

POLLEN EFFECT (XENIA) FOR EVALUATING BREEDING MATERIALS IN MAIZE

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Pollen effect (xenia) plays an important role in modifying biochemical constituents of maize (*Zea mays* L.) kernels. The objectives of this study were to i) evaluate the effect of filial generations on certain genetic estimations; ii) compare general (GCA) and specific combining ability (SCA) effects obtained from Griffing's diallel analyses between parental (F₀) and F₁ generations; iii) determine the relationships between pollen effect and genetic estimations; and iv) examine the possible utility of pollen effect for improving kernel-quality traits (protein and oil contents). We conducted two experiments (F₀ in 2011 and F₁ in 2013) and examined kernel protein and oil contents. Individual pollen effects (IPE) and specific individual pollen effects (SIPE) were computed. The results showed that entries (E) and filial generations (G) and E × G interaction variances were significant for both protein and oil contents, whereas changes in genetic estimates between generations were highly variable. The signs and magnitudes of GCA effects were similar and highly correlated ($r > 0.80$) between F₀ and F₁ generations for all four diallel methods. In addition, GCA effects were highly correlated with IPE estimates for all four diallel methods. Specific combining ability (SCA) estimates between F₀ and F₁ generations were moderately correlated ($r = 0.50$) in Method IV for oil and highly negatively correlated ($r = -1.00$) in Method III for protein content. Heterosis analyses showed that hybrids could not be evaluated on the basis of the F₀ generation to predict their F₁ performances. Individual pollen effects between generations showed higher correlation for protein content ($r = 1.00$) than for oil content ($r = 0.40$). Specific individual pollen effects of parents were also slightly higher for protein content ($r = 0.74$) than for oil content ($r = 0.62$). We concluded that the direct or indirect utilization of pollen effect (xenia) was possible for parental evaluation but not suitable for hybrid evaluation for kernel oil and protein contents.

Key words: combining ability, diallel analysis, kernel quality, oil content, protein content, *Zea mays*

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INTRODUCTION

The term “xenia” refers to the effects of pollen from different sources on readily discernible characteristics of seeds and fruits during the period immediately following fertilization (BOZINOVIC *et al.*, 2015). KIESSELBACH (1960) showed an effect of the origin and nature of pollen on kernel development in maize. He noted a large reciprocal effect relative to kernel weight and a difference in weight between kernels that resulted from self-fertilization and those that resulted from cross fertilization; the latter increased kernel weight, on average, by 10.1% (11.8% for embryos, 10.4% for endosperm, and 3.2% for pericarp).

NAGUR *et al.* (1991) considered the term “xenia” for direct pollen effects on embryo and endosperm, and “metaxenia” for pollen effects on maternal plant tissue. According to DENNEY (1992), direct, or immediate, pollen effects on seeds and fruits are called “xenia” and include differences in size, shape, color, developmental timing, and chemical composition of seeds and fruits, resulting from fertilization by genetically different pollen grains. DENNEY (1992) explained that xenia included metaxenia and that, initially, xenia referred only to pollen effects on maternal tissues, such as seed coat and pericarp. DENNEY (1992) dwelled at length on the confusion between xenia and metaxenia and listed different definitions of xenia in a review article.

The pollen effect has been discussed in scientific studies under two main topics, i.e., “individual pollen effect” and “pollen-parent effect.” Individual pollen effect (IPE) is the immediate effect of pollen parent on female parent, which is observed only during pollination (F_0) (BULANT *et al.*, 2000); whereas pollen-parent effect is measured in the next generation (F_1), following pollination. Research on individual-pollen effect has shown a significant effect of pollen source on kernel biochemical constituents in maize (TSAI and TSAI, 1990; LETCHWORT and LAMBERT, 1998; WEINGARTNER *et al.*, 2004; VANCETOVIC *et al.*, 2009). TANAKA *et al.* (2009) reported that embryo/kernel ratio was significantly affected by the pollen effect and kernel’s biochemical structure. There were significant changes in protein, oil and fatty acid composition of normal maize genotypes when plants were pollinated by ‘high-oil’ or ‘high-protein’ maize genotypes (DONG, 2007). Some conflicting findings about the pollen effect on biochemical traits also exist in scientific literature. For example, protein content was not significantly affected by pollen effect in the study by LETCHWORT and LAMBERT (1998); whereas other studies have reported a significant effect of xenia on protein and amino acid content (PIXLEY and BJARNASON, 1994; VANCETOVIC *et al.*, 2009). This issue still remains unresolved.

To exploit pollen effect in maize on the basis of the results of pollen-effect studies, several systems have been developed. One of the well-known examples of these systems is TopCross Blend® licensed by Optimum Quality Grains (THOMISON *et al.*, 2002). In this method, a high-yielding, elite hybrid was pollinated with a high-oil parent to improve its oil yield. Recently, this system was tested to determine the effectiveness of pollen effect in modifying antioxidant constituents in different materials (VANCETOVIC *et al.*, 2014). WANG *et al.* (2009) reported that yield increase was higher in ‘three-effect-utilization system’ (TEU) than in the TopCross system. In TEU, yield increase would be possible, together with increased oil production, by using a high-oil maize pollinator possessing high yield. Another system, namely, Plus-hybrid effect, has also been developed, which relates to pollen effect, combined with cytoplasmic male sterility, and has been used to improve yield in maize (WEINGARTNER *et al.*, 2002a, b).

The research on IPE and its exploitation have enabled the development of various practical methods. However, no study currently exists on the possible use of IPE for evaluating

breeding materials in maize. In general, hybrid maize-breeding experiments cover parental generation (F_0) and later generations, such as F_1 , F_2 , etc. Breeding materials obtained from parental generation (F_0) have previously been evaluated via different genetic analyses, which provided combining abilities of evaluated materials (BERTAN *et al.*, 2007; YAO *et al.*, 2013). Usually, statistical analyses were performed on F_1 progeny and/or later generations in studies involving plant characteristics and grain yield. However, pollen effect could potentially cause changes in the biochemical constituents of maize kernels, and it could enable researchers to conduct combining ability analyses in the parental generation (F_0) in studies aimed at improving kernel-quality traits. AHUJA and MALHI (2008) used a line \times tester design for determining combining ability effects of parents and hybrids based on F_0 seeds for oil content in maize. However, they did not compare the estimated effects in the F_1 generation. Several studies have compared combining abilities from later generations (F_1 and F_2) in self-pollinated species, such as wheat (JOSHI *et al.*, 2004; YAO *et al.*, 2014). In scientific literature, there has been some speculation about selection of suitable breeding materials on the basis of estimations of pollen effect. OLFATI *et al.* (2010) suggested that combining ability effects could be identified on the basis of IPE in different plant species.

Heterosis is another important genetic estimation for breeders interested in hybrid development. There are examples of studies that predict heterosis in later generations, e.g., F_1 and F_2 (XU and ZHU, 1999). However, there is no conceptual work about relationships of pollen effect and heterosis in maize experiments as well as about differences between parental (F_0) and F_1 generations. Thus, there is a need for clarifying use of pollen effect for selecting appropriate materials in studies aimed at improving kernel-quality traits. Therefore, the current study was intended to determine, by using a 4-parent diallel cross as an example, (i) whether results from combining ability and heterosis analyses based on parental generation (F_0) and F_1 progeny will be the same or different, (ii) whether results from Griffing's different diallel methods (Griffing's Method I, Method II, Method III and Method IV) would be the same or different between F_0 and F_1 generations, (iii) whether or not relationships exist among pollen effect estimations, combining abilities, maternal/non-maternal effects and midparent heterosis, and (iv) whether pollen effect can be used to evaluate breeding materials without genetic analyses.

MATERIALS AND METHODS

In this study, a 4×4 complete diallel set (parents, F_1 s and reciprocal F_1 s) was used. The parental material included three inbred lines and one open-pollinated variety (see Table 1). Two parental lines, IHO (high oil) and Q2 (high protein), were specialty types of maize. We used parents having different kernel colors and biochemical characteristics to be able to measure the pollen effect (Table 1).

Field trials were conducted at the Dardanos Research and Application Center of Çanakkale Onsekiz Mart University, Northwest Turkey. The trials included parental generation trial (F_0) and F_1 progeny evaluation trial. Field experiments were arranged in a randomized complete-block design with three replications. Each genotype was planted at a seeding rate of 71000 ha⁻¹. Each experimental plot consisted of two rows (each row 2-m long), with 0.70 m spacing between rows. Parental generation trial (F_0) was conducted in 2011 with only the parental lines, whereas the parents and hybrids were included in the F_1 evaluation trial conducted in 2013. To prevent pollen contamination among the genotypes, controlled pollination was used, as suggested elsewhere (ANONYMOUS, 2015). In the parental generation (F_0), parents were self-

pollinated and crossed in all possible combinations (a full diallel set). In the F₁ progeny evaluation trial, five randomly selected plants per genotype were self-pollinated. Drip irrigation was applied to meet water needs of the plants. Three hand-pollinated ears per plot were harvested and dried at 40°C to uniform moisture content. Afterwards, dried ears were shelled and kernel samples kept at 4°C until needed for further evaluation.

Table 1. The experimental material used.

Parent	Specialty	Kernel color	Source†
IHO	High oil	White	NCRPIS, USA
Q2	High protein quality	Yellow	NCRPIS, USA
OPV	Normal	Yellow-Orange	Trabzon, Turkey
PR	Normal	Purple	ÇOMÜ, Turkey

†NCRPIS: North Central Regional Plant Introduction Station; ÇOMÜ: Çanakkale Onsekiz Mart University.

Protein and oil contents were determined using a near-infra red (NIR) instrument (Spectrastar 2400D, Unity Scientific, Brookfield, CT, USA). For this purpose, kernel samples were ground in a laboratory mill (Fritsch, Pulverisette 14, Germany) and passed through a 0.5 mm sieve. Ground samples were placed in a rotary sample cup of the NIR instrument, and then scanned between 1200 and 2400 nm, with 1 nm scanning intensity. A local calibration was used to estimate protein and oil contents of the samples using Infostar software (Unity Scientific, Brookfield, CT, USA).

Diallel analyses were performed via DIALLEL-SAS05 program (ZHANG *et al.*, 2005), using SAS Version 8 (SAS INSTITUTE, 1999). Griffing's diallel methods (Method I, Method II, Method III and Method IV) were used to estimate GCA of parents and SCA of hybrid combinations. A fixed-effects model was applied for the diallel analyses. The t-test was used to examine the significance of estimated combining ability effects. Statistical explanation of the methods used herein is presented in Table 2. The following general linear model was used:

$$Y_{ijkl} = \mu + \alpha_l + b_{kl} + v_{ij} + (\alpha v)_{ijl} + e_{ijkl}$$

where Y_{ijkl} = observed value from each experimental unit; μ = population mean; α_l = generation effect; b_{kl} = block or replication effect within l th generation; v_{ij} = F₁ hybrid effect [$v_{ij} = g_i + g_j + s_{ij} + r_{ij}$; where g_i = GCA of the i th parent; g_j = GCA of j th parent; s_{ij} = SCA for the ij th F₁ hybrid; and r_{ij} = reciprocal effect (REC) for ij th F₁ hybrid; further, $r_{ij} = m_i + m_j + n_{ij}$; m_i = maternal effect (MAT) of parental line i , m_j = maternal effect of parental line j ; n_{ij} = non-maternal effect (NMAT) of ij th F₁ hybrid]; $(\alpha v)_{ijl}$ = interaction effect between ij th F₁ hybrid and l th generation [$(\alpha v)_{ijl} = (ag)_{il} + (ag)_{jl} + (as)_{ijl} + (ar)_{ijl}$; where $(ag)_{il}$ = interaction between GCA effect for i th parent and l th generation; $(ag)_{jl}$ = interaction between GCA effect for j th parent and l th generation; $(as)_{ijl}$ = interaction between SCA effect for ij th F₁ hybrid and l th generation; $(ar)_{ijl}$ = interaction between reciprocal effect for ij th F₁ hybrid and l th generation; further, $(ar)_{ijl} = (am)_{il} + (am)_{jl} + (an)_{ijl}$; $(am)_{il}$ = interaction between l th generation and maternal effect of parental line i ; $(am)_{jl}$ = interaction between l th generation and maternal effect of parental inbred j ; and $(an)_{ijl}$ = interaction between l th generation and non-maternal effect of ij th F₁ hybrid]; and e_{ijkl} = random residual effect. Model components in Griffing's methods are shown in Table 2. The F₀ (parents) and F₁ means were separately compared via the Least Significant Difference (LSD) test.

Table 2. Model components of Griffing's diallel methods.

Method	Materials included	Model components†
Method I	Parents, F _{1S} and reciprocals	$v_{ij} = g_i + g_j + s_{ij} + r_{ij}$, $(av)_{ijl} = (ag)_{il} + (ag)_{jl} + (as)_{ijl} + (ar)_{ijl}$, $r_{ij} = m_i + m_j + n_{ij}$, and $(ar)_{ijl} = (am)_{il} + (am)_{jl} + (an)_{ijl}$.
Method II	Parents and F _{1S}	$v_{ij} = g_i + g_j + s_{ij}$ $(av)_{ijl} = (ag)_{il} + (ag)_{jl} + (as)_{ijl}$.
Method III	F _{1S} and reciprocals	$v_{ij} = g_i + g_j + s_{ij} + r_{ij}$, $(av)_{ijl} = (ag)_{il} + (ag)_{jl} + (as)_{ijl} + (ar)_{ijl}$, $r_{ij} = m_i + m_j + n_{ij}$, and $(ar)_{ijl} = (am)_{il} + (am)_{jl} + (an)_{ijl}$.
Method IV	F _{1S}	$v_{ij} = g_i + g_j + s_{ij}$ $(av)_{ijl} = (ag)_{il} + (ag)_{jl} + (as)_{ijl}$.

†Model components explained in the text.

Midparent heterosis (MPH) was computed by dividing the difference between parental means and hybrid value by parental mean (FALCONER and MACKAY, 1996). The MPH calculations were made according to the following formula:

$$MPH = ((F_1 - MP) / MP) \times 100$$

where F₁ = the mean of the F₁ hybrid performance and MP = (P₁ + P₂) / 2, where P₁ and P₂ are the means of the inbred parents. These calculations were made for each generation and the variation in MPH values from different generations was compared.

We used the approach proposed by BULANT *et al.* (2000) to determine individual pollen effect in F₀ and F₁ generations. Specific individual pollen effect (SIPE) was computed by subtracting pollen parent mean from F₁ hybrid value, where a specific parent was involved. Individual pollen effect (IPE) was average of SIPE values for each parental line in the F₀ generation, whereas pollen parent effect (IPE_{F1}) was similarly estimated in the F₁ generation. These values were used to evaluate the relationships of pollen effect with combining ability and heterosis.

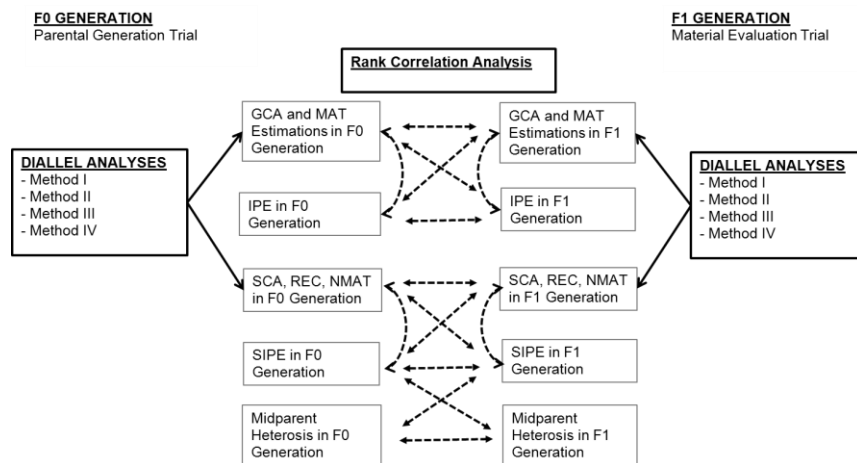


Figure 1. The outline of data evaluation related to genetic estimations.

The PROC CORR statement of SAS package (SAS INSTITUTE, 1999) was used to compute Spearman's rank correlations to evaluate the relationship between genotypic means, combining ability values (GCA, SCA) and other genetic components (REC, MAT and NMAT) of the two generations. The same procedure was applied to investigate the relationships between individual pollen effects and estimated genetic parameters. We have presented the relationships between genetic estimations (GCA, SCA, REC, MAT, and NMAT) in different generations using scatter plots. The number of visible points in scatter plots varied according to Griffing's diallel method used. An outline of investigated relationships is presented in Figure 1.

RESULTS AND DISCUSSION

Effect of Generation on Mean Values and Genetic Estimations

Analysis of variance showed that there were significant differences between generations (G) for protein content. Entry (E) and entry \times generation (E \times G) interaction effects were significant for both oil and protein contents (Table 3). The significant E \times G interaction indicated that oil and protein values for entries differed significantly between F₀ and F₁ generations.

Table 3. Mean squares (analysis of variance) for oil content (%) and protein content (%) across F₀ and F₁ generations involving 16 entries.

Source of variation	df	Oil content	Protein content
Generations (G)	1	0.000001	6.58**
Replications within Generations	4	2.87**	16.88**
Entries (E)	15	25.86**	10.09**
E \times G	15	3.59**	2.10**
Error	60	0.07	0.65
CV (%)		4.06	7.48

*, ** Significant at the 0.05 and 0.01 level of probability, respectively.

We separated the entries into parents and hybrids to detect changes in protein and oil contents in parents and hybrids. Between F₀ and F₁ generations, mean values for parents were highly correlated for oil ($r = 0.80$) and protein content ($r = 1.00$) (Figure 2). In general, F₀ values were lower than F₁ values for both traits. The reason for the high correlations might be that protein and oil contents are controlled by additive gene action in maize, as pointed out by COOK *et al.* (2012). This type of gene action is less affected by environmental conditions compared with non-additive gene action, such as dominance effects and epistatic interactions. Additive type of gene action is more pronounced in selfed progenies or inbred lines, which are generally developed by successive selfing in classical maize breeding. Our results suggested that additive type of gene action was stable between generations. Our field trials (F₀ and F₁) were conducted in separate years. Environmental differences might have had some effect on additive type of gene action because parental rankings were similar but not identical for the observed traits (Figure 2).

Correlations between F₀ and F₁ values for hybrids were non-significant for both oil ($r = 0.41$) and protein content ($r=0.54$). Six crosses had higher oil content in F₀ compared with F₁ generation, whereas five crosses had lower protein content in F₀ than in F₁ generation (Figure 2). These results showed that parents had more stable ranking in different generations compared with

crosses for both the traits. Thus, it should be possible to simply select the parents with good protein and oil contents based on their F_0 performance; however, it would be difficult to do the same for crosses. Nevertheless, one could focus on hybrids possessing high protein and oil contents in the F_1 generation for improving these traits. On the other hand, between-generation rank changes for crosses certainly affected rankings for combining ability values.

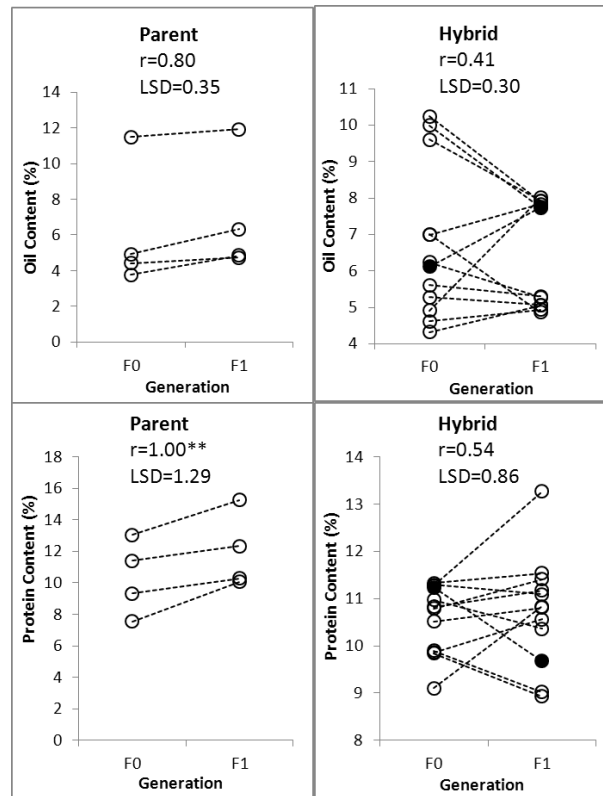


Figure 2. Means of parents and hybrids for oil and protein content in F_0 and F_1 generations.

The GCA effects were significant for both protein and oil content in all four Griffing's diallel methods. However, significance of SCA effects was variable across the four diallel methods for observed traits. The SCA effect was significant in Methods I and II for protein content, whereas for oil content, SCA was significant in Methods I, II and IV. The GCA \times generation interaction was significant in Method IV for both protein and oil contents (Table 4). However, SCA \times generation interaction was significant in all four diallel methods for both traits. These results revealed that GCA estimations were less affected by generation, whereas SCA effects were modified by generation effect. For protein content, REC, MAT and NMAT effects were not significantly affected by generations (Table 4). However, for oil content, these estimations were significantly affected by generations (Table 4).

Table 4. Mean squares from diallel analysis based on Griffing's Methods I through IV for oil content (%) and protein content (%).

Source of variation	df	Oil content				Protein content			
		Method I	Method II	Method III	Method IV	Method I	Method II	Method III	Method IV
GCA†	3	112.7**	110.4**	112.8**	46.6**	43.9**	47.1**	43.9**	3.80**
SCA‡	2	1.31**	0.69**	0.19	0.57**	2.14**	2.43**	0.21	0.24
REC§	3	6.95**	-	6.95**	-	1.09	-	1.09	-
MAT¶	3	13.4**	-	13.4**	-	1.86*	-	1.86*	-
NMAT#	6	0.55**	-	0.55**	-	0.31	-	0.31	-
GCA × G††	3	0.11	0.03	0.11	4.17**	1.45	1.16	1.45	1.88*
SCA × G	2	1.69**	1.80**	0.59**	0.48**	3.83**	3.93**	2.40*	2.20*
REC × G	3	7.24**	-	7.24**	-	0.70	-	0.70	-
MAT × G	3	13.9**	-	13.9**	-	0.60	-	0.60	-
NMAT × G	6	0.57**	-	0.57**	-	0.80	-	0.80	-

* ** Significant at the 0.05 and 0.01 probability level, respectively.

†GCA: General combining ability.

‡SCA: Specific combining ability.

§REC = Reciprocal effect.

¶MAT = Maternal effect.

#NMAT = Non-maternal effect.

††G = Generations.

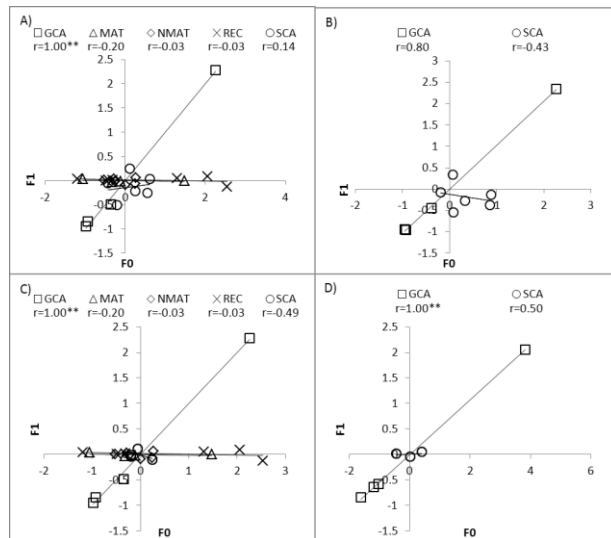


Figure 3. Relationships between genetic estimations in different generations for oil content determined via Griffing's Diallel Method I (A), Method II (B), Method III (C) and Method IV (D).

Genetic estimations for oil content via Griffing's methods are shown in Figure 3. The GCA estimations via all four diallel methods showed a perfect linear relationship between F_0 and F_1 generations ($r = 1.00$, $p < 0.01$). Correlation values for MAT, NMAT and REC effects were found to be equal in Method I and Method III. This would be expected because both Method I and Method III involved reciprocal F_1 crosses (Table 2). However, relationships between SCA values for F_0 and F_1 generations differed across diallel methods. For oil content, correlations between generations for SCA values in Method I, Method II, Method III and Method IV were 0.14, -0.43, -0.49 and 0.50, respectively (Figure 3). These results showed that GCA values could be evaluated based on F_0 analysis for oil content in all four methods, whereas SCA values could not be. Hybrids could be partially evaluated based on F_0 analysis using Methods II, III and IV. However, caution must be exercised, as the correlation coefficients were relatively small for these three methods; relationships explained only a small proportion of total variation ($R^2=0.18$ for Method II, $R^2=0.24$ for Method III, and $R^2=0.25$ for Method IV). The ranks of parents and crosses based on their combining abilities and IPE and SIPE estimations in F_0 and F_1 generations are summarized in Table 5. Genotypic ranks for GCA values were identical (IHO>OPV>Q2>PR) in Method I and Method III for oil content; whereas genotypic ranks differed in Method II and IPE estimations. Some crosses [(IHO \times Q2) = (PR \times OPV) and (IHO \times PR) = (PR \times Q2)] had identical SCA estimates for oil content in Method IV. This case resulted in fewer visible points (3 points) than expected (6 points) (see Figure 3). Only two crosses (OPV \times IHO and Q2 \times IHO) had same rank in F_0 and F_1 generation based on their SIPE estimations for oil content (Table 5). For protein content, correlations between genetic estimates showed differences according to the estimation method used (Figure 4). Method I and Method III gave identical rank correlations between F_0 and F_1 generations for GCA, NMAT and REC estimates for both traits. Rank correlation for GCA estimates between generations was lower for protein content than for oil content in Method IV. Rankings of the hybrid combinations based on their SCA values were negatively correlated for protein content in all four diallel methods. For protein content, Methods I, II, III, and IPE had identical results (IHO>OPV>PR>Q2) for parental ranks (Table 5). Only one cross (Q2 \times PR) had the same rank in different generations relative to SCA. The SIPE estimations of crosses between generations had completely different rankings for protein content (Table 5).

The GCA effects are related to additive gene action, whereas SCA effects are related to non-additive gene action (SPRAGUE and TATUM, 1942). The GCA estimations were less affected than SCA values by the generations for both oil and protein content in this study. The same rankings of parental lines were observed for oil content based on their GCA values for Griffing's Methods I, II, and III. The GCA values were identical for protein content in Method I and Method III only. For oil content, evaluation of parental lines based on their GCA values in F_0 generation would permit prediction of their GCA values in the F_1 generation. We may partly attribute this finding to specialty characteristics of parents used in the current study. We used a high-oil parent to generate our diallel set and inclusion of specialty maize in experimental material would affect genetic estimations and/or their relationships between different generations. Our results revealed that use of genotypes having different biochemical characteristics could enable one to observe/measure the pollen effect in studied material. Inclusion of a specialty parent in a diallel set could strengthen the relationships between GCA estimations in F_0 and F_1 generations. If someone wanted to utilize this relationship in their own study, they would need to use specialty maize having different characteristics relative to their target traits. The relationship between F_0 and F_1 generations for SCA effects was weak to moderate for oil content.

Table 5. Rankings of genotypes based on general combining ability (GCA), specific combining ability (SCA) values and their individual pollen effect (IPE) and specific pollen effects (SIPE) in F_0 and F_1 generations (F_0/F_1) for oil content (%) and protein content (%) using Griffing's diallel methods I through IV.

	Oil content				
	Method I	Method II	Method III	Method IV	IPE&SIPE
IHO	1/1†	1/1	1/1	1/1	1/1
OPV	2/2	2/2	2/2	3/3	3/2
PR	4/4	3/4	4/4	4/4	2/4
Q2	3/3	4/3	3/3	2/2	4/3
IHO×OPV	10/8	6/2	6/1	1/1	12/10
IHO×PR	8/12	4/6	8/8	5/3	11/12
IHO×Q2	6/10	2/5	4/10	3/5	10/11
OPV×IHO	3/3	NE‡	3/4	NE	4/4
OPV×PR	12/4	NE	12/5	NE	3/9
OPV×Q2	4/5	1/3	6/1	1/1	6/8
PR×IHO	1/9	NE	1/12	NE	7/1
PR×OPV	5/11	3/4	4/10	3/5	8/7
PR×Q2	7/1	5/1	8/8	5/3	9/5
Q2×IHO	2/2	NE	2/3	NE	2/2
Q2×OPV	9/6	NE	10/6	NE	1/4
Q2×PR	11/7	NE	11/7	NE	5/6

	Protein content				
	Method I	Method II	Method III	Method IV	IPE&SIPE
IHO	1/1	1/1	1/1	1/2	1/1
OPV	2/2	2/2	2/2	3/1	2/2
PR	3/3	3/3	3/3	2/3	3/3
Q2	4/4	4/4	4/4	4/4	4/4
IHO×OPV	10/7	4/3	10/1	5/1	11/10
IHO×PR	12/9	6/5	5/6	3/5	10/11
IHO×Q2	1/12	2/6	1/9	1/3	9/12
OPV×IHO	8/11	NE	8/12	NE	7/3
OPV×PR	7/1	NE	7/3	NE	8/9
OPV×Q2	6/2	5/1	10/1	5/1	12/8
PR×IHO	9/6	NE	9/8	NE	4/1
PR×OPV	3/5	3/2	1/9	1/3	5/4
PR×Q2	2/8	1/4	5/6	3/5	6/7
Q2×IHO	5/10	NE	4/11	NE	1/2
Q2×OPV	11/3	NE	12/4	NE	2/5
Q2×PR	4/4	NE	3/5	NE	3/6

†Number on left of/ indicates the F_0 rank; the number on right indicates F_1 rank.

‡NE: Non-estimable.

Interestingly, Method III gave a perfect but negative relationship between F_0 and F_1 generations ($r = -1.00$, $p < 0.001$) for protein content. The rankings of genotypes based on their NMAT, MAT and REC effects were also variable for oil and protein contents. For both traits, there was a weak correlation for REC effects between F_0 and F_1 generations. According to FAN *et al.* (2014), the REC effects in diallel analysis were estimated from NMAT and MAT effects. Thus, correlations calculated between different generations for REC effects may be expected to be similar to correlations calculated for NMAT and MAT effects. In our study, we observed a weak correlation between F_0 and F_1 generations for NMAT, MAT and REC effects for oil content (Figure 3a, Figure 3c). However, an inverse case was observed for protein content in our study. Although, positive correlations were observed between F_0 and F_1 generations for MAT ($r = 0.80$) and NMAT ($r = 0.37$) effects, the correlation observed for REC effects ($r = 0.03$) between F_0 and F_1 generations was much lower than expected (Figure 4a, Figure 4c). This finding showed that relationship between REC effects and its estimators (NMAT and MAT effects) varied for oil content and protein content.

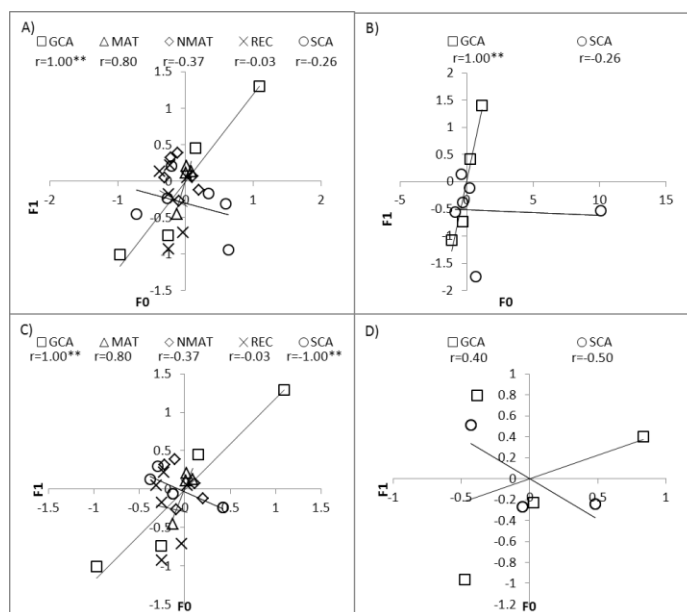


Figure 4. Relationships between genetic estimations in different generations for protein content determined via Griffing's Diallel Method I (A), Method II (B), Method III (C) and Method IV (D).

Mid-parent heterosis values for oil content (Figure 5a) had a much higher range in F_0 than in F_1 generation (heterosis values ranged from 35.6% to 50.2% in F_0 and -14.3% to 5.64% in F_1 generation). For protein content, MPH values varied from -11.8% to 17.2% in F_0 and from -23.5% to -3.32% in F_1 generation (Figure 5b). Four hybrids had similar values for both protein and oil contents in F_0 and F_1 generations. For protein content, most of the hybrids had lower MPH values in F_1 generation than in F_0 generation (Figure 5b). Conversely, two hybrids (PR×IHO and Q2×IHO) showed higher heterosis for oil content in F_1 generation than in F_0 generation (Figure 5a). Similarly, two hybrids (OPV×IHO and OPV×Q2) had higher values of heterosis in F_1

generation than in F₀ generation for protein content (Figure 5b). These results revealed that hybrids had lower values in the F₁ generation for both protein and oil content than their parental means in F₀ generation. Low rank correlations between generations for protein ($r = 0.24$) and oil content ($r = 0.10$) showed that the ranking of the crosses for MPH values changed significantly between generations.

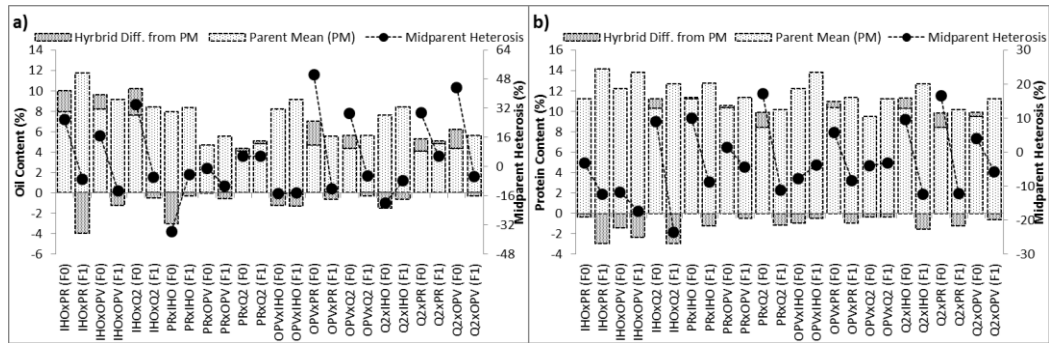


Figure 5. Heterosis values in F₀ and F₁ generations for oil content and protein content.

Heterosis is an important genetic estimator for evaluating hybrid performances in breeding experiments (XU and ZHU, 1999). Positive heterosis was observed for plant traits and grain yield in maize and it was related to dominant gene action (DRINIĆ *et al.*, 2012). Some previous studies found low or negative heterosis for kernel-quality traits (DRINIĆ *et al.*, 2012); whereas positive heterosis was reported in some others (OLIVEIRA *et al.*, 2006; KAHRIMAN *et al.*, 2015). These differences could be attributed to the specific characteristics of parental lines used in the above-mentioned studies. We observed positive heterosis in seven hybrids for oil content and in nine hybrids for protein content in the F₀ generation (Figure 5). The observed heterosis in F₀ generation was directly related to the pollen effects of male parents on the female parents. However, this effect disappeared in the F₁ generation and negative heterosis was observed for both traits. These results can be explained in two ways. Firstly, protein and oil contents are quantitatively inherited traits (HWANG *et al.*, 2014), which are affected by environmental factors. Heterosis was affected by environmental fluctuations, and the conventional estimation method of heterosis on the basis of data from parents only did not show the effect of these changes (XU and ZHU, 1999). We used conventional estimation method in this study, which is one of the reasons for the weak relationships between F₀ and F₁ generations in the expression of heterosis. Secondly, inbreeding depression had an effect on heterosis. BURTON and BROWNIE (2006) speculated that heterosis would be reduced in the case of overdominance because of the loss of heterozygosity and it would be reduced in the case of dominance because of the increasing number of unfavorable alleles in the homozygous state. We can explain the changes in heterosis between generations in this study as follows: F₀ heterosis was attributable to pollen effect on female parents, whereas F₁ heterosis was the result of combined environmental and genetic effects. This study revealed that F₀ heterosis for kernel-quality traits was higher than heterosis calculated for the F₁ generation. We could say that heterosis evaluation based on F₀ generation was not useful for making decisions on F₁ performances of genotypes, because rankings of crosses differed greatly between F₀ and F₁ generations for the observed traits. This implies that heterosis analysis

based on F_0 generation would not give accurate results for hybrid evaluation without conducting an evaluation trial of the F_1 generation.

Relationships between Pollen Effect and Genetic Estimations and Using Pollen Effect in Genetic Evaluations

A perfect correlation ($r = 1.00$, $p < 0.01$) was observed between individual pollen effect and GCA estimations in Method I, Method II and Method III for protein content for all possible pairs of generations (F_0 - F_0 , F_1 - F_1 and F_0 - F_1). However, relationships between pollen effect and GCA estimations for oil content were significant only for the F_1 generation (Table 6). These results indicated that parental evaluations could be made on the basis of estimates of individual pollen effect without computing GCA estimates for protein content. On the other hand, Griffing's diallel methods affected the relationship between pollen effect and GCA effects (Table 6). Also, relationships between individual pollen effects and combining ability values showed significant differences for the observed traits. Protein content showed stable relationships for both the generations, whereas IPE and GCA effects had variable relationships for oil content (Table 6). These results suggested that pollen effect could be successfully used in maize breeding experiments for protein content to help make decisions on parental value of the genotypes in both generations, but not for oil content. Specific individual pollen effect (SIPE) and SCA estimates in all four diallel methods showed moderate relationships for protein content in F_0 generation; however, Method I showed a strong relationship ($r = 0.89$, $p < 0.01$) for oil content (Table 6). We found weak correlations between pollen effect and certain genetic estimations (MAT, NMAT and REC). Significant relationships were observed between $SIPE_{F_0}$ and $SIPE_{F_1}$ for protein ($r = 0.74$, $p < 0.01$) and oil ($r = 0.62$, $p < 0.05$) content. A perfect relationship was observed between IPE_{F_0} and IPE_{F_1} estimations for protein content ($r=1.00$, $p < 0.01$) but not for oil content ($r=0.40$). This result showed that IPE in the F_0 generation was higher than the pollen parent effect in the F_1 generation for oil content, whereas pollen parent effect was higher than IPE for protein content. Specific individual pollen effects and MPH values showed a significant relationship for protein content in F_0 generation ($r = 0.61$, $p < 0.05$).

Investigations on individual pollen effects of parental lines enabled us to know how to utilize pollen effect in maize breeding experiments. Relationships between pollen effect estimates and genetic estimations within (F_0 - F_0 and F_1 - F_1) and between generations (F_0 - F_1) have significant implications. For protein content, individual pollen effect of parents (IPE) in the F_0 generation was significantly correlated with that obtained in the F_1 generation. However, oil content only had a low to moderate relationship. Specific individual pollen-effect estimations, i.e., special effect of any parental line on any of the female parents, showed pollen effect of parents in the F_0 generation to persist in the F_1 generation. We observed significant differences for relationships between pollen effect estimations and genetic effect estimations (GCA, SCA, REC, MAT and NMAT) by generations (F_0 - F_0 , F_1 - F_1 and F_0 - F_1) for protein and oil content. Evaluations based on IPE values of parental lines could be useful for selecting appropriate parental lines relative to their GCA effects. We could attribute this finding to the fact that estimation of pollen effect is part of GCA estimation. The GCA estimation in diallel analyses is via subtraction of parental values from the means of hybrid combinations (GRIFFING, 1956a; 1956b). Because of this, we found a strong relationship between IPE and GCA values in this study. Interestingly, we did not observe this relationship for oil content. This result showed that the relationship between IPE/SIPE and genetic estimations varied with the trait. Diallel methods also had important effects

on relationships between pollen effect and genetic estimations in this study. Method IV, which included F₁ hybrids only, was not highly satisfactory for utilizing pollen effect in breeding experiments.

Table 6. Relationships (correlation coefficients) between pollen effect and genetic estimations obtained from Griffing's Methods I, II, III, and IV, within and between generations for kernel oil content (%) and protein content (%).

Relations of Pollen Effect with Genetic Estimations									
Relation		Oil content			Protein content				
		Method I	Method II	Method III	Method IV	Method I	Method II	Method III	Method IV
†IPE _{F0}	§GCA _{F0}	0.40	0.80	0.40	0.20	1.00**	1.00**	1.00**	0.80
IPE _{F1}	GCA _{F1}	1.00**	1.00**	1.00**	0.80	1.00**	1.00**	1.00**	0.80
IPE _{F0}	GCA _{F1}	0.40	0.40	0.40	0.20	1.00**	1.00**	1.00**	0.80
IPE _{F0}	¶MAT _{F0}	0.40	NE¶¶	0.40	NE	-0.80	NE	-0.80	NE
IPE _{F1}	MAT _{F1}	-0.20	NE	-0.20	NE	-0.40	NE	-0.40	NE
IPE _{F0}	MAT _{F1}	0.80	NE	0.80	NE	-0.40	NE	-0.40	NE
‡SIPE _{F0}	#SCA _{F0}	0.94**	0.71	0.24	0.12	0.54	0.66	0.84*	0.84*
SIPE _{F1}	SCA _{F1}	0.66	0.77	0.00	0.00	0.71	0.71	0.00	0.00
SIPE _{F0}	SCA _{F1}	0.31	0.14	-0.12	-0.12	-0.26	-0.26	-0.84*	-0.60
SIPE _{F0}	††REC _{F0}	-0.26	NE	-0.26	NE	0.09	NE	0.09	NE
SIPE _{F1}	REC _{F1}	-0.03	NE	-0.03	NE	-0.71	NE	-0.71	NE
SIPE _{F0}	REC _{F1}	0.60	NE	0.60	NE	-0.20	NE	-0.20	NE
SIPE _{F0}	‡‡NMAT _{F0}	-0.37	NE	-0.37	NE	0.37	NE	0.37	NE
SIPE _{F1}	NMAT _{F1}	-0.60	NE	-0.60	NE	0.60	NE	0.60	NE
SIPE _{F0}	NMAT _{F1}	0.14	NE	0.14	NE	0.14	NE	0.14	NE
Relations of Pollen Effect with Heterosis									
		Oil content			Protein content				
SIPE _{F0}	§§MPH _{F0}	0.13				0.61*			
SIPE _{F1}	MPH _{F1}	0.20				0.48			
SIPE _{F0}	MPH _{F1}	0.01				0.07			
SIPE _{F0}	SIPE _{F1}	0.62*				0.74**			
IPE _{F0}	IPE _{F1}	0.40				1.00**			

*, ** Significant at the 0.05 and 0.01 probability level, respectively.

†IPE: Individual pollen effect.

‡SIPE: Specific individual pollen effect.

§GCA: General combining ability.

¶MAT = Maternal effect.

#SCA: Specific combining ability.

††REC = Reciprocal effect.

‡‡NMAT = Non-maternal effect.

§§MPH: Midparent heterosis.

¶¶NE: Non-estimable.

CONCLUSION

Our findings revealed that pollen effect could be used for evaluating performances of parental lines in kernel quality-related breeding experiments conducted via Griffing's diallel methods. The GCA estimations in F_0 generation for protein content showed a strong relationship with their estimations in F_1 generation. Method I and Method III were more appropriate for oil content than Method II and Method IV. If methods that allow making other genetic estimations based on GCA values could be developed, it would be possible to benefit from pollen effect for making decisions about selection of appropriate materials in breeding experiments. In conclusion, parental evaluation based on F_0 generation using pollen effect should be possible in experiments targeted at studying kernel-quality traits. Diallel methods used here had a significant effect on utilization of pollen effect for the investigated traits. Therefore, different experiments conducted with additional materials and kernel-quality traits should be useful in the future.

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EFEKAT POLENA (KSENIJA) ZA OCENU OPLEMENJIVAČKOG MATERIJALA KOD KUKURUZA

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Izvod

Efekat ksenija kod polena kukuruza (*Zea mays* L.) ima značajnu ulogu u promenama biohemijskog sastava zrna. Ciljevi ovog rada bili su: i) ocena efekta potomstva na određene genetičke parametre; ii) poređenje efekta opšte (GCA) i specifične kombinacione sposobnosti (SCA) dobijene Griffing-ovom dialelnom analizom između roditeljske (F₀) i F₁ generacije; iii) određivanje odnosa između efekta polena i genetičkih parametara; i iv) mogućnost iskorišćavanja efekta polena za popravku kvaliteta zrna (sadržaj proteina i ulja). Postavljena su dva eksperimenta: (F₀ u 2011 i F₁ u 2013) i ispitivan sadržaj proteina i ulja u zrnu. Izračunati su individualni efekti polena (IPE) i specifični individualni efekti polena (SIPE). Rezultati su pokazali da su varijanse kod početne (E) i generacije potomstva (G), kao i interakcija E × G, bile značajne za sadržaj i proteina i ulja, dok su promene u genetičkoj oceni između generacija bile visoko varijabilne. Znaci i rasponi efekta GCA bili su slični i visoko zavisni ($r > 0.80$), između F₀ i F₁ generacija za sva četiri modela dialela. Pored toga, efekti GCA bili su visoko korelisani sa ocenom IPE za sva četiri dialelna modela. Procene SCA između F₀ i F₁ generacije bili su umereno zavisne ($r = 0.50$) po metodu IV za sadržaj ulja i visoko zavisne ($r = -1.00$) po metodu III za sadržaj proteina. Analiza heterozisa pokazala je da se performanse hibrida u F₁ generaciji ne mogu proceniti na osnovu F₀ generacije. Individualni efekat polena između generacija pokazao je veću međuzavisnost za sadržaj proteina ($r = 1.00$) u odnosu na sadržaj ulja ($r = 0.40$). SIPE roditelja je takođe bio nešto viši za sadržaj proteina ($r = 0.74$) u odnosu na sadržaj ulja ($r = 0.62$). Zaključili smo da je direktna ili indirektna upotreba efekta ksenija kod polena moguća za ocenu roditelja, ali da nije pogodna za ocenu hibrida za sadržaj ulja i proteina u zrnu.

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