INHERITANCE OF SOME YIELD COMPONENTS IN SUNFLOWER

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Abstract

In order to study the mode of inheritance and gene effects for seed set, autofertility and
self-fertility, half diallel crosses with five divergent sunflower inbred lines were made.
The effects of additive, dominant and epistatic gene effects were investigated by the
generation mean analysis method related to parents and their progenies (F1, F2, BC1 and
BC2). Seed set was determined by the most dominant gene effects. Additive gene effects
were predominant in the inheritance of autofertility and self-fertility.

Introduction

Sunflower (*Helianthus annuus* L.) seed yield is a product of three major components,
namely plant number per unit area x seed number per unit area x seed mass (Merrien, 1992).
Seed number has the largest direct effect on seed yield (Škorić, 1974; Marinković, 1987;
Dušanić, 1998). Seed number per sunflower head depends on the number of disc flowers
formed, seed set, attractiveness to pollinators, and environmental factors at flowering and
pollination (Škorić, 1992).

Marinković (1984) found intermediacy, partial dominance, dominance and heterosis in
the inheritance of seed set. Joksimović (1992) and Joksimović et al. (1995) found cases of
dominant and superdominant inheritance, while Lande et al. (1998) found superdominance.
Additive and nonadditive gene action both play a role in the inheritance of seed set, but the
nonadditive component of genetic variance has greater importance (Joksimović, 1992 and
Joksimović et al., 1995). According to Marinković (1984), on the other hand, the additive
component is the more significant of the two. Holtom et al. (1995) found larger significance
of dominant gene effects and the absence of epistatic effects in the expression of seed set.
Gangappa et al. (1997), by contrast, found two-gene epistases in the inheritance of this trait.
Effects that proved the most important were those of dominant genes and dominant x
dominant interaction accompanied by duplicate epistasis. Additive gene effects were not
significant, but the additive x additive gene interaction was.

In actual commercial sunflower production, it is relatively common for pollination to take
place without the presence of genetically distant pollen and insect pollinators, i.e., in virtual
self-pollinated conditions. When pollination occurs without the presence of foreign pollen and
insect pollinators, seed set is called autofertility. If, however, foreign pollen is absent but
insect pollinators are not, seed set is referred to as self-fertility (George et al., 1980). Many
authors have studied the inheritance mechanism of autofertility and self-fertility. Vranceanu et
al. (1978) established that self-fertility is a complex trait both in terms of expression and
inheritance. The same authors determined that most often partial dominance manifests itself in
the inheritance of this trait in the F1 generation. They also found intermediate inheritance in

28% of the crosses, complete dominance in 15%, and superdominance in 6%. Fick (1978) concluded that high self-fertility is most probably controlled by a larger number of recessive genes, which means that in order to obtain a highly self-fertile hybrid both parental components need to be characterized by a high degree of self-fertility. Olivieri et al. (1988) indicated additiveness in the inheritance of self-fertility and possibility of breeding success in selection for this trait. They also found classical complementary epistatic gene effects in some of the crosses. The inheritance of self-fertility is influenced by a number of genes, according to Kovaik and Škaloud (1996). In their study, they found cases of incomplete dominance, which were positive for self-fertility and negative for autofertility, as well as cases of the intermediate mode of inheritance. The most common mode of inheritance in hybrids was positive dominance. Additive gene effects were significant for genetic control, but in some crossing combinations dominance and nonallelic interactions were more important. Sunflower autofertility is a complex phenomenon that is polygenetic in nature. The number of genes that control this trait ranges from 5 to 12 (Soare, 1996).

Materials and Methods

For our analysis of the mode of inheritance and gene effects on seed set, autofertility and self-fertility in sunflower we chose five self-pollinated sunflower lines that had been shown in preliminary studies to be divergent from each other with respect to the traits studied. In the first year of our experiment, the lines were subjected to half diallel crosses. The following year, backcrosses with both parents were made and the F1 hybrids were selfed to obtain the F2 generation. A comparative trial with three replicates was set up according to a randomized block design using the parental lines, F1s and F2s, and backcrosses. Thirty plants were taken from the parental lines, hybrids and backcrosses and 90 open-pollinated ones from the F2 generation. In order to determine autofertility and self-fertility, an identical number of plants in each generation were placed in complete self-pollination by isolation using natron bags and self-pollination facilitated by rubbing with cotton swabs every other day. Seed set was obtained from the relationship between the total number of disc flowers and number of seeds, i.e., the number of fertilized disc flowers forming seeds. Autofertility and self-fertility were determined according to the formula provided by George et al. (1980): autofertility (%) = (seed set in self pollination/seed set in open pollination) x 100; self-fertility (%)= (seed set in facilitated pollination/seed set in open pollination) x 100. Gene effects were estimated by genetic analysis of generation means (Mather and Jinks, 1977 and 1982).

Results and Discussion

Seed Set. When the additive-dominant model was applied and its adequacy checked, it proved to be adequate for two of the 10 combinations, namely R-15 x R-17 and CMS-77 x CMS-19 (Table 1). In both these crosses, seed set was influenced much more by dominant genes than by additive ones, as the estimated values of the effects of the former were about seven times higher than those of the latter (Table 2). Similar results have been reported by Holtom et al. (1995), who found higher significance of dominant gene effects and absence of epistatic effects in seed set expression. In the other crossing combinations, seed set was found to have been influenced by epistatic gene effects as well, as indicated by individual and joint tests. Joksimović (1992) and Joksimović et al. (1995) determined that both the additive and

nonadditive components of genetic variance play a role in the inheritance of this trait, but that the nonadditive component has greater importance.

Table 1. Estimated values of additive and dominant gene effects for sunflower seed set.

Cross	m	[d]	[h]	Individual tests			χ^2 test	
				A	B	C	χ^2	P
R-15 x Kiz	39.32	13.60	11.04	15.51	16.18	33.40*	10.33	< 0.01
R-15 x R-17	49.85	-0.43	6.86	-5.07	0.75	-11.46	3.66	= 0.95
R-15 x Cms-19	46.85	5.53	8.54	2.59	-8.79	-29.78**	22.28	< 0.01
R-15 x Cms-77	46.95	-1.69	9.51	-17.49**	-6.65	-20.60	21.97	< 0.01
Cms-77 x Kiz	34.27	7.19	28.95	-18.36**	19.37**	47.92**	53.66	< 0.01
Cms-77 x R-17	48.06	-0.53	25.44	0.55	7.53	-12.00*	12.21	< 0.01
Cms-77xCms-19	45.97	1.74	15.68	-10.75	-1.76	-12.07	5.36	= 0.84
Cms-19 x Kiz	32.92	5.66	32.24	-5.00	11.29**	-8.29	50.33	< 0.01
Cms-19 x R-17	44.54	1.91	21.89	2.42	-18.26**	-31.69**	45.28	< 0.01
R-17 x Kiz	38.08	12.21	18.68	-5.68	5.78	30.13**	15.72	< 0.01

Table 2. Estimated values of gene effects for seed set using the six-parameter model in crosses in which epistases were found to have been present.

Cross	m	[d]	[h]	[i]	[j]	[l]
R-15 x Kiz	40.10*	12.85**	33.79	-1.71	-0.66	-29.98
R-15 x Cms-19	24.65*	3.01	48.28*	23.59*	11.38	-17.39
R-15 x Cms-77	53.68**	1.11	-20.91	-3.55	-10.84	27.69
Cms-77 x Kiz	84.20**	11.74**	-66.70**	-46.91**	-37.73**	45.89**
Cms-77 x R-17	29.36**	-0.40	72.52**	20.07*	-6.98	-28.15*
Cms-19 x Kiz	20.80**	9.84**	60.63**	14.59*	-16.29**	-20.88
Cms-19 x R-17	31.68**	-2.30	34.99	15.85	20.69**	-0.01
R-17 x Kiz	67.73**	12.14**	-41.93	-30.04*	-11.46	29.95

The six-parameter model detected high significance of additive gene effects on seed set expression in four of the combinations. In all those cases, one of the parental components was line Kiz, which had by far the lowest seed set of all the lines used. In two of the combinations (R-15 x Kiz and R-17 x Kiz), the additive effect was the most important of all the gene effects studied, and the same has been reported by Marinković (1984) as well. In the other two combinations (CMS-77 x Kiz and CMS-19 x Kiz), a highly significant dominant gene effect was found and its estimated values were around six times higher than those of additive gene effects. A highly significant effect of dominant genes was also found in CMS-77 x R-17. In all cases where dominant gene effects were found to be significant, their estimated values were higher than those of any of the other gene effects studied. Of the two-gene epistases, the one that stood out slightly in terms of its importance in seed set inheritance was epistasis between additive and dominant genes, which was highly significant in three of the combinations. Interaction among additive genes was highly significant in one cross and significant in four. Interaction among dominant genes was highly significant in one cross and significant in another. In both cases, the effects of dominant x dominant gene epistasis had the opposite sign from those of dominant genes, i.e., duplicate epistasis was manifested. The

estimated values of two-gene epistases were higher than the corresponding estimated values of additive genes but lower than those of dominant genes. Gangappa et al. (1997) have also determined that the most important effects in seed set inheritance are those of dominant genes, followed by those of two-gene epistases.

Autofertility. The use of the additive-dominant model and testing of its adequacy revealed that epistatic effects had no significance in autofertility expression in two of the crosses. In R-15 x R-17, additive and dominant gene effects had an almost identical negative effect in the inheritance of autofertility (Table 3). A negative estimated value of dominant gene action was also found in another cross (R-15 x CMS-77), for which the additive-

Table 3. Estimated values of additive and dominant gene effects for autofertility.

Cross	m	[d]	[h]	Individual tests			χ^2 test	
				A	B	C	χ^2	P
R-15 x Kiz	24.90	17.98	-16.35	-20.26*	2.52	-30.34	11.60	< 0.01
R-15 x R-17	61.86	-15.87	-20.62	-12.79	0.90	-14.27	3.13	=0.96
R-15 x Cms-19	34.44	7.84	5.80	-41.16*	2.30	-50.61**	23.66	< 0.01
R-15 x Cms-77	41.18	8.41	-3.27	-0.49	-5.05	6.69	0.87	=0.98
Cms-77 x Kiz	16.93	11.58	-13.20	8.46	18.68*	-21.08**	33.42	< 0.01
Cms-77 x R-17	51.64	7.54	-16.65	13.00	-47.81**	-3.21	28.99	< 0.01
Cms-77xCms-19	28.60	0.34	15.60	-2.46	10.94*	6.72	13.49	< 0.01
Cms-19 x Kiz	14.54	8.12	7.28	-21.19**	23.38	59.42	20.24	< 0.01
Cms-19 x R-17	41.09	-15.35	-5.97	20.50	-45.26**	-13.38	48.72	< 0.01
R-17 x Kiz	17.45	8.69	-17.18	-57.07**	7.55	-10.59	61.65	< 0.01

dominant model was adequate, but in that cross the influence of additive genes, whose estimated value was positive, was twice as big. In the other eight combinations where the additive-dominant model proved inadequate based on the results of individual and joint tests, gene effects were estimated by analysis of generation means with six parameters. The results of this analysis indicated that additive gene effects had a significant role in the expression of autofertility, as their high significance was found in six of the crosses (Table 4). The two

Table 4.   Estimated values of gene effects for autofertility using the six-parameter model in crosses in which epistases were found to have been present.

Cross	m	[d]	[h]	[i]	[j]	[l]
R-15 x Kiz	14.91	21.64**	-10.68	12.59	-22.78*	5.15
R-15 x Cms-19	26.63	10.77*	-11.61	11.75	-43.45*	27.11
Cms-77 x Kiz	-28.63*	13.72**	-108.05**	48.21**	-10.22	-75.35**
Cms-77 x R-17	87.51**	-22.61**	-119.63**	-31.59*	60.81**	66.40**
Cms-77 x Cms-19	27.29**	4.26	24.07	1.76	-13.39*	-10.24
Cms-19 x Kiz	72.55	9.46**	-105.43	-57.23	-44.57*	55.03
Cms-19 x R-17	63.03**	-26.87**	-60.90	-11.37	65.76**	36.13
R-17 x Kiz	81.13**	36.33**	-169.16**	-38.93**	-64.62**	88.46**

combinations in which no highly significant effects of additive genes were found, R-15 x CMS-19 and CMS-77 x CMS-19, were also the only crosses in which there was no increase in the mean value of autofertility in the F2 generation compared with the relevant hybrids. Dominant gene effects were highly significant in only three of the crosses, which may suggest that additive gene effects play the more significant role in the inheritance of this trait. However, the estimated values of dominant gene effects in crosses where their high significance was established were by far the highest of all the gene effects studied, including

those with negative values. The efects of two-gene epistases had approximately the same significance and in most cases the values were negative. The estimated values of the effects of major two-gene epistases were higher than those of additive gene effects. The two-gene epistasis that had a slightly higher importance was that between dominant and additive genes, which in the inheritance of autofertility had a highly significant effect in three crosses and a significant one in four. Interaction among dominant genes had a highly significant effect in three of the combinations. In all cases where we found significance of dominant gene effects, epistasis among dominant genes was found to have significant effect as well. In two crosses (CMS-77 x R-17 and R-17 x Kiz), the estimated values of epistasis among dominant genes had the opposite sign relative to those of dominant gene effects. Since dominant gene effects were negative, the less unfavorable type of duplicate epistasis manifested itself. In CMS-77 x Kiz, these two gene effects had the same negative value. In this cross, the F1 and F2 generations obtained were almost autosterile. The epistatic gene effect of additive x additive genes had a highly significant influence on autofertility in two combinations and a significant effect in one.

Self-fertility. Analysis of generation means by the three-parameter model revealed that epistatic gene effects were present in the expression of self-fertility in eight of the crosses (Table 5). The additive-dominant model was adequate for R-15 x Kiz and CMS- 19 x Kiz;

Table 5. Estimated values of additive and dominant gene effects for self-fertility.

Cross	m	[d]	[h]	Individual tests			χ^2 test	
				A	B	C	χ^2	P
R-15 x Kiz	45.17	17.18	-26.77	27.21	4.20	9.80	5.78	= 0.84
R-15 x R-17	63.48	-9.52	-9.14	-0.67	-9.51	-46.20**	22.29	< 0.01
R-15 x Cms-19	48.31	-0.44	-7.60	-39.98**	-20.12	-98.25**	55.63	< 0.01
R-15 x Cms-77	44.13	5.78	0.73	-23.66	-10.72	-41.00**	22.39	< 0.01
Cms-77 x Kiz	33.97	5.55	-24.31	24.85**	15.39	-39.93*	30.46	< 0.01
Cms-77 x R-17	53.95	-14.51	0.52	17.51	-27.02**	-12.20	22.93	< 0.01
Cms-77xCms-19	43.39	-3.27	11.75	7.16	-15.84*	17.18	29.83	< 0.01
Cms-19 x Kiz	39.13	11.20	4.56	-24.92	-2.45	-15.64	6.34	= 0.83
Cms-19 x R-17	62.03	-15.88	-6.29	-16.68*	9.07	-53.02*	15.77	< 0.01
R-17 x Kiz	46.78	21.76	-39.52	-28.11*	27.58	-24.03*	22.89	< 0.01

self-fertility expression in these crosses was influenced by the effects of additive and dominant genes. In R-15 x Kiz, dominant gene effects were negative and higher than additive gene ones, which were positive. In CMS-19 x Kiz, on the other hand, both of these gene effects were positive and the estimated values of additive gene effects on self-fertility inheritance were twice as high as those of dominant gene ones in the inheritance of this trait. Additive gene effects were the most important gene effects in the expression of self-fertility even in crosses where epistatic gene effects were present, as they were highly significant in four combinations and significant in two (Table 6). Additiveness in
the inheritance of self-fertility has been noted by Olivieri et al. (1988). Dominant gene effects were highly significant and significant in only one cross each. In those two crosses, however, their estimated values were the highest of all gene effects. Significant influence of dominant genes is accompanied by significant influence of epistatic effects among dominant genes and the occurrence of duplicate epistasis, which significantly reduces their effect on the expression of self-fertility. Epistatic effects among dominant genes were the least significant of all two-gene epistases. Interaction between additive and dominant genes was the most

important two-gene epistasis, because its effects were highly significant in three crosses, in which its estimated values were also higher than those of the other highly significant gene effects. Effects of epistasis among additive genes were highly significant in the inheritance of self-fertility in one cross and significant in three. Overall, the estimated values of significant two-gene epistases were higher than the corresponding estimated values of significant additive gene effects.

Table 6. Estimated values of gene effects for self-fertility using the six-parameter model in crosses in which epistases were found to have been present.

Cross	m	[d]	[h]	[i]	[j]	[l]
R-15 x R-17	33.40*	-10.51*	52.90	36.02*	8.84	-25.84
R-15 x Cms-19	-1.68	2.45	52.86	58.15*	-19.86	1.95
R-15 x Cms-77	42.38	9.92**	-19.05	6.62	-12.95	27.76
Cms-77 x Kiz	-46.72*	5.63	176.74**	80.17**	9.46	-120.40**
Cms-77 x R-17	56.81**	-20.43**	-8.88	2.70	44.53**	6.80
Cms-77 x Cms-19	72.40**	-7.47*	-55.11*	-25.85*	23.00**	34.53*
Cms-19 x R-17	21.57	-12.96**	73.94	45.41	-25.75	-37.79
R-17 x Kiz	30.38	26.06**	1.13	23.50	-55.69**	-22.97

Conclusions

High significance of additive gene effects in seed set expression was found in four crosses, which all had a common parental component with a very low seed set. Dominant gene effects were significant in six crossing combinations, which also had the most significant gene effects in seed set inheritance. Epistatic effects were not present in R-15 x R-17 and CMS-77 x CMS-19. Estimated values of two-gene epistases were higher than those of additive gene effects but smaller than dominant gene effects. Interaction between additive and dominant genes was found in three of the crosses, additive x additive epistasis in five, and interaction among dominant genes with duplicate epistasis in two. The most important two-gene epistasis in seed set inheritance was the effect of additive x dominant gene epistasis.

Additive gene effects were the most important in the inheritance of autofertility, as their significance was found in nine of the ten crosses. Dominant gene effects were highly significant and negative in five crosses, and in CMS-77 x Kiz, CMS-77 x R-17 and R-17 x Kiz their estimated values were considerably higher than those of the other gene effects studied. In the inheritance of autofertility, epistasis was not found in R-15 x R-17 and R-15 x CMS-77. In the other crosses, estimated values of two-gene epistases were higher than the corresponding estimated values of additive gene effects. Among two-gene epistases, the one that stood out slightly was that between additive and dominant genes, while the additive x additive and dominant x dominant ones were at the same level.

Additive gene effects on self-fertility expression were the largest among the gene effects studied, since their significance was found in eight of the crosses. Dominant gene effects were significant in four crosses. In two, they were smaller or on a par with those of additive gene, while in the other two they had the highest estimated values. Epistatic gene effects had no effect on the inheritance of self-fertility in R-15 x Kiz and CMS-19 x Kiz. Interaction between additive and dominant genes was the most significant two-gene epistasis in the rest of the crosses, in three of which it was highly significant and had the highest estimated values. In self-fertility expression, the effects of additive x additive gene epistasis were highly

significant in one cross and significant in three. The lowest significance was exhibited by epistasis among dominant genes, which was accompanied by duplicate epistasis.

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