



A priori choice of hybrid parents in plants

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ABSTRACT. Plant breeding deals with high-yielding genotypes. However, how best to choose parents of these genotypes remains an unsolved question. Here, we focus on *a priori* choice based on parental distances by means of agronomic and molecular data. Despite numerous theoretical and empirical studies, *a priori* choice continues to be a controversial procedure. Both success and failure are commonly reported. We looked at these ambiguous results in order to investigate their possible causes. A total of 139 articles on genetic divergence were sampled to examine aspects such as type and number of markers utilized. We suggest that the mean number of 160, 281 and 25 for RAPD and RFLP markers, and SSR loci, respectively, which we found in these papers, should be increased for accurate analysis. A second sample composed of 54 articles was used to evaluate the divergence-heterosis association. Most of them (28) detected positive divergence-heterosis association, whereas 26 revealed negative or inconclusive results. We exam-

ined several causes that influence *a priori* choice positively and negatively.

Key words: *A priori* choice of hybrid parents, Morphological markers, Molecular markers, Plant species

INTRODUCTION

Plant breeding deals with high-yielding genotypes. However, how best to choose parents of these genotypes remains an unsolved question. Research on parent selection may be approached in two ways (Baenziger and Peterson, 1992): *a priori* and *a posteriori* choice. The former consists of selection methods based on *per se* parent performance, such as midparental value, divergence according to coefficient of parentage, character complementation, multivariate analysis and parental distances, least squares, parental complementation, and ideal genotype. In the latter, parents are evaluated on the basis of F_1 , F_2 data and advanced generations. A long period of time is necessary to choose parents in this way, especially in perennial plants. Here, we focused on *a priori* choice based on parental distances determined from agronomic and molecular data. Its predictive nature avoids the need for hundreds of crossings, as only predictively promising crosses are made and evaluated, saving labor, financial resources, materials, and time.

The *a priori* choice is based on the fact that heterosis is a relative measure of two generations - the parental and the progeny. For a given quantitative trait, the amount of heterosis following a cross between two populations is a function of the square of the difference of gene frequency between the populations and of the dominance deviations (Falconer, 1989). If the populations that are crossed do not differ in gene frequencies, there will be no heterosis. Likewise, loci without dominance cause neither inbreeding depression nor heterosis. Falconer (1989) argues that: i) the occurrence of heterosis is dependent on directional dominance and its absence is not sufficient grounds for concluding that the loci show no dominance; ii) the amount of heterosis is specific to each particular cross, and iii) for inbred lines, heterosis is the sum of the dominance deviations of those loci that have different alleles in the two lines.

When the divergence-heterosis association is found to be high, it is possible to use the divergence estimate as a solid criterion for parental selection and, subsequently, for the synthesis of heterotic hybrids, as argued by Dias and Resende (2001). The *a priori* choice was initially made based on morphological descriptors and further reinforced by data from molecular markers; this choice assumed that the divergence between any two parents expresses the allelic differences between them. Despite numerous theoretical and empirical studies, *a priori* choice continues to be a controversial procedure. Success and failure are common results in these studies (Dias et al., 2003). We examined these ambiguous results in order to investigate the causes.

MATERIAL AND METHODS

First, a total of 139 articles (Table 1), dealing with genetic divergence, were sampled to investigate the causes of the ambiguous results. In spite of the limitations and difficulties inher-

ent to this type of sample, some of the aspects of this kind of study, such as type and number of markers, could be examined. Subsequently, a second sample was investigated; this time it was composed of 54 articles (Table 2), involving 21 plant species, to evaluate the divergence-heterosis association in particular.

RESULTS AND DISCUSSION

Genetic divergence

Genetic distance estimates were mostly based on morphological, biochemical (isoenzymes), and molecular markers [random amplified polymorphic DNA (RAPD), restriction fragment length polymorphism (RFLP), amplified fragment length polymorphism (AFLP), simple sequence repeats (SSR), and sequence-tagged site-polymerase chain reaction (STS-PCR)] (Table 1). Some of the articles also used pedigree information (relationship coefficient) separately, or in combination with other markers. In the measures of divergence, RAPD markers were most commonly used, comprising the largest number of species and reported papers (Table 1). This observation may be due to the fact that the RAPD technique (Williams et al., 1990) facilitates automation, and has a low operational cost, besides its simplicity, speed, and good degree of polymorphism, in addition to wide genome coverage. Such features mitigate its negative properties, such as low reproducibility and dominant heritage.

Table 1. Number of articles (N), plant species (S) and appraised average number of markers, loci or probes (n) and range (A) of sampled morphological, biochemical and molecular markers applied in divergence studies.

| | Morphological/ agronomic | Isoenzyme (loci) | RFLP | | RAPD | Microsatellite (SSR) | | AFLP | STS-PCR |
|---|-----------------------------|---------------------|---------|--------|--------|-------------------------|-------|---------|---------|
| | | | Markers | Probes | | Markers | Loci | | |
| N | 22 | 19 | 31 | | 78 | 22 | | 19 | 3 |
| S | 13 | 12 | 12 | | 68 | 17 | | 16 | 2 |
| n | 14.91 | 15.11 | 281.41 | 85.45 | 160.18 | 101.88 | 25.08 | 1294.12 | 235.67 |
| A | 5-34 | 7-31 | 47-1202 | 34-257 | 27-932 | 26-211 | 6-68 | 55-5094 | 93-505 |

RFLP markers are frequently used for estimating genetic diversity. These markers are co-dominant, reliable, and they have a high information content; however, this technique demands a considerable amount of good quality DNA, it is laborious, and it often requires the use of radioactive substances. The use of fluorescence, instead of radioactivity, with a well-equipped laboratory and good staff gives this system a further advantage. RFLP has the advantage of allowing the selection of probes that target desirable DNA sequences associated with specific yield or resistance traits. Some of the probes used in the studies that succeeded in associating genetic distance with hybrid prediction were cDNA clones. These advantages help explain why RFLP is the most commonly employed in research on genetic distance-heterosis associations (see Table 2).

When compared to other kinds of molecular markers, AFLP is promising, as it combines the specificity, resolution and sampling power of enzyme restriction, with the simplicity of PCR polymorphism. Furthermore, the large number of markers generated with this technique is

Table 2. Favorable and unfavorable association of divergence estimates based on morphological and molecular markers with heterosis in plant species.

| Reference | Genetic distance/marker | Crop or species | Divergence-heterosis association | |
|---|---|--|---|---|
| | | | Favorable | Inconclusive/unfavorable |
| Ramanujam et al. (1974) | Mahalanobis distance/ morphological | <i>Phaseolus aureus</i> | Positive association of genetic divergence-heterosis | |
| Srivastava and Arunachalam (1977) | Mahalanobis distance/ morphological | <i>triticale</i> | Association divergence-heterosis and clustering of divergent genetic groups | |
| Arunachalam et al. (1984) | Mahalanobis distance/ morphological | <i>Peanut</i> | Heterosis associated with moderate parental divergence | |
| Arunachalam and Bandyopadhyay (1984) | Mahalanobis distance/ morphological | <i>Peanut</i> and <i>Brassica campestris</i> | Positive association for the limits of divergence and heterosis | |
| Ghaderi et al. (1984) | Mahalanobis distance/ morphological | <i>Phaseolus vulgaris</i> and <i>Vicia faba</i> | Positive and significant correlations | |
| Shamsuddin (1985) | Mahalanobis distance/ morphological | <i>Triticum</i> | Positive and significant association of heterosis and genetic divergence | |
| Frei et al. (1986) | Pedigree/alloenzymes | <i>Zea mays</i> | Yield and pedigree distance positive associations | Dependence on similar pedigree background with isoenzymes |
| Prasad and Singh (1986) | Mahalanobis distance/ morphological | <i>Zea mays</i> | Heterosis associated with moderate parental divergence | |
| Cowen and Frey (1987a) | Genealogical distance/ morphological | <i>Avena sativa</i> | Positive association of genealogical distance and genetic variance | Negative association of genealogical distance and diversity, significant as well as nonsignificant correlations |
| Cowen and Frey (1987b) | Three types of distance/ morphological | <i>Avena sativa</i> | | Inconsistent associations of genetic distance and transgressive segregants, heterosis and genetic variance |
| Lee et al. (1989) | RFLP | <i>Zea mays</i> | Significant correlation of genetic distance with grain yield and combining ability | |
| Smith and Smith (1989) | Morphological/ isoenzymes | <i>Zea mays</i> | | Lack of congruence of estimated kinship and non-accurate correlation between isoenzymes, pedigree and heterosis in estimating lineage relationship |

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Table 2. Continued

| Reference | Genetic distance/marker | Crop or species | Divergence-heterosis association | |
|---------------------------|---|---------------------|--|---|
| | | | Favorable | Inconclusive/unfavorable |
| Melchinger et al. (1990) | RFLP | <i>Zea mays</i> | Positive but small correlations of genetic distance with F_1 performance, specific combining ability and heterosis for yield and yield components. Consistent association of clusters based on genetic distance and pedigree | |
| Smith et al. (1990) | Pedigree/RFLP | <i>Zea mays</i> | Higher correlation for RFLP similarity and heterosis and grain yield | |
| Dudley et al. (1991) | RFLP and isoenzymes | <i>Zea mays</i> | Congruence of clustering analysis based on genetic distances and pedigree | Estimates not always correlated with production and no relationship of genetic distance and hybrid yield was observed |
| Bernardo (1992) | RFLP | Simulation study | Positive relationship based on simulation data | |
| Boppenmaier et al. (1992) | RFLP | <i>Zea mays</i> | Consistent association of RFLP-genetic distance clustering with pedigree | Absence of significant correlation of F_1 performance and genetic distance |
| Melchinger et al. (1992) | RFLP | <i>Zea mays</i> | Moderate, positive and significant correlation of genetic distance and F_1 performance. Consensus of cluster analysis based on genetic distance and pedigree | |
| Cruz et al. (1994) | Mahalanobis distance/morphological | <i>Zea mays</i> | Positive association divergence-heterosis for grain yield | |
| Gerdes and Tracy (1994) | Pedigree/RFLP | <i>Zea mays</i> | Positive correlations between pedigree and RFLP-distance clustering | Morphological markers and isoenzymes clustering did not agree with pedigree |
| Moser and Lee (1994) | Genealogical and multivariate distance/RFLP | <i>Avena sativa</i> | Positive association of RFLP genetic variance with genealogical distance | Heterosis and genetic variance prediction based on RFLP seemed not to be efficient |
| Zhang et al. (1994) | RFLP and microsatellites | <i>Oryza sativa</i> | Marker highly significant effects on yield on its component traits. Heterozygosity significantly correlated with performance and heterosis | |

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Table 2. Continued

| Reference | Genetic distance/marker | Crop or species | Divergence-heterosis association | |
|-----------------------------------|---|------------------------|--|--|
| | | | Favorable | Inconclusive/unfavorable |
| Ali et al. (1995) | Multivariate distance/ morphological | <i>Canola</i> | Positive and significant correlations | |
| Bar-Hen et al. (1995) | Isoenzymes | <i>Zea mays</i> | Positive relationship although dependent on genotype | |
| Martin et al. (1995) | Kinship coefficient/ STS-PCR | <i>Triticum</i> | Hybrid performance correlations with genetic distance and complement of the kinship, showing similar magnitude and direction | Estimates did not predicted hybrid performance |
| Diers et al. (1996) | RFLP | <i>Brassica napus</i> | Genetic distance and hybrid yield correlation | Estimates were not consistent in indicating the best crossings |
| Dubreuil et al. (1996) | Pedigree/RFLP | <i>Zea mays</i> | Significant correlation between pedigree and genetic distance | |
| Baril et al. (1997) | RAPD | <i>Eucalyptus</i> | Positive association of genetic distance and inter-specific hybrid performance | |
| Cerna et al. (1997) | RFLP and isoenzymes | <i>Glycine max</i> | Positive relationship between parental distance and yield components in their hybrids | Nonsignificant relationship |
| Dias and Kageyama (1997) | Mahalanobis distance/ yield components | <i>Theobroma cacao</i> | | |
| Helms et al. (1997) | RAPD | <i>Glycine max</i> | | Lack of correlation of kinship coefficient and genetic variance with RAPD genetic distance |
| Kisha et al. (1997) | Genealogical distance/ RFLP | <i>Glycine max</i> | Correlation of genetic distance and agronomic traits | Positive and negative genetic distance associations with genetic variance in different population groups |
| Lanza et al. (1997) | RAPD | <i>Zea mays</i> | | |
| Manjarrez-Sandoval et al. (1997a) | Kinship coefficient/ RFLP | <i>Glycine max</i> | Coefficient association with yield and correlation between coefficient and genetic similarity | |

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Table 2. Continued

| Reference | Genetic distance/marker | Crop or species | Divergence-heterosis association | |
|-----------------------------------|--|---------------------------|---|---|
| | | | Favorable | Inconclusive/unfavorable |
| Manjarrez-Sandoval et al. (1997b) | Kinship coefficient/ RFLP | <i>Zea mays</i> | Significant correlation between coefficient and genetic similarity in heterosis prediction | Limited correlation between estimates |
| Saghai Maroof et al. (1997) | RFLP and SSR | <i>Oryza sativa</i> | Significant genetic distance correlations with heterozygosity and hybrid performance | Estimates dependent on germplasm |
| Burkhamer et al. (1998) | Kinship coefficient/ STS-PCR and AFLP | <i>Triticum</i> | | Genetic distance estimates were not strong predictors for a variance of traits |
| Charcosset et al. (1998) | Isoenzymes and RFLP | <i>Zea mays</i> | Efficient models on prediction of specific combining ability and hybrid performance | |
| Chowdari et al. (1998) | RAPD and microsatellite | <i>Pennisetum glaucum</i> | | Genetic distance and heterosis correlation mostly nonsignificant |
| Fabrizius et al. (1998) | Kinship coefficient/ morphological | <i>Triticum</i> | | Lack of adequate explanation of F ₂ heterosis and genetic distance |
| Garcia et al. (1998) | Pedigree/RAPD and morphological | <i>Cucumis melo</i> | Relationship among distance matrixes based on RAPD, pedigree and morphological markers. Data suggesting suitable hybrid performance based on RAPD | |
| Perenzin et al. (1998) | Kinship coefficient/ RFLP and RAPD | <i>Triticum</i> | Correlation between genetic diversity and hybrid performance | Weak correlation estimates |
| Tenkouano et al. (1998) | Microsatellite and pedigree | <i>Musa</i> | | Hybrid performance nonrelated to similarity pedigree and microsatellite indexes |
| Bohn et al. (1999) | Kinship coefficient/ AFLP, RFLP and SSR | <i>Triticum</i> | Significant genetic similarity and co-ancestry coefficient correlations | Nonsignificant genetic variance estimated on genetic similarity |
| Joyce et al. (1999) | RAPD | <i>White clover</i> | | Genetic distance negatively related with heterosis |

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Table 2. Continued

| Reference | Genetic distance/marker | Crop or species | Divergence-heterosis association | |
|-------------------------|---------------------------|------------------------|---|---|
| | | | Favorable | Inconclusive/unfavorable |
| Kidwell et al. (1999) | RFLP | <i>Alfalfa</i> | | Lack of consistent effects of markers on selection for yield |
| Sant et al. (1999) | RAPD and microsatellite | <i>Chick-pea</i> | Positive heterosis values for most evaluated traits, and parental mean and Mahalanobis distance predicting hybrid performance | Significant non-linear relationship |
| Pandini et al. (2001) | Mahalanobis distance | <i>Glycine max</i> | | |
| Parentoni et al. (2001) | RAPD | <i>Zea mays</i> | Phylogeny obtained with RAPD agreed with pedigree data. Weak, positive and significant correlation between RAPD genetic distance and specific combining ability yield | |
| Kown et al. (2002a) | Pedigree/ RAPD and SSR | <i>Oryza sativa</i> | Genetic distance clustering agreeing with pedigree data | Nonsignificant genetic distance and F_1 performance correlations, with some exceptions. No correlation with heterosis, besides hybrid performance prediction dependent on germplasm |
| Kown et al. (2002b) | AFLP | <i>Oryza sativa</i> | | Nonsignificant distance correlation, with few exceptions. No correlation of genetic distance with heterosis was observed |
| Barbosa et al. (2003) | SSR and AFLP | <i>Zea mays</i> | Cluster analysis according to assignment for heterotic groups and significant genetic distance correlation with yield | |
| Dias et al. (2003) | Yield components/ RAPD | <i>Theobroma cacao</i> | Positive association divergence-heterosis for both yield components and RAPD markers | |
| Jordan et al. (2003) | RFLP | <i>Sorghum bicolor</i> | Significant correlation of genetic distance and yield, although weak for identifying superior hybrids | |

obvious from Table 1. However, it gives limited genetic information per locus, and it is a dominant marker, as is RAPD, from which it differs by a need for higher quality DNA and more protocol steps (Ferreira and Grattapaglia, 1998). On the other hand, microsatellites or SSR are the most polymorphic markers. SSR polymorphism is based on differences in simple repetitive sequences that are flanked by conserved borders; they are distributed all over the genome, making them the most suitable for paternity studies. It is important to bear in mind that the information content does not differ significantly among RFLP, AFLP and SSR, as argued by Bohn et al. (1999). For a detailed review of biochemical and molecular markers, see Ferreira and Grattapaglia (1998).

In search of the optimum number of bands, Tivang et al. (1995) observed that, regardless of the restriction enzyme used, the average number of polymorphic RFLP bands provided an equivalent amount of information, although 284 to 377 bands were necessary for genetic distance estimates for 37 inbred maize lines associated with a fixed 10% coefficient of variation. Similarly, Fanizza et al. (1999) evaluated 10 accessions of *Vitis vinifera* and concluded that the optimum number of RAPD markers for evaluating genetic divergence was above 400. The cluster formed with 400 markers did not present distortion when compared to the cluster formed with all polymorphic markers (932 bands), and the coefficient of variation of the genetic distances was only 5%. Picoli et al. (2004) obtained similar results in a study of 84 *Eucalyptus* genotypes. In spite of the limitations that this value (~400 bands) may have for other gene pools or plant species, it is a reference point that should be taken into account in diversity studies. Based on these findings, the mean number (160) of markers that we found in our sample (Table 1) should have been larger.

An analogous effort was made for microsatellites, for which 44 primer pairs were required for a correlation value of 95 and 6.44% stress, comparable to a standard sample of 57 primer pairs (Morales, 2003). This suggests that the respective mean numbers of 160, 281 and 25 for RAPD and RFLP markers, and SSR loci that we found in the articles that we examined (Table 1) should be larger to achieve accurate analysis. The low number of markers seems to be the major drawback for the use of isoenzymes (Table 1), besides the restricted coverage of the genome, weak correlation with other markers and possible environmental influence (Tsegaye et al., 1996). To some extent, morphological markers suffer these same limitations, although phenotype assessment is essential for evaluating the traits of interest.

Divergence-heterosis association

Noteworthy in the second sample of articles (Table 2), 28 of them detected positive divergence-heterosis association, whereas 26 revealed negative or inconclusive results. There are several reasons that could explain these results. Besides the deviations of dominance, genotypic divergence and complementation already reported, additional conditions for divergence-heterosis association have been inferred on the basis of simulation studies (Bernardo, 1992): i) manipulation of traits with high heritability; ii) variation of the allelic frequencies of the parents within narrow limits; iii) that at least 30 to 50% of quantitative trait loci (QTL) be linked to the markers, and iv) that less than 20 to 30% of the markers be randomly distributed or not linked to QTL.

In practice, the success of *a priori* choice has confirmed that moderate/high heritability of the traits is decisive (Dias and Resende, 2001; Dias et al., 2003), as much as marker linkage

to QTL (Vencovsky and Rumin, 2000), based on items i and iv, above. Nevertheless, this last condition may only be partially valid in species for which linkage maps are unavailable, where wide genome coverage may result in a “blind” prediction, according to item iv. Additionally, the parents with maximum relative divergence will not necessarily originate the most heterotic crossings, in agreement with item ii. For instance, Dias and Resende (2001) and Dias et al. (2003) found higher frequencies of heterotic hybrids and a larger magnitude of heterosis for yield components in the crosses involving parents of moderate divergence. They obtained success with *a priori* choice of hybrid parents, using yield components, as well as DNA markers (RAPD).

There are many other conditions negatively influencing *a priori* choice, such as: i) increased genetic similarity in a gene pool due to strong selection pressure (Barbosa et al., 2003); ii) lack of linkage between genes controlling the traits and the markers used (Bernardo, 1992); iii) differences in the contributions of the marked DNA regions (Kwon et al., 2002a,b); iv) gene pool with a narrow genetic base (Marrof et al., 1997); v) a lack of linkage disequilibrium (Charcosset et al., 1991); vi) epistasis (Boppenmaier et al., 1992); vii) high degree of improvement of the gene pool used (Dias et al., 2003), and viii) genotype-environment interactions (Dias et al., 2003). These remarks suggest that divergence and heterosis do not always associate linearly. Non-linear relationships support this reasoning, as revealed by Sant et al. (1999), a feature that may explain the erratic results in many studies.

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