	-12,10	2,408 ^{**}	-17,18	-10,74
14	RHA-R-PL-2/1	1,00 ^{**}	-0,506	-106,75	-1,07
15	RHA-N-49	4,12 ^{**}	0,583 ^{**}	239,75 ^{**}	5,86 ^{**}
16	RUS-RF-OL-168	-5,12	-0,077	-133,01	-4,78
	LSD 0.05 (1-13)	1,25	0.174	16,37	3,23
	LSD 0.01	1,88	0.261	24,56	4,84
	LSD 0.05 (14-16)	0,29	0.084	7,86	0,78
	LSD 0.01	0,44	0.126	11,80	2,33
	SCA				
	F ₁	PH	HD	TSN	SY
1	1x14	-1,75	0,520 ^{**}	-6,64	-0,90
2	1x15	6,30 ^{**}	0,761 ^{**}	-65,56	0,79
3	1x16	-4,55	0,231	72,20 ^{**}	0,12
4	2x14	-2,44	0,409 [*]	-53,95	0,77
5	2x15	3,35 ^{**}	0,845 ^{**}	1,97	3,33
6	2x16	-0,91	-0,513	51,98 ^{**}	-4,10
7	3x14	-1,41	-0,916	32,61 [*]	-2,37
8	3x15	1,46	1,076 ^{**}	-38,11	-2,09
9	3x16	-0,05	-0,524	5,50	4,46

10	4x14	-1,14	-0,747	-90,29	-4,19
11	4x15	2,24*	-0,127	22,51	-4,38
12	4x16	-1,10	-0,474	67,78**	8,57**
13	5x14	-0,72	-0,541	50,14**	1,65
14	5x15	-2,93	-0,911	-44,01	6,40*
15	5x16	3,65**	-0,478	-6,13	-8,05
16	6x14	0,06	-0,700	-10,97	-3,37
17	6x15	3,02*	-0,705	83,38**	7,63*
18	6x16	-3,08	-0,752	-72,41	-4,26
19	7x14	3,75**	1,131**	-32,10	1,01
20	7x15	-7,29	0,312*	39,61*	0,63
21	7x16	3,53**	0,103	-7,51	-1,64
22	8x14	3,53**	-0,472	-33,73	-3,24
23	8x15	-2,59	-0,077	22,21	-3,72
24	8x16	2,23*	1,684**	11,52	6,97*
25	9x14	2,78*	0,895**	174,13**	7,18*
26	9x15	-1,59	-0,030	-133,59	-11,34
27	9x16	-1,19	0,391*	-40,54	4,16
28	10x14	-1,78	-0,284	-56,52	1,37
29	10x15	3,69*	0,468**	31,26*	10,80**
30	10x16	-1,91	0,296	25,26	-12,17
31	11x14	1,39	-0,093	-23,70	3,04
32	11x15	-2,90	-0,618	114,64**	-6,52
33	11x16	1,51	0,604**	-90,94	3,48
34	12x14	0,72	-1,179	53,65**	-1,08
35	12x15	-2,73	0,996**	-92,39	-5,49
36	12x16	2,01	0,824**	38,74*	6,57*
37	13x14	0,17	-1,557	-2,64	0,14
38	13x15	-0,04	-0,421	58,07**	3,97
39	13x16	-0,13	0,571**	-55,43	-4,11
LSD 0.05		2,17	0.300	28,35	5,59
LSD 0.01		3,26	0.450	42,53	8,39
GCA		5,59	0,178	1909	8,03
SCA		17,96	0,570	13852	75,05
GCA/SCA		0,31	0,312	0,14	0,11

Significant positive SCA value for all traits were demonstrated by NS-G-9xRHA-R-PL-2/1 and NS-G-10xRHA-N-49. Hybrid NS-GS-10xRHA-N-49, which had been obtained by crossing one parent with a poor PH, TSN and SY GCA to another one that has a highly positive GCA for this traits (Tab.2). These results support those obtained by Škorić *et al.* (2000), who determined that crosses with a good plant height SCA usually involve one parent with high and one with low GCA values. Highly significant positive value for PH, HD and SY were demonstrated by NS-G-8xRUS-Rf-OL-168 and for HD, TSN and SY were demonstrated by NS-G-12xRUS-Rf-OL-168. The greatest highly significant positive SCA value for PH was found in NS-G-1xRHA-N-49, HD in NS-G-8xRUS-Rf-OL-168, TSN per head in NS-G-9xRHA-R-PL-2/1 and SY per plant in NS-G-10xRHA-N-49 (Tab.2). In the inheritance of the PH, HD, TSN and SY per plant the non-additive component of the genetic variance had a predominant role as shown by the analysis of variance of combining abilities and analysis of genetic variance components. This is supported by the GCA/SCA ratio for PH (0.31), HD (0.31), TSN per plant (0.14) and SY per plant (0.11) in the F₁ generation, which was below the value of one (Tab.2). A higher contribution of non-additive genetic variance has been reported by Škorić *et al.* (2000) for the inheritance of PH, Hladni *et al.* (2004) and Parameswari *et al.* (2004) for the inheritance of HD, Goksoy *et al.* (2004) for the inheritance of TSN per head, Škorić *et al.* 2000 and Gvozdenović *et al.* 2008 for the inheritance of SY. By contrast, research found the additive component to be have been more significant in the inheritance of PH Marinković (2005), in the inheritance of HD Ashok *et al.* (2000), in the inheritance of TSN per head Goksoy *et al.* (2000), in the inheritance of SY Marinković *et al.* (2000). In this research the largest average contribution in the expression of PH, HD and SY per plant was that of the female A-line while the average contribution of Rf testers was higher in the TSN per head expression (Tab.3).

Table 3. Average percentage contribution of female lines and tester lines and their interactions to expression of plant height and head diameter

Average contribution	PH	HD	TSN	SY
	%	%	%	%
Female line	80,29	66,91	25,93	69,33
Tester line	10,96	7,86	63,19	10,80
Line x tester	8,75	25,24	10,89	19,8

According to (Škorić *et al.*, 2000; Farrokhi *et al.*, 2008) the mother lines had a significant proportion in the expression of the plant height (55.8%; 54.9%) and seed yield (51.4%; 62.8%). A higher average contribution of the interaction line/tester for seed yield (53.8%) was determined by Marinković *et al.* (2000). By studying the proportional contribution of inbred lines, testers and their crosses in the total variability, breeders come to different results with the same trait. The differences in the conclusions of different authors mentioned in this work can be explained by the differences in the plant material used in their studies. Studying GCA in relation to the origin lines we can observe that the lines of interspecies populations PRA-RUN the best general combiners for PH and SY per plant, lines from interspecies population DES are the best general combiners for HD, while the lines originating interspecies populations DEB-SIL and RES the best general combiners for TSN per head. The exception is a line from interspecies population DES NS-G-11 which is the best general combiners for TSN per head. The worst GCA for PH, TSN per head and SY per plant have lines originating from interspecies population DES, while for PH, HD and SY per plant have lines originating from interspecies population RES. It is very difficult to combine all positive traits in one combination. High significant positive SCA values are possessed by NS-G-9xRHA-R-PL-2/1 and NS-G-10xRHA-N-49 hybrids for SY and morphophysiological components PH, HD and TSN per head. These researches can be significant for the creation of new high-yielding sunflower hybrids on the basis of interspecies hybridization.

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