Does Genetic Distance of Parental Forms Affect Specific Combining Ability and Heterosis Effects in F_1 and F_2 of Spring Rape Diallel Cross?

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Summary

This paper aims to probe into relationships between genetic diversity of inbred lines, estimated through the Mahalanobis distance and the effects of specific combining ability (SCA) and heterosis. The SCA and heterosis effects were analyzed for nine quantitative traits of eight inbred lines and their diallel cross hybrids of spring rape. The field experiments (with F_1 and F_2 generations) were carried out in a partly balanced square design with four replications. The results show that the Mahalanobis distances for inbred lines and SCA effects of the hybrids were mostly positively correlated. However, the Mahalanobis distances were usually not related, or very weakly, with the heterosis effects. On this basis we conclude that it is possible that the genetic diversity of crossed lines does not have to affect heterosis effects in the hybrids derived from the crossing. Since, as far as could be determined, this is the first conclusion of this type in literature, it calls for further research to study this phenomenon.

Key words

genetic distance, heterosis, Mahalanobis distance, phenotypic correlations, SCA, spring rape

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Introduction

Within- and inter-species crossing is one of the most often used plant breeding methods that provide genetic variability. Gene segregation and genetic recombination in hybrid generations allow breeders to obtain desirable genotypes; crossing well-chosen parental forms can provide valuable hybrids. The application of suitable crossing schemes (for example diallelic crossing) allows performing genetic analysis of quantitative traits and recognition of different types of gene action into inbred line populations (Dobek et al., 1983).

The fundamental goal in breeding programs is proper selection of parental forms for simple as well as diallelic crossing. Such selection can be done in two ways: (i) parental forms are a random sample selected from a certain population about which one wants to make conclusions, or (ii) parental forms are chosen intentionally. In the second method, with which we deal in this paper, a selection criterion plays a crucial role.

One such criterion, the Mahalanobis distance (Mahalanobis, 1936), is based on multivariate analysis of variance (MANOVA). For winter rape, this method, along with canonical variate analysis, was used for example in the study of fatty acid composition by Kaczmarek et al. (2005). The Mahalanobis distance measures the diversity of genotypes in respect to the traits of interest. Generally, it is assumed that the larger the genetic distance between the crossing lines, the larger the heterosis and specific combining ability (SCA) effects should be. Such a phenomenon suggests that greater heterosis effects can be obtained from crossing lines that are genetically diverse. Such a situation was detected for example by Knaak and Ecke (1995), who studied the genetic distance between 64 spring rape cultivars on the basis of RFLP analysis. In their studies, the heterosis effect for seed yield was 16%, but correlation coefficient between heterosis effects in F_1 generation and genetic distance between parents was 0.72.

The aim of this paper was to estimate the correlation between the genetic diversity, estimated through the Mahalanobis distance, of parental forms in F_1 and F_2 generations of spring rape diallel crosses and the effects of specific combining ability and heterosis.

Model and estimators

The model of the observations y_{ij} for full diallel cross is (Griffing, 1956)

$$y_{ij}=\mu+g_i+g_j+s_{ij}+r_{ij}+e_{ij}, \tag{1}$$

where y_{ij} is the mean value for the genotype obtained by crossing the i-th and j-th parental forms, μ is the grand mean, g_i (g_j) is the effect of general combining ability of the i-th (j-th) parental line, s_{ij} is the effect of specific combining ability of the hybrid obtained by crossing the i-th and j-th parental lines, r_{ij} is the effect of the inverted crossing and e_{ij} is the random error, $i, j = 1, 2, \ldots, p$.

The estimators of parameters from the model (1), obtained by the ordinary least squares, have the form of (Griffing, 1956)

$$\begin{aligned}
\hat{\mu} &= \frac{1}{p^2}\sum_{i=1}^{p}\sum_{j=1}^{p} y_{ij}, \\
\hat{g}_i &= \frac{1}{2p}\left(\sum_{j=1}^{p} y_{ij} - \sum_{j=1}^{p} y_{ji}\right) - \hat{\mu}, \\
\hat{s}_{ij} &= \frac{1}{2}\left(y_{ij} + y_{ji}\right) - \hat{g}_i - \hat{g}_j - \hat{\mu}, \\
\hat{r}_{ij} &= \frac{1}{2}\left(y_{ij} - y_{ji}\right).
\end{aligned} \tag{2}$$

Occurring in hybrids of F_1 generation heterosis appears when the hybrid exceeds a better parent or the mean for both parental forms in terms of a particular trait of interest. Heterosis can be estimated either by comparison of the hybrid with the better parent, in terms of the trait of interest, or, as we did in this paper, by comparison of the hybrid with the trait mean over both parents

Mahalanobis distance

Usually a number of traits are observed. One of the tools that help in selection is the Mahalanobis distance calculated for each parental genotype and its hybrids. It assesses the genetic distance between two lines. The Mahalanobis distance d_{ij} between the i-th and j-th genotypes on the basis of t traits is defined as (Mahalanobis, 1936)

$$d_{ij} = \left[\left(\mathbf{y}_i - \mathbf{y}_j\right)'\mathbf{S}^{-1}\left(\mathbf{y}_i - \mathbf{y}_j\right)\right]^{1/2}, \tag{3}$$

where $\mathbf{y}_i$ and $\mathbf{y}_j$ denote the t-dimensional vectors of means of individual traits for the i-th and j-th parental forms, respectively, and $\mathbf{S}$ denotes the covariance matrix.

Example for spring rape

Plant material and methods

As plant material for the experiment we used 64 genotypes obtained by diallel cross of eight spring rape inbred lines (type I according to Griffing, 1956). The inbred lines, obtained from Strzelce Plant Breeding Station, represented wide genetic diversity of major traits of this species useful in breeding programs in Poland. The F_1 and F_2 (after F_1-selfing) hybrids were sowed at the field of the Experimental Station of the Poznań Agriculture University (currently Poznan University of Life Sciences) in Dłoń in 2002 and 2003. The field experiments were established in a partly balanced square design (Cochran and Cox, 1957) with four replications. In each of both experiments (F_1 and

F_2), there were 256 one-row plots, 1-meter long and with 0.5m between-row distance. During the vegetation period and after harvesting, the following quantitative traits were measured on 15 plants from each plot: diameter of root neck, plant height, number of branches per plant, distance to first branch, number of pods per plant, number of seeds per plant, 1000-seed weight, number of seeds per pod and seed yield per plant.

Based on the data, the effects of specific combining ability and heterosis effects for F_1 and F_2 generations in each year were estimated by the formula (2). In further analyses, mean values of these effects from both years of the experiment were considered. The Mahalanobis distances among the eight parental forms were calculated using the formula (3) on the basis of the quantitative traits for both years pooled.

The relationships between the criteria of hybrid breeding value, namely the SCA and heterosis effects, and the Mahalanobis distances of initial forms were assessed based on Pearson's correlation coefficient.

Results

The correlation coefficients between the Mahalanobis distances between parental lines and SCA and heterosis effects in the F_1 and F_2 generations are shown in Table 1. The SCA effects were significantly positively correlated with the Mahalanobis distances of particular parental inbred lines for all traits studied in generation F_1. Still significant in most of the cases, usually the corresponding correlation coefficients in generation F_2 were smaller. Nonetheless, heterosis effects were rather weakly correlated with the Mahalanobis distances, exceeding 0.50 only for plant height in generation F_1.

The example of the relations studied is presented in Figures 1-2, which represent, respectively, the Mahalanobis distances versus the SCA effects for plant height (positive correlation for both generations) and the Mahalanobis distances versus the heterosis effects (positive correlation in F_1 and very weak correlation in F_2).

Discussion

Genetic diversity of initial plant material is crucial at the beginning of a breeding program. Selection of suitable parents after correct and exact determination of gene action responsible for qualitative and quantitative traits can be performed on the basis of progeny of the parental forms. In our experiment, the results for eight parental lines of spring rape showed the positive correlation between the Mahalanobis distances and specific combining ability effects of the hybrids in both F_1 and F_2 generations. Because the significance of SCA effects indicates epistatic gene action in inheritance of quantitative traits analyzed, we can expect that epistatic effects of the hybrids should increase with increasing diversity of their parental forms. Lower correlation between the SCA effects and the Mahalanobis distances in the F_2 generation than that in the F_1 generation can be an evidence of the decreasing in the epistatic effects in the subsequent generations.

Interestingly, the Mahalanobis distances of parental lines and heterosis effects were rather unrelated; in several cases the correlation coefficient was significant, but its magnitude was rather negligible. Quite likely it is the result of a small number of significant heterosis effects obtained in this experiment (Łuczkiewicz et al., 2006). This in turn might be a consequence of high phenotypic diversity of parental lines with small genotypic diversity. Of course it is necessary to simultaneously perform the phenotypic and molecular genetic analyses, the molecular biology methods being a final tool for genotype selection for parental forms for recombinant and heterosis breeding. Ofori and Becker (2008) also noted small heterosis effects in crosses between European winter *B. rapa* cultivars. In Piętka et al.'s (2005) study, heterosis effects for glucosinolate contents in winter rape seeds significantly decreased in F_2 generation.

Table 1. Correlation coefficients between the Mahalanobis distances and the SCA and heterosis effects in F_1 and F_2 generations of spring rape

Effect	Diameter of root neck	Plant height	No. of branches per plant	Distance to first branch	No. of pods per plant	No. of seeds/plant	No. of seeds per pod	1000-seed weight	Seed yield/plant
				F_1 generation					
SCA	0.53***	0.76***	0.55***	0.35*	0.64***	0.68***	0.56***	0.70***	0.67***
Heterosis	0.03	0.62***	0.30*	0.27*	0.00	–0.09	0.09	0.10	0.13
				F_2 generation					
SCA	0.33*	0.60***	0.44**	0.39*	0.45**	0.35*	0.22	0.51***	0.33*
Heterosis	–0.13	0.30*	0.12	0.37**	0.06	0.04	0.24	0.19	0.03

*, **, *** significant at α=0.05, α=0.01 and α=0.001, respectively

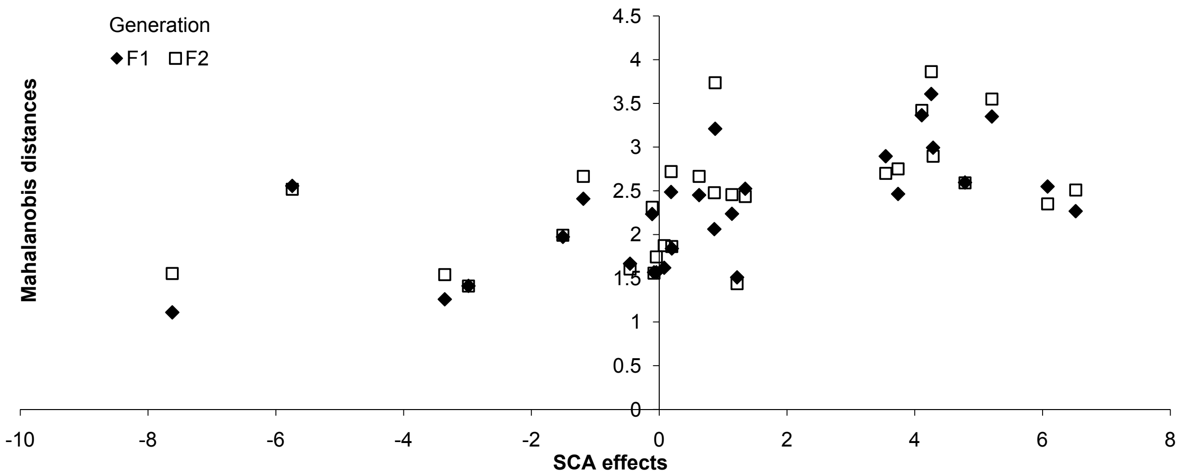

Figure 1. The Mahalanobis distances and SCA effects for plant height in F_1 and F_2 generations

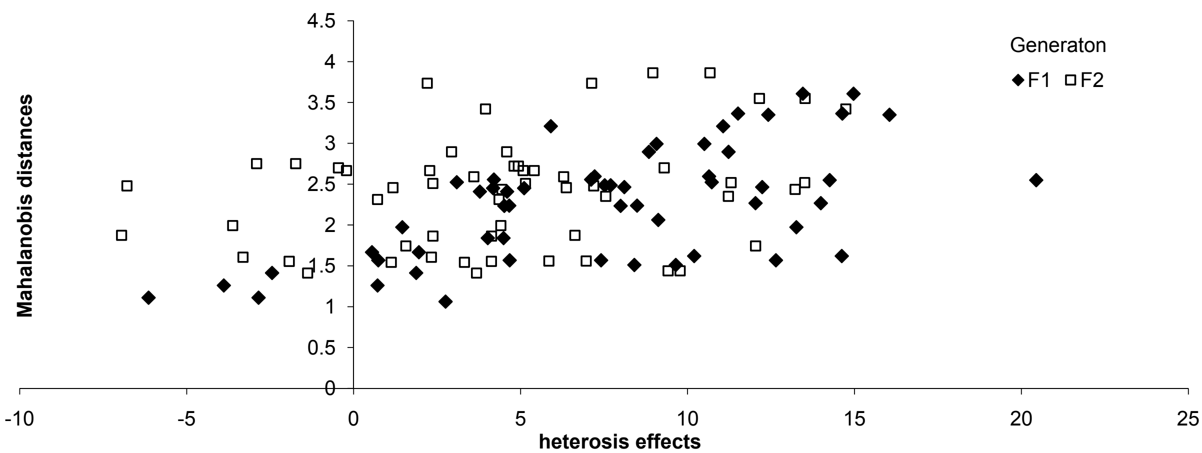

Figure 2. The Mahalanobis distances and heterosis effects for plant height in F_1 and F_2 generations

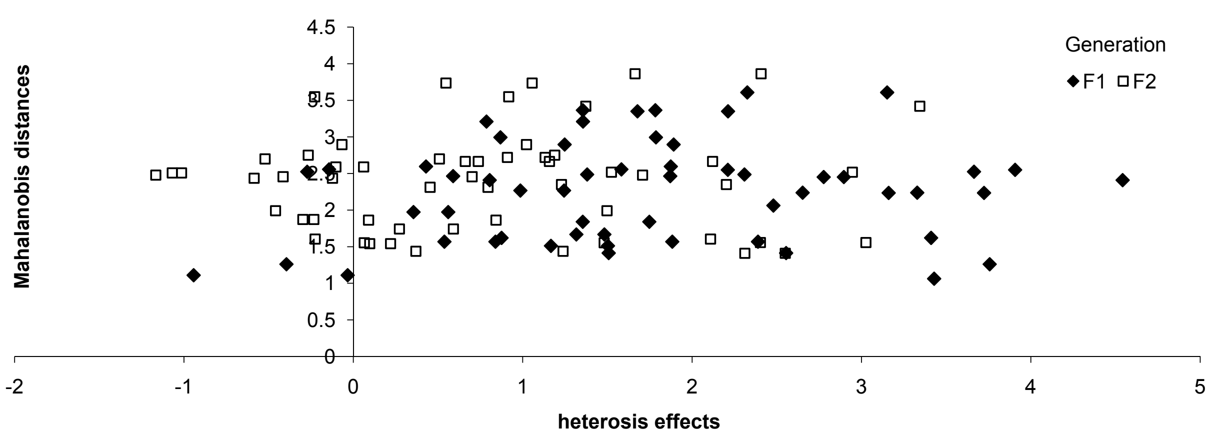

Figure 3. The Mahalanobis distances and heterosis effects for seed yield per plant in F_1 and F_2 generations

Yet the correlations between the heterosis effects and the Mahalanobis distances in both F_1 and F_2 generations were so small and non-important may seem surprising because it suggests that two lines that are genetically diverse may provide similar heterosis as two lines that are genetically similar. This is easily seen from Figures 2 (for plant height) and especially Figure 3 (for seed yield per plant). We were surprised indeed to see this result, and have never come across any other source that would suggest such a phenomenon to that extent. For example, if we take seed yield per plant, of course the most important trait for plant breeders and producers, we see that the heterosis effect is practically independent of the genetic distance of the parental lines (see Table 1 and Figure 3). Hence, should spring rape breeders at all pay attention to the genetic diversity of lines taken to the cross? Or, maybe, even genetically non-distant lines can be taken with no actual risk that heterosis will be noticeably smaller? Is heterosis indeed independent of the genetic distance of parental lines?

Our study suggests the three 'yes' answers to these three questions. Yet we are aware that our analysis is the first that leads such conclusions, and as such is not sufficient to give the definite 'yes' answers. But it is sufficient to suggest that the genetic diversity of the lines used in crossing does not necessarily have to affect heterosis effects in the hybrids derived from the crossing. Such line of research should be taken up to probe into this phenomenon, potentially interesting for plant breeders of spring rape, and also of other crop plant species.

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