

Partitioning of General and Specific Combining Ability Effects for Estimating Maternal and Reciprocal Effects

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Abstract

General and specific combining ability effects were partitioned according to a proposed model to estimate general and specific combining ability effects for each parent when it is used as a female or a male in its hybrid combinations. A working example includes a full-diallel among eight parents was used so that all possible hybrid combinations were included. The objectives of this study were: (1) to compare the GCA and SCA effects before and after partitioning, (2) to evaluate the relative contribution of each parent to its cross combination when it is used as a male or female parent, (3) to estimate maternal effects in the form of GCA and SCA effects, and (4) to estimate the relationship between maternal and reciprocal effects. Results revealed that estimated GCA effects according to Griffing's method is equal to the average of GCA effects of each parent, after partitioning, when it is used as a male and a female in its hybrid combinations. In addition, the average of the difference between female and male GCA effects would provide precise estimation of the maternal effect. This would prove that maternal effect provides precise estimation to the favorable alleles, which is mainly additive. The SCA effects calculated according to Griffing's method is the average of SCA effects of each cross and its reciprocal. The average of the difference between SCA effects of each cross and its reciprocal, according to the proposed model, is equal to the reciprocal effect. This would prove that reciprocal effect provides precise estimation to the interaction effect between nuclear and cytoplasmic genes given that the interaction between male and female alleles inside the nucleus of the cross is similar to its reciprocal hybrid.

Keywords: Partitioning, Full-diallel, GCA, SCA, Maternal effect, Reciprocal effect

1. Introduction

The diallel cross has been proven to be of considerable value to plant breeders in making decisions concerning the type of breeding system to use and in selecting breeding materials that show the greatest promise for success (Gardner and Eberhart, 1966). Widstrom et al. (1992) reported that diallel assessment of specific combining ability effects provides: 1) information about paired populations to be exposed to a reciprocal recurrent selection program; 2) the basis for choosing paired populations for extraction of new and high performing inbred lines.

Griffing (1956) defined diallel crosses, which have been used extensively in plant breeding. However, general and specific combining ability effects are commonly based on the average effect of the parent when it is used as a female or a male in its hybrid combinations assuming that they are likely to be similar as proposed by Yates, (1947). Griffing's methods 1 and 3 where crosses and their reciprocals are included, the fixed models, only one GCA effect value for each parent and one SCA effect value for each cross combination are estimated. These estimated effects do not, separately, show the contribution of each parent to the cross combination when this particular parent is used as a male or, alternatively, female.

Partitioning of the general and specific combining ability effects would provide additional information about each parent when it is used as a female or a male in its hybrid combinations (Mahgoub, 2004). It should, also provide precise information about the nature of the interaction between the best combinations among parents. Therefore, a proposed model is presented as follows:

1.1 Griffing's method 1 model 1 (all crosses, their reciprocals and parents are included) $n = p^2$

Various effects are estimated according to Griffing (1956) as follows:

$$\hat{g}_i = \left(\frac{1}{2p}\right) (X_i + X_{.i}) - \left(\frac{1}{p^2}\right) X_{..}$$

$$\hat{s}_{ij} = \left(\frac{1}{2}\right) (x_{ij} + x_{ji}) - \left(\frac{1}{2p}\right) (X_i + X_{.i} + X_j + X_{.j}) + \left(\frac{1}{p^2}\right) X_{..}$$

$$\hat{r}_{ij} = \left(\frac{1}{2}\right) (x_{ij} - x_{ji}).$$

Maternal effect is estimated according to Cockerham (1963) using Griffing's notations as follows:

$$\hat{m}_i = \left(\frac{X_i - X_{.i}}{2p}\right),$$

where X_i is the sum of the i th female over all males; $X_{.i}$ is the sum of the i th male over all females; X_j is the sum of the j th female over all males; $X_{.j}$ is the sum of the j th male over all females; x_{ij} is the mean for the F1 resulting from crossing the i th female and the j th male parents, x_{ji} is the mean for the F1 resulting from crossing the j th female and the i th male parents; \hat{g}_i is the general combining ability effect of the i th parent, \hat{s}_{ij} is the specific combining ability effect for the cross between the i th female and the j th male parents ($\hat{s}_{ij} = \hat{s}_{ji}$); \hat{r}_{ij} is the reciprocal effect involving the i th and j th parents, \hat{m}_i is the maternal effect of the i th parent, \hat{s}_{ij} is the SCA effect of the i th female and the j th male parent, and \hat{s}_{ji} is the SCA effect of the reciprocal, the j th female and the i th male parent, and $X_{..}$ is the grand total.

A proposed model where GCA effect \hat{g}_i is partitioned to estimate GCA effect for the parent when it is used as a female in its hybrid combination \hat{g}_{fi} ; and GCA effect for the parent when it is used as a male in its hybrid combination \hat{g}_{mi} as follows:

$$\hat{g}_{fi} = \left(\frac{1}{p}\right) (X_{i.}) - \left(\frac{1}{p^2}\right) X_{..}$$

$$\hat{g}_{mi} = \left(\frac{1}{p}\right) (X_{.i}) - \left(\frac{1}{p^2}\right) X_{..}$$

where \hat{g}_{fi} is the deviation of the mean performance of the i th parent when it is used as a female, averaged over a set of P males, from the grand mean and \hat{g}_{mi} is the deviation of the mean performance of the i th parent when it is used as a male, averaged over a set of P females, from the grand mean where:

$$\hat{g}_i = \left(\frac{1}{2}\right) (\hat{g}_{fi} + \hat{g}_{mi}) \text{ and,}$$

$$\hat{g}_{fi} - \hat{g}_{mi} = \left[\left(\frac{1}{p}\right) (X_{i.}) - \left(\frac{1}{p^2}\right) X_{..} - \left(\frac{1}{p}\right) (X_{.i}) - \left(\frac{1}{p^2}\right) X_{..}\right] = \left[\left(\frac{1}{p}\right) (X_{i.}) - \left(\frac{1}{p}\right) (X_{.i})\right] = \left[\left(\frac{1}{p}\right) (X_i - X_{.i})\right],$$

by dividing both sides of the equation by 2; $\left(\frac{1}{2}\right) (\hat{g}_{fi} - \hat{g}_{mi}) = \left(\frac{1}{2p}\right) (X_i - X_{.i})$

This proves that the average of the difference between \hat{g}_{fi} and \hat{g}_{mi} is exactly equal to maternal effect. In other words, estimation of $\hat{g}_{fi} - \hat{g}_{mi}$ would provide precise estimation for the maternal effect. General combining ability effect provides estimation for the additive effect. Therefore, maternal effect is mainly additive and expresses how much additive effect is involved.

Specific combining ability effect is partitioned to estimate SCA effect for the cross \hat{s}_{ij} and for its reciprocal \hat{s}_{ji} as follows:

$$\hat{s}_{ij} = x_{ij} - \left(\frac{1}{2p}\right) (X_i + X_{.i} + X_j + X_{.j}) + \left(\frac{1}{p^2}\right) X_{..}$$

$$\hat{s}_{ji} = x_{ji} - \left(\frac{1}{2p}\right)(X_i + X_{.i} + X_j + X_{.j}) + \left(\frac{1}{p^2}\right)X_{..}$$

where the average of the partitioned \hat{s}_{ij} and \hat{s}_{ji} is equal to \hat{s}_{ij} calculated according to Griffing's method.

$$\hat{s}_{ij} - \hat{s}_{ji} = \left[x_{ij} - \left(\frac{1}{2p}\right)(X_i + X_{.i} + X_j + X_{.j}) + \left(\frac{1}{p^2}\right)X_{..}\right] - \left[x_{ji} - \left(\frac{1}{2p}\right)(X_i + X_{.i} + X_j + X_{.j}) + \left(\frac{1}{p^2}\right)X_{..}\right],$$

$$\hat{s}_{ij} - \hat{s}_{ji} = x_{ij} - x_{ji}.$$

Therefore,

$$\left(\frac{1}{2}\right)(\hat{s}_{ij} - \hat{s}_{ji}) = \left(\frac{1}{2}\right)(x_{ij} - x_{ji}) = \text{reciprocal effect}$$

This proves that the average of the difference between SCA effect of the cross and its reciprocal is exactly equal to the estimated reciprocal effect. Accordingly, this difference provides precise estimation for the reciprocal effect. This suggests that the difference in SCA effects between each cross and its reciprocal provides a precise estimation of the interaction that might be existed between nuclear and cytoplasmic genes. This proves that partitioning of SCA effects provided additional information to plant breeders about estimating the magnitude of the interaction between nuclear and cytoplasmic genes. Consequently, it is expected that estimated reciprocal effect would underestimate the real difference that might be existed between the cross \hat{s}_{ij} and its reciprocal \hat{s}_{ji} in terms of SCA effects. Specific combining ability effect provides estimation for the dominance effect. Therefore, the real difference that might be existed between the cross \hat{s}_{ij} and its reciprocal \hat{s}_{ji} in terms of SCA effects reveals and expresses how much interaction between nuclear and cytoplasmic genes is involved.

1.2 Griffing's method 3 model 1 (all crosses and their reciprocals, excluding parents) $n=p(p-1)$

Various effects are estimated according to Griffing's method 3 as follows:

$$\hat{g}_i = \left(\frac{1}{2p(p-2)}\right)(p(X_i + X_{.i}) - 2X_{..}),$$

$$\hat{s}_{ij} = \left(\frac{1}{2}\right)(x_{ij} + x_{ji}) - \left(\frac{1}{2(p-2)}\right)(X_i + X_{.i} + X_j + X_{.j}) + \left(\frac{1}{(p-1)(p-2)}\right)X_{..},$$

$$\hat{r}_{ij} = \left(\frac{1}{2}\right)(x_{ij} - x_{ji}).$$

Estimated effects after partitioning according to the proposed model are calculated as follows:

$$\hat{g}_{fi} = \left(\frac{X_i}{p-2}\right) - \left(\frac{X_{..}}{p(p-2)}\right),$$

$$\hat{g}_{mi} = \left(\frac{X_{.i}}{p-2}\right) - \left(\frac{X_{..}}{p(p-2)}\right),$$

$$\hat{g}_i = \left(\frac{1}{2}\right)(\hat{g}_{fi} - \hat{g}_{mi}),$$

$$\hat{g}_{fi} - \hat{g}_{mi} = \left[\left(\frac{X_i}{p-2}\right) - \left(\frac{X_{..}}{p(p-2)}\right) - \left(\frac{X_{.i}}{p-2}\right) + \left(\frac{X_{..}}{p(p-2)}\right)\right],$$

$\hat{g}_{fi} - \hat{g}_{mi} = \left(\frac{X_i - X_{.i}}{p-2}\right)$, by multiplying the right hand side of the equation by $\left(\frac{p-1}{p-1}\right)$ and dividing both sides of the equation by 2;

$$\left(\frac{1}{2}\right)(\hat{g}_{fi} - \hat{g}_{mi}) = \left(\frac{X_i - X_{.i}}{2(p-1)}\right)\left(\frac{p-1}{p-2}\right),$$

i. e. the average of the difference between \hat{g}_{fi} and \hat{g}_{mi} is exactly equal to the maternal effect multiplied by a constant, $\left(\frac{p-1}{p-2}\right)$. In other words, estimation of \hat{g}_{fi} and \hat{g}_{mi} would provide an estimation for the maternal effect,

simply, by multiplying $\left(\frac{1}{2}\right)(\hat{g}_{fi} - \hat{g}_{mi})$ by $\left(\frac{p-2}{p-1}\right)$ for Griffing's method 3. The SCA effects are partitioned as follows:

$$\begin{aligned}\hat{s}_{ij} &= x_{ij} - \left(\frac{1}{2(p-2)}\right)(X_i + X_i + X_j + X_j) + \left(\frac{1}{(p-1)(p-2)}\right)X_{..}, \\ \hat{s}_{ji} &= x_{ji} - \left(\frac{1}{2(p-2)}\right)(X_i + X_i + X_j + X_j) + \left(\frac{1}{(p-1)(p-2)}\right)X_{..}, \\ \hat{s}_{ij} - \hat{s}_{ji} &= \left[x_{ij} - \left(\frac{1}{2(p-2)}\right)(X_i + X_i + X_j + X_j) + \left(\frac{1}{(p-1)(p-2)}\right)X_{..}\right] - \\ &\quad \left[x_{ji} - \left(\frac{1}{2(p-2)}\right)(X_i + X_i + X_j + X_j) + \left(\frac{1}{(p-1)(p-2)}\right)X_{..}\right] \\ \hat{s}_{ij} - \hat{s}_{ji} &= x_{ij} - x_{ji}.\end{aligned}$$

Therefore,

$$\left(\frac{1}{2}\right)(\hat{s}_{ij} - \hat{s}_{ji}) = \left(\frac{1}{2}\right)(x_{ij} - x_{ji}) = \text{reciprocal effect}$$

Thus, the average of the difference between \hat{s}_{ij} and \hat{s}_{ji} = the estimated reciprocal effect as indicated above in method 1. This would prove that the difference between the interaction effect of the cross and its reciprocal is due mainly to the interaction between the nuclear and the cytoplasmic genes as indicated above. Cytoplasm of the female parent may represent different environment that differs from one parent to another and therefore, interacts with nuclear genes differently. Interaction between the nuclear and the cytoplasmic genes was reported by Cooper et al. (1990); Singh and Brown (1991); Ekiz and Konzak (1991a, b, and c); Maan (1992); & Voluevich and Bulovich (1992).

Improving the precision of the statistical model used for estimating GCA and SCA effects may provide a precise tool for selecting the breeding method as well as the paired populations to be used in a reciprocal recurrent selection program.

The objectives of the present study were: (1) to compare the GCA and SCA effects before and after partitioning, (2) to evaluate the relative contribution of each parent to its cross combination when it is used as a male or a female parent, (3) to estimate the relationship between maternal and GCA effects, (4) to estimate the relationship between SCA effect, reciprocal effect, and the interaction between nuclear and cytoplasmic genes.

2. Materials and methods

A working example using data kindly cited from Singh and Chaudhary (1985) was used, where a diallel cross among eight parents, where all possible hybrid combinations were included. Therefore, data were analyzed according to Griffing's method 1 model I, and according to the proposed model, where GCA and SCA effects were partitioned to study the contribution of each parent when it is used as a male or a female in its hybrid combinations, but not on the average performance of male and female parents.

3. Results and discussion

3.1 General combining ability

The GCA effects calculated according to Griffing's method showed that parent 3 and 7 had high positive GCA effects; while parent 8 had high negative effects (Table 1). Partitioning of the GCA effects to estimate male and female effects revealed that the average of \hat{g}_{fi} and \hat{g}_{mi} effects calculated according to Griffing's method might underestimate the breeding value of the parent if it showed better performance when it is used as a female or a male in its hybrid combinations (parent 3 and 7, Table 1). Data in Table 1 show that the average of the difference between \hat{g}_{fi} and \hat{g}_{mi} is exactly equal to maternal effect, which is based on the average of the females over all associated males. Population 3 had higher GCA effects when it was used as a female rather than a male (higher \hat{g}_{fi} than \hat{g}_{mi}). In contrast, Population 7 showed higher \hat{g}_{mi} than \hat{g}_{fi} . The average of \hat{g}_{fi} and \hat{g}_{mi} effects calculated according to Griffing's method underestimated the breeding value of the parent 3 compared with its breeding value when it was used as a female parent. Likewise, the average of \hat{g}_{fi} and \hat{g}_{mi} effects calculated according to

Griffing's method underestimated the breeding value of the parent 7 compared with its breeding value when it was used as a male parent. Parent 3 revealed much higher \hat{g}_{fi} than parent 7. This indicated that more favorable alleles were provided by the female plants of population 3 to the offspring than the male ones of the same parent and GCA effects calculated according to Griffing's method do not show the magnitude of the difference between parents 3 and 7 when they were used as female parents. Therefore, a breeding method, where the progeny test is based mainly on the performance of the offspring of the male plants (e. g. half sib family selection), may be less effective in detecting the high \hat{g}_{fi} and consequently less effective in improving of population 3, but this breeding method would be more effective with population 7 (higher \hat{g}_{mi} than \hat{g}_{fi}). The significance of \hat{g}_{fi} of population 3 may indicate that some gain from selection is expected if the progeny test was based on the performance of the offspring of the female plants (e.g. S1 family selection). In contrast, reciprocal recurrent selection is expected to be less effective for this population and would be more effective for population 7 since \hat{g}_{mi} is higher than \hat{g}_{fi} of this population. Source materials and environmental conditions under which recurrent selection trials are conducted may be as important as the selection method used (Genter and Eberhart, 1974). This indicates that the GCA effects calculated on the average of male and female effects (Griffing's method) underestimated the value of the populations 3 and 7 when they were used as male or female in their hybrid combinations, respectively.

Accordingly, this provides another explanation to the question "why some plant breeders are able to get more gain from selection from the same population than others?". Genter and Eberhart 1974 did not find an improvement in crosses of BSK (S) and BSSS (HT), while previous evaluation had shown much improvement in general combining ability of the advanced populations (Burton *et al* 1971 and Eberhart *et al* 1973). Similarly, the advanced population of NHG did not show as much improvement by Genter and Eberhart 1974 as had been reported by Gardner 1961 and 1969.

The average of the difference between \hat{g}_{mi} and \hat{g}_{fi} is exactly equal to the maternal effect calculated according to Cockerham (1963), which is based on the average of the females over all associated males. Therefore, partitioning of the GCA effects provided additional information to plant breeders about estimating maternal effect.

Estimation of maternal effects, which is based on the average of the females over all associated males would underestimate maternal effect of some specific cross combinations, which may be more important. Therefore, partitioning of the maternal effects leads to estimation of the reciprocal effects, which provides estimation of the maternal effects on a hybrid combination basis rather than on the average of all associated male parents.

3.2 Specific combining ability

The SCA effects, calculated according to Griffing's method and the partitioned SCA effects are presented in Tables 2. Cross (2 x 3) had much higher SCA effects (after partitioning) compared with its reciprocal (3 x 2). But SCA effects, calculated according to Griffing's method assumed that SCA effects are the same for each cross and its reciprocal and do not show this additional information. Likewise, crosses (1 x 5), (6 x 7), and (7 x 8) had much higher SCA effects (after partitioning) compared with their reciprocals (5 x 1), (7 x 6), and (8 x 7), respectively. The SCA effects calculated according to Griffing (1956) underestimated the SCA effects of the crosses (3 x 2), (5 x 1), (7 x 6), and (8 x 7) compared with their reciprocals, which were overestimated. The SCA effects calculated according to Griffing (1956) provides one value for each cross combination assuming that the interaction between males and females is mainly due to the interaction between the nuclear genes of male and female plants, neglecting an important part of the interaction, which is between nuclear and cytoplasmic genes. Partitioning of the SCA effects to estimate a value for each cross and a different value for its reciprocal could reflect the magnitude of the interaction between nuclear and cytoplasmic genes. This suggests that differences between SCA effects of a cross and its reciprocal are due to the direct effect of the cytoplasm and/or the mitochondrial genes of the female parent as well as the interaction between the nuclear genes and the cytoplasm of the female parent. Cytoplasm of the female parent represents a different environment from that of the other parent, where the embryo develops and this interaction might be considered as a different type of genotype (G) x environment (E) interaction. Cytoplasm from a number of cultivated and wild species had modifying effects on the expression of the nuclear genes controlling quantitative resistance (Volvevich and Bulovich, 1992). Ekiz and Konzak (1991a) found significant nuclear x cytoplasm genetic interactions in two subsets of alloplasmic lines of wheat having common cytoplasm but different nuclear genotypes. The occurrence of reciprocal differences for all components of anther culture response,

indicated that the cytoplasm of maternally inherited factors interact with nuclear genes to control the response of wheat genotypes to anther culture Ekiz and Konzak (1991c). Cooper *et al.* (1990) reported that maize nuclear background influenced number and size of transcripts from the gene encoding subunit 2 of cytochrome *c* oxidase (*cox 2*) in *Zea perennis* and *Zea diploperennis* mitochondria but it had no influence on *cox 2* transcript pattern in lines carrying *Z. luxurians* cytoplasm.

For simplicity, SCA effects, calculated according to Griffing's method and the proposed method of the top high-yielding crosses and their reciprocals, arranged in descending order are presented in Table 3. The SCA effects calculated according to Griffing's method underestimated the SCA effects of the crosses 7x8, 6x7, 1x5, and 4x1. In contrast, the SCA effects of their reciprocals were overestimated. Cytoplasm of a good combiner parent represents a different internal environment from the cytoplasm of the other parent, which might interact differently with the nuclear genes. This suggests that partitioning of the SCA effects according to the proposed model provides a precise estimation of these effects for each cross and its reciprocal.

Partitioning of GCA and SCA effects provided precise and more precise procedure for estimating genetic effects. Genter and Eberhart (1974) suggested that information regarding selection progress can be extracted from population diallel experiments if properly designed and analyzed. Therefore, Griffing's methods 2 and 4, where reciprocal crosses are not included, would underestimate the value of the best performing cross combinations. The present results revealed that the proposed model would provide valuable information about each parent when it is used as a female or a male in its hybrid combination and further calculations for estimating reciprocal effects are no longer required.

The proposed model would provide additional information to the plant breeder about each parent when it is used as a male or a female and precise information about the nature of the interaction between the best parental combinations.

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Table 1. The GCA effects \hat{g}_i , \hat{g}_{fi} and \hat{g}_{mi} , and maternal effects of the eight parent populations

	(1)	(2)	(3)	(4)	(5)
				<u>Maternal effect</u>	
Parents	\hat{g}_i	\hat{g}_{fi}	\hat{g}_{mi}	$(\hat{g}_{fi} - \hat{g}_{mi})/2$	$\hat{m}_i = \left(\frac{X_{i.} - X_{.i}}{2p}\right)$
1	006	015	-003	009	009
2	047	115	-021	068	068
3	903	999	806	096	096
4	-344	-261	-427	083	083
5	-233	-314	-151	-082	-082
6	-194	-174	-213	020	020
7	724	598	849	-126	-126
8	-910	-978	-841	-069	-069

Table 2. The SCA effects calculated according to Griffing’s method (bold, upper) and SCA effects calculated according to the proposed method (italics, lower)

		Male							
		1	2	3	4	5	6	7	8
Female	1	-523	-743	-348	2966	2730	-2019	1040	-3104
		<i>-523</i>	<i>-427</i>	<i>-934</i>	<i>2757</i>	<i>3180</i>	<i>-2033</i>	<i>959</i>	<i>-2908</i>
	2	-743	658	782	096	1252	-1700	-572	228
		<i>-1059</i>	<i>658</i>	<i>1133</i>	<i>039</i>	<i>1104</i>	<i>-1602</i>	<i>-081</i>	<i>353</i>
	3	-348	782	-3474	532	-618	239	298	2589
		<i>239</i>	<i>431</i>	<i>-3474</i>	<i>431</i>	<i>-317</i>	<i>304</i>	<i>452</i>	<i>2705</i>
	4	2966	096	532	777	-065	2185	-3350	-3142
		<i>3174</i>	<i>153</i>	<i>634</i>	<i>777</i>	<i>030</i>	<i>2042</i>	<i>-3010</i>	<i>-3136</i>
	5	2730	1252	-618	-065	-3200	-043	-1532	1474
		<i>2280</i>	<i>1400</i>	<i>-919</i>	<i>-159</i>	<i>-3200</i>	<i>-234</i>	<i>-1372</i>	<i>1549</i>
	6	-2019	-1700	239	2185	-043	1351	2259	-2273
		<i>-2004</i>	<i>-1799</i>	<i>173</i>	<i>2329</i>	<i>148</i>	<i>1351</i>	<i>2556</i>	<i>-2598</i>
	7	1040	-572	298	-3350	-1532	2259	-1426	3283
		<i>1121</i>	<i>-1063</i>	<i>143</i>	<i>-3690</i>	<i>-1691</i>	<i>1962</i>	<i>-1426</i>	<i>3638</i>
	8	-3104	228	2589	-3142	1474	-2273	3283	944
		<i>-3300</i>	<i>102</i>	<i>2472</i>	<i>-3147</i>	<i>1399</i>	<i>-1948</i>	<i>2928</i>	<i>944</i>

Table 3. Rank, SCA partitioned (SCAp), and SCA according to Griffing's method of the high-yielding crosses (bold) and their reciprocals (italic) in a descending order

Number	Rank	F	M	Yield	SCAp	SCA
1	1	7	8	1253	364	328
2	<i>5</i>	<i>8</i>	<i>7</i>	<i>1182</i>	<i>293</i>	<i>328</i>
3	2	6	7	1216	256	226
4	<i>7</i>	<i>7</i>	<i>6</i>	<i>1157</i>	<i>196</i>	<i>226</i>
5	3	1	5	1203	318	273
6	<i>12</i>	<i>5</i>	<i>1</i>	<i>1113</i>	<i>228</i>	<i>273</i>
7	4	4	1	1191	317	297
8	<i>9</i>	<i>1</i>	<i>4</i>	<i>1150</i>	<i>276</i>	<i>297</i>
9	6	3	8	1177	271	259
10	<i>8</i>	<i>8</i>	<i>3</i>	<i>1154</i>	<i>247</i>	<i>259</i>
11	10	2	3	1116	113	78
12	<i>18</i>	<i>3</i>	<i>2</i>	<i>1046</i>	<i>43</i>	<i>78</i>
13	11	3	7	1115	45	30
14	<i>15</i>	<i>7</i>	<i>3</i>	<i>1085</i>	<i>14</i>	<i>30</i>
15	13	7	1	1093	112	104
16	<i>16</i>	<i>1</i>	<i>7</i>	<i>1076</i>	<i>96</i>	<i>104</i>
17	14	6	4	1087	233	219
18	<i>17</i>	<i>4</i>	<i>6</i>	<i>1058</i>	<i>204</i>	<i>219</i>
19	19	5	2	1029	140	125
20	<i>24</i>	<i>2</i>	<i>5</i>	<i>999</i>	<i>110</i>	<i>125</i>
21	20	4	3	1027	63	53
22	<i>23</i>	<i>3</i>	<i>4</i>	<i>1007</i>	<i>43</i>	<i>53</i>
23	21	3	1	1022	24	-35
24	<i>30</i>	<i>1</i>	<i>3</i>	<i>905</i>	<i>-93</i>	<i>-35</i>
25	22	3	6	1009	30	24
26	25	6	3	996	17	24

Table 4. Reciprocal effects calculated according to Griffing's method

		Male							
		1	2	3	4	5	6	7	8
Female	1	000	316	-586	-209	450	-014	-081	196
	2	-316	000	351	-057	-148	099	491	125
	3	586	-351	000	-102	301	066	155	117
	4	209	057	102	000	095	-144	340	006
	5	-450	148	-301	-095	000	-191	159	075
	6	014	-099	-066	144	191	000	297	-325
	7	081	-491	-155	-340	-159	-297	000	355
	8	-196	-125	-117	-006	-075	325	-355	000