

Note

Impact of Interpopulation Divergence on Additive and Dominance Variance in Hybrid Populations

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ABSTRACT

We present a theoretical proof that the ratio of the dominance *vs.* the additive variance decreases with increasing genetic divergence between two populations. While the dominance variance is the major component of the variance due to specific combining ability (σ_{SCA}^2), the additive variance is the major component of the variance due to general combining ability (σ_{GCA}^2). Therefore, we conclude that interpopulation improvement becomes more efficient with divergent than with genetically similar heterotic groups, because performance of superior hybrids can be predicted on the basis of general combining ability effects.

AN increasing number of crops as well as animal populations are improved by using interpopulation recurrent selection schemes. Interpopulation selection entails subdivision of the germplasm into at least two populations denoted as heterotic groups (MELCHINGER and GUMBER 1998). Genetic variation is generated in each breeding cycle within each heterotic group but progenies are evaluated for performance of testcrosses with genotypes from the opposite heterotic group (HALLAUER and MIRANDA 1988).

For establishment of heterotic groups, two approaches have been outlined in the literature. On the basis of results of a simulation study, CRESS (1967) suggested combining all genetic materials into one synthetic population. Heterotic groups are subsequently established by two random samples of genotypes from this synthetic. The work of CRESS (1967) focused mainly on maximum yield potential, which cannot be reached in a breeding scheme with two separate groups if the favorable alleles are absent in one of them, assuming a degree of dominance smaller than one. However, it is questionable whether maximum yield potential is a suitable criterion to evaluate selection strategies for short- and medium-term breeding programs.

Alternatively, MELCHINGER (1999) suggested starting with genetically divergent populations as heterotic groups. This approach has the following advantages: (1) maximum exploitation of heterosis and hybrid performance

from the very beginning and (2) a lower ratio of dominance (σ_D^2) *vs.* additive variance (σ_A^2). While the validity of the first point was demonstrated on the basis of quantitative genetic theory (FALCONER and MACKAY 1996) and experimental data (MELCHINGER 1999), a theoretical proof of the latter claim is still missing. Our objective was to examine the influence of genetic divergence between heterotic groups on the absolute size of σ_D^2 and σ_A^2 as well as their ratio, on the basis of quantitative genetic theory.

Theory: Assume two different base populations π_1 and π_2 with two alleles and linkage equilibrium among the loci in the base populations. For the following considerations we assume a one-locus model, where $p_{\pi_1} \in [0, 1]$ and $p_{\pi_2} \in [0, 1]$ stand for the frequency of the favorable allele in the base populations π_1 and π_2 . In addition, a and d refer to the additive and dominance effects (FALCONER and MACKAY 1996). For the hybrid population $\pi_1 \times \pi_2$, σ_A^2 and σ_D^2 are

$$\sigma_A^2 = p_{\pi_1}(1 - p_{\pi_1})[a - (2p_{\pi_2} - 1)d]^2 + p_{\pi_2}(1 - p_{\pi_2})[a - (2p_{\pi_1} - 1)d]^2, \quad (1)$$

$$\sigma_D^2 = 4d^2 p_{\pi_1} p_{\pi_2} (1 - p_{\pi_1})(1 - p_{\pi_2}) \quad (2)$$

(GRIFFING 1962; SCHNELL 1965).

Assume that both populations π_1 and π_2 are combined into one synthetic, which is randomly intermated for several generations so that linkage equilibrium is reached. Following CRESS (1967), two populations are subsequently established by random samples of genotypes

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from this synthetic. Under the assumption of an infinite population size, the variances

$$\sigma_{A^*}^2 = 2\bar{p}(1 - \bar{p})[a - (2\bar{p} - 1)d]^2, \quad (3)$$

$$\sigma_{D^*}^2 = 4d^2\bar{p}^2(1 - \bar{p})^2 \quad (4)$$

are obtained, with $\bar{p} = (p_{\pi 1} + p_{\pi 2})/2$.

There are parameter values, *e.g.*, $\{a = 0.25, d = 0.5, p_{\pi 1} = 0.2, p_{\pi 2} = 1\}$ for which $\sigma_{A^*}^2 \geq \sigma_A^2$ and others, *e.g.*, $\{a = 0.25, d = 0.5, p_{\pi 1} = 0.2, p_{\pi 2} = 0.8\}$ for which $\sigma_{A^*}^2 \leq \sigma_A^2$. Thus, neither $\sigma_{A^*}^2 \leq \sigma_A^2$ generally holds nor the opposite applies. However, we prove in the following that (1)

$$\sigma_{D^*}^2 \geq \sigma_D^2$$

and (2)

$$\frac{\sigma_{D^*}^2}{\sigma_{A^*}^2} \geq \frac{\sigma_D^2}{\sigma_A^2}$$

for arbitrary parameter values.

Proof of inequality 1: Let $\theta = (p_{\pi 1} - p_{\pi 2})/2$. Then $\sigma_{D^*}^2 \geq \sigma_D^2$ is equivalent to $4d^2\bar{p}^2(1 - \bar{p})^2 \geq 4d^2(\bar{p} + \theta)(\bar{p} - \theta)(1 - \bar{p} + \theta)(1 - \bar{p} - \theta)$ or $\bar{p}^2(1 - \bar{p})^2 \geq (\bar{p}^2 - \theta^2)((1 - \bar{p})^2 - \theta^2)$. Thus, for all $d, p_{\pi 1}$, and $p_{\pi 2}$, $\sigma_{D^*}^2 \geq \sigma_D^2$ with equality if $\theta^2 = 0$, *i.e.*, if $p_{\pi 1} = p_{\pi 2}$.

Proof of inequality 2: $\sigma_{D^*}^2/\sigma_{A^*}^2 \geq \sigma_D^2/\sigma_A^2$ is equivalent to

$$F(a, d, p_{\pi 1}, p_{\pi 2}) = [2(1 - p_{\pi 1} - p_{\pi 2})^2 + p_{\pi 1}(1 - p_{\pi 1}) + p_{\pi 2}(1 - p_{\pi 2})](a + d)^2 - 4adp_{\pi 1}p_{\pi 2}(p_{\pi 1} + p_{\pi 2}) \geq 0$$

(see APPENDIX A).

Let $p_{\pi 1}$ and $p_{\pi 2}$ be fixed but otherwise arbitrarily chosen constants. For the moment, we assume that $0 < p_{\pi 1} < 1$ and $0 < p_{\pi 2} < 1$. Then F gives rise to the definition of the following family of functions:

$$F_{p_{\pi 1}, p_{\pi 2}}(a, d) = F(a, d, p_{\pi 1}, p_{\pi 2}).$$

It can be shown (APPENDIX B) that each of these functions has only one critical point and this is $(a_0, d_0) = (0, 0)$. Since the Hessian matrix (see APPENDIX B) of $F_{p_{\pi 1}, p_{\pi 2}}$ at the critical point is positive definite (due to positive eigenvalues), its determinant, $\det(H(F_{p_{\pi 1}, p_{\pi 2}}))$, is also positive. Thus, $F_{p_{\pi 1}, p_{\pi 2}}$ has a local minimum at $(0, 0)$ (PRICE 1984). Moreover, since the Hessian matrix is positive definite at *any* point (a, d) , the function $F_{p_{\pi 1}, p_{\pi 2}}$ is convex and $(0, 0)$ is its global minimum. As $F_{p_{\pi 1}, p_{\pi 2}}(0, 0) = 0$, it follows that $\sigma_{D^*}^2/\sigma_{A^*}^2 \geq \sigma_D^2/\sigma_A^2$.

It remains to be proved that $\sigma_{D^*}^2/\sigma_{A^*}^2 \geq \sigma_D^2/\sigma_A^2$ if one of the alleles is fixed. Owing to the symmetric structure of $F(a, d, p_{\pi 1}, p_{\pi 2})$ with respect to $p_{\pi 1}$ and $p_{\pi 2}$, it suffices to show that $F(a, d, p_{\pi 1}, p_{\pi 2}) \geq 0$ if $p_{\pi 1} = 0$ and $p_{\pi 1} = 1$. The assertion immediately results from $F(a, d, p_{\pi 1} = 0, p_{\pi 2}) = (1 - p_{\pi 2})(2 - p_{\pi 2})(a + d)^2 \geq 0$ and $F(a, d, p_{\pi 1} = 1, p_{\pi 2}) = p_{\pi 2}(1 + p_{\pi 2})(a - d)^2 \geq 0$. This completes the proof.

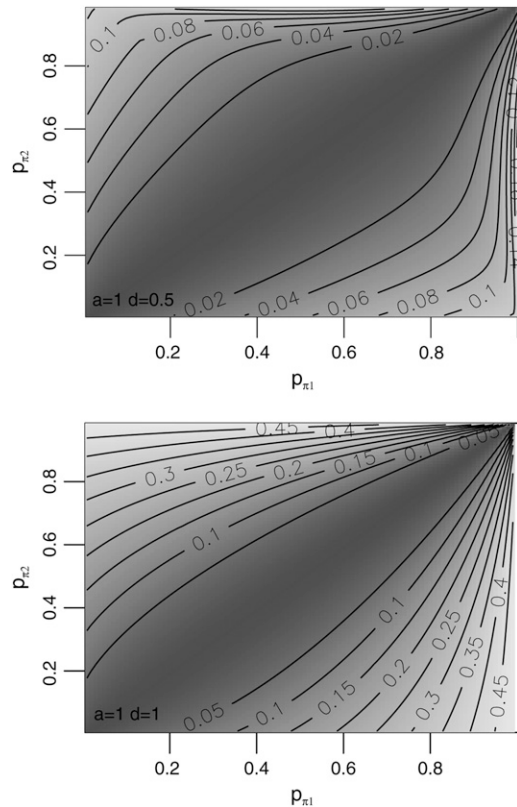


FIGURE 1.—Difference $\sigma_{D^*}^2/\sigma_{A^*}^2 - \sigma_D^2/\sigma_A^2$, where σ_D^2 and σ_A^2 denote the dominance and additive variance for the strategy of divergent heterotic groups, and $\sigma_{D^*}^2$ and $\sigma_{A^*}^2$ refer to the dominance and additive variance for the strategy of sampling the heterotic groups out of one synthetic established using both heterotic groups. The frequencies of the favorable alleles in the divergent populations $\pi 1$ and $\pi 2$ are denoted as $p_{\pi 1}$ and $p_{\pi 2}$, and a and d refer to the additive and dominance effects.

Discussion: Under the assumption (1) that the parents used for producing hybrids are homzygous inbred lines, *i.e.*, the inbreeding coefficients $F_{\pi 1} = F_{\pi 2} = 1$, and (2) of absence of epistasis, σ_A^2 equals the variance due to general combining ability (σ_{GCA}^2), and σ_D^2 equals the variance due to specific combining ability (σ_{SCA}^2) (WRICKE and WEBER 1986). The ratio of $\sigma_{SCA}^2/\sigma_{GCA}^2$ is of central importance for predicting hybrid performance from GCA effects (MELCHINGER *et al.* 1987). With predominance of σ_{GCA}^2 over σ_{SCA}^2 , early testing becomes more effective and superior hybrids can be identified and selected mainly on the basis of their prediction from GCA effects. Therefore, the results of our quantitative genetic investigations show that in the absence of epistasis divergent heterotic groups lead to a predominance of σ_{GCA}^2 over σ_{SCA}^2 . These theoretical findings are in accordance with experimental data of genetically divergent heterotic groups in various crops such as maize (SCHRAG *et al.* 2006), rye (MIEDANER and GEIGER 1996), and sunflower (KAYA 2005) and explain the high prediction accuracy of hybrid performance based on GCA effects.

The assumption of absence of epistasis is critical because results from model organisms suggest that epistatic interactions among QTL also contribute substantially to the genetic variation in complex traits (CARLBORG and HALEY 2004). For homozygous inbreds and epistatic interactions involving two loci, $\sigma_{GCA}^2 = \sigma_A^2 + \sigma_{AA}^2/2$ and $\sigma_{SCA}^2 = \sigma_D^2 + \sigma_{AA}^2/2 + \sigma_{AD}^2 + \sigma_{DD}^2$, where σ_{AA}^2 , σ_{AD}^2 , and σ_{DD}^2 refer to variance due to additive \times additive, additive \times dominance, and dominance \times dominance interactions (LYNCH and WALSH 1998). As $\sigma_{AA}^2/2$ is a component of σ_{SCA}^2 and σ_{GCA}^2 , its influence on $\sigma_{SCA}^2/\sigma_{GCA}^2$ is expected to be low. Nevertheless, the remaining epistatic variance components may have an influence on the ratio of $\sigma_{SCA}^2/\sigma_{GCA}^2$ but information on their relative importance is limited.

The advantage of divergent populations is illustrated on the basis of numerical examples assuming different degrees of dominance (Figure 1). The advantage of divergent heterotic groups is pronounced with (1) an enhanced genetic divergence between both populations π_1 and π_2 , (2) an increased degree of dominance, and (3) higher frequencies of the favorable alleles. Considering the slow changes in allele frequencies in breeding programs due to selection (FALCONER and MACKAY 1996), it takes a long time to recover a favorable ratio of $\sigma_{SCA}^2/\sigma_{GCA}^2$ that increases by intermating genetic divergent heterotic groups. Consequently, suitable choice of parental populations for interpopulation improvement is of fundamental importance to warrant a high short- and medium-term selection gain.

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APPENDIX A

$\sigma_{D^*}^2/\sigma_{A^*}^2 \geq \sigma_D^2/\sigma_A^2$ is equivalent to $\sigma_A^2\sigma_{D^*}^2 - \sigma_{A^*}^2\sigma_D^2 \geq 0$. The left-hand side can be simplified to

$$\begin{aligned} \sigma_A^2\sigma_{D^*}^2 - \sigma_{A^*}^2\sigma_D^2 &= \{p_{\pi_1}(1 - p_{\pi_1})[a - (2p_{\pi_2} - 1)d]^2 + p_{\pi_2}(1 - p_{\pi_2})[a - (2p_{\pi_1} - 1)d]^2\} \\ &\quad \times 4d^2\bar{p}^2(1 - \bar{p}^2) - 2\bar{p}(1 - \bar{p})[a - (2\bar{p} - 1)d]^2 4d^2 p_{\pi_1} p_{\pi_2} (1 - p_{\pi_1})(1 - p_{\pi_2}) \\ &= \frac{1}{4}d^2(p_{\pi_1} + p_{\pi_2})(2 - p_{\pi_1} - p_{\pi_2})(p_{\pi_1} - p_{\pi_2})^2 F(a, d, p_{\pi_1}, p_{\pi_2}) \end{aligned}$$

with

$$\begin{aligned} F(a, d, p_{\pi_1}, p_{\pi_2}) &= [2(1 - p_{\pi_1} - p_{\pi_2})^2 + p_{\pi_1}(1 - p_{\pi_1}) + p_{\pi_2}(1 - p_{\pi_2})](a + d)^2 \\ &\quad - 4adp_{\pi_1}p_{\pi_2}(p_{\pi_1} + p_{\pi_2}). \end{aligned}$$

The inequality $\sigma_A^2\sigma_{D^*}^2 - \sigma_{A^*}^2\sigma_D^2 \geq 0$ is therefore equivalent to $F(a, d, p_{\pi_1}, p_{\pi_2}) \geq 0$.

APPENDIX B

The critical value ($a_0 d_0$) of $F_{p_{\pi_1}, p_{\pi_2}}$ is obtained by solving the system of linear equations

$$\frac{\partial F_{\pi_1, \pi_2}}{\partial a} = 2[2(1 - p_{\pi_1} - p_{\pi_2})^2 + p_{\pi_1}(1 - p_{\pi_1}) + p_{\pi_2}(1 - p_{\pi_2})](a + d) - 4dp_{\pi_1}p_{\pi_2}(p_{\pi_1} + p_{\pi_2}) = 0$$

$$\frac{\partial F_{\pi_1, \pi_2}}{\partial d} = 2[2(1 - p_{\pi_1} - p_{\pi_2})^2 + p_{\pi_1}(1 - p_{\pi_1}) + p_{\pi_2}(1 - p_{\pi_2})](a + d) - 4ap_{\pi_1}p_{\pi_2}(p_{\pi_1} + p_{\pi_2}) = 0,$$

leading to $(a_0, d_0) = (0, 0)$.

The Hessian matrix H of $F_{p_{\pi_1}, p_{\pi_2}}$ at any point (a, d) is of the form

$$H(F_{\pi_1 \pi_2}) = \begin{pmatrix} \frac{\partial^2 F_{\pi_1, \pi_2}}{\partial a^2} & \frac{\partial^2 F_{\pi_1, \pi_2}}{\partial a \partial d} \\ \frac{\partial^2 F_{\pi_1, \pi_2}}{\partial d \partial a} & \frac{\partial^2 F_{\pi_1, \pi_2}}{\partial d^2} \end{pmatrix}_{(a, d)}$$

with $\partial^2 F_{\pi_1, \pi_2} / \partial a^2 = \partial^2 F_{\pi_1, \pi_2} / \partial d^2 = 4(1 - p_{\pi_1} - p_{\pi_2})^2 + 2p_{\pi_1}(1 - p_{\pi_1}) + 2p_{\pi_2}(1 - p_{\pi_2})$ and $\partial^2 F_{\pi_1, \pi_2} / \partial a \partial d = \partial^2 F_{\pi_1, \pi_2} / \partial d \partial a = 4(1 - p_{\pi_1} - p_{\pi_2})^2 + 2p_{\pi_1}(1 - p_{\pi_1}) + 2p_{\pi_2}(1 - p_{\pi_2}) - 4p_{\pi_1}p_{\pi_2}(p_{\pi_1} + p_{\pi_2})$. Note that the Hessian matrix does not depend on a or d but only on the choice of p_{π_1} and p_{π_2} . $H(F_{\pi_1, \pi_1})$ is positive definite because both eigenvalues $\lambda_1 = 4p_{\pi_1}p_{\pi_2}(p_{\pi_1} + p_{\pi_2})$ and $\lambda_2 = 4(2 - p_{\pi_1} - p_{\pi_2})(1 - p_{\pi_1})(1 - p_{\pi_2})$ are positive, which ensures that its determinant $\det(H(F_{\pi_1, \pi_2})) = \lambda_1\lambda_2$ is also positive.