Parental Selection Strategies in Plant Breeding Programs

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Abstract

Selection of the appropriate parents to be used in artificial crosses is one of the main decisions faced by plant breeders that will facilitate the exploitation of maximum genetic variability and production of superior recombinant genotypes. Several techniques have been used in aiding the identification of genotypes with promising and desirable agronomical traits for hybridization. In this way, the objective of the present review is to gather available information for the selection of parents based on different breeding designs and analytical tools showing their similarities and highlighting the main advantages and disadvantages of their use.

Key words: genetic constitutions, genetic variability, artificial crosses.

Introduction

Plant-breeding experiments concerning self-pollinated plants have been traditionally performed with single crosses between two parents, followed by production of segregating progeny populations. This method generally results in a reasonable amount of genetic variability needed for selection and attainment of complete homozygosis. In cross-pollinated or out-crossing plants, where heterosis leads to superior hybrid genotypes, parental combination is sought to obtain the maximum expression of desirable agronomical traits. Selecting the best hybrid combinations is the initial breeding step that determines the degree of success achieved by the program because it is fundamental that genetic variability be present in the initial population/progeny to obtain superior genotypes. However, for both self-pollinating and out-crossing plants, breeders find it difficult to identify the best parents that when crossed with each other, give rise to hybrid populations of superior performance. Therefore, the selection of genotypes to serve as parents in crosses is one of the most important decisions that a plant breeder has to face. The decision has to be as close to ideal as possible, because populations with reduced genetic potential may lead to a waste of time and money. Thus, each individual's high performance, wide adaptability, and yield stability have been the

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major features taken into account for choosing parental genotypes.

Different statistical procedures employed for the characterization of variability between and within plant species have become important auxiliary tools for the definition of crosses. Methods predicting the performance of hybrid combinations can be estimated on the basis of morphological (Cruz and Regazzi 1997), molecular (Diniz Filho 2000; Oliveira 1998), or pedigree (Barbosa Neto et al. 1996; Cao et al. 1997; Van Beuningen and Bush 1997) evaluations. However, selecting parental lines based only on target traits is often insufficient to guarantee the presence of superior genotypes in the progeny because any genetic gain that occurs in progenies originating from the selected parents were due to their phenotypic attributes, and may be random and non-repeatable (Gandin 1982). Thus, it is essential that the genotypes used in the crosses have a sufficient degree of combining ability to generate favorable recombinants at a high frequency.

The best way to determine the combining ability of parents is the diallel analysis. This technique has its rationale based on the crossing of a pre-determined number of parents and the evaluation of the progenies in different degrees of relatedness, essential to the investigation of genetic properties of agronomically important traits. There are many methods for the evaluation of diallel crosses however; one of the most used is still Griffing's Method 2 (Lorencetti et al. 2005). This method enables one to

estimate the general combining ability (GCA) and specific combining ability (SCA) that is related mainly to the additive gene effects and non-additive gene effects (dominance and epistasis), respectively. Despite its wide use, the diallel analysis (Javaid et al. 2001; Masood and Kronstad 2000) has a disadvantage based on the fact that some hybrids may be difficult to obtain and the workload involved in the evaluations. In addition, when the number of parental genotypes is high, the number of hybrid populations available for evaluation can potentially render the experiment unfeasible. In this sense, the top-cross method can be used as an alternative to diallel crosses to estimate the combining ability between genotypes, but because these values are obtained relative to a tester (high GCA), the difficulty faced here is to find good testers (Carvalho C et al. 2003). The best linear unbiased predictor (BLUP) approach was formerly used for animal breeding. However, current trends show a greater adoption of this technique by plant breeders (Balzarini et al. 2002) for predicting cross performance and choosing parental lines. The BLUP is an estimation procedure under the mixed-linear model approach (Searle et al. 1992). Taking advantage of the fact that parental genotypes or elite inbred lines are treated as fixed and environmental and genotype-by-environment effects are treated as random, the mixed model is considered the most appropriate approach (Balzarini et al. 2002). The predictive accuracy of BLUPs against a fixed model approach has been compared using sugar-cane data, showing that while the fixed-model approach produced errors of 11.406 Mg ha^{-1}, mixed models mean values obtained ranged from 9.738 to 9.959 Mg ha^{-1} (Balzarini et al. 2002). Therefore, mixed models have the potential to aid the breeder in finding the best predictions for parental performances and selecting the most appropriate genotypes for the hybridizations.

Quantitative genetics and statistical analyses have been used by numerous plant breeding programs (Balzarini et al. 2002; Flachenecker et al. 2006; Lstiburek et al. 2005; Milligan et al. 2003; Perkins and Jinks 1968; Piepho and Williams 2006), to select parental combinations that will translate into major heterotic effects on their progenies, increasing the possibility of obtaining superior recombinants. Therefore, the present review will discuss some aspects related to the main strategies and their strengths and pitfalls.

Parental screening based on phenotypic data

Individual genotype performance

Ideotype breeding is based on the modification of plant architecture to reassemble the ideal ideotype (Khush 2005). In practice, plant breeders take several decisions in order for their selection to resemble an ideotype. Although many advances in biotechnology and bioinformatics tools have been made, it is still common for the breeder to select parents based on their phenotypic performance regarding specific characteristics. This kind of decision depends on the subjective goals of each breeder, i.e. he/she could select those genotypes with the best means for targeted characters, such as yield components, grain quality, vegetative and reproductive cycle, and pest and disease resistance. However, it is not possible to capture the combining ability among parents based solely on their individual performance. The breeder must obtain crosses and evaluate the progenies or use techniques that allow the prediction of a specific genotype combination before the cross is performed (Mihaljevic et al. 2005).

Adaptability and stability

Similar to the superior individual performance, parental selection for crosses can take into account high adaptability traits (genotype ability to positively react to environmental stimuli) and yield stability (genotype ability to respond vis-à-vis the environment's yield potential). Considering these points, the selection of parents is also highly important for breeding programs aiming for a broader area of coverage, mainly for locations that show distinct soil and climate conditions. Many statistical models were developed to make genotype x environment interactions more precise and to facilitate the understanding of adaptability and stability of evaluated genotypes. Several research groups including Plaisted and Paterson (1959), Finlay and Wilkinson (1963), Eberhart and Russell (1966), Tai (1971), Wricke (1965), Francis and Kannenberg (1978), Verma et al. (1978), Lin et al. (1986), and Cruz et al. (1989) were pioneers in the landmark development of prediction techniques. Currently, studies concerning adaptability and stability, developed from genotype x environment analyses, are presented constantly in the literature; e.g. for soybeans (Oliveira et al. 2003), common beans (Jobim et al. 1999), canola (Coimbra et al. 1999), wheat (Felício et al. 1998), maize (Flachenecker et al. 2006; Scapim et al. 2000), oat (Benin et al. 2003), and sugarcane (Milligan et al. 2003) among other important crop species.

The work performed by Benin et al. (2003) is an example of using the bi-segmental model described by Cruz et al. (1989), where 19 oat (*Avena sativa* L.) genotypes were evaluated in nine regions of Southern Brazil. Using an environmental stratification allowed by the method, the environments were scored as favorable and unfavorable to oat cultivation according to a criterion based on a performance that was superior or inferior to the overall mean of studied environments (Table 1).

Adaptability and stability are measured by the significances of b_1 and $\hat{\sigma}^2_{\delta i}$ parameters, where R^2 corresponds to the adjustment of the regression model for each genotype. Significant values for b_1 and $\hat{\sigma}^2_{\delta i}$ when present on both environmental classes (favorable and unfavorable), as observed for the genotypes UFRGS 17, URS 21, and OR 2, indicate wide adaptability and stability of grain yield in the production regions sampled by the nine locations used (Table 1). This method has been extensively used

Table 1. Grain yield in ha⁻¹ (GY), adaptability (b₁), and stability (δ²ᵢ) parameters obtained for nine locations from Southern Brazil, in 2002 and 2003, according to the performances in favorable and unfavorable environments for the white oat crop (Benin et al. 2003).

Genotypes	Favorable environments				Unfavorable environments			
	GY	b_1	δ^2_{di}	R^2	GY	b_1	δ^2_{di}	R^2
UPF 15	3455	a[1]	0.85ⁿˢ	195220*	82	1951	b[1]	0.85ⁿˢ	64969*	89
UPF 16	3558	a	1.07ⁿˢ	407223*	65	2072	b	0.89ⁿˢ	76531*	89
UPF 17	3340	a	1.33*	150650*	84	1872	b	0.93ⁿˢ	347134*	71
UPF 18	3559	a	1.31*	240324*	81	2228	a	0.93ⁿˢ	166075*	83
UPF 19	3818	a	0.98ⁿˢ	135522*	85	2283	a	1.07ⁿˢ	169564*	83
UPFA 20	3738	a	1.04ⁿˢ	29342*	90	2513	a	1.19*	45934*	90
UFRGS 14	3635	a	0.77*	126742*	86	2417	a	1.29*	23367ns	91
UFRGS 15	3275	a	0.77*	318150*	80	1730	b	0.92ⁿˢ	136917*	84
UFRGS 16	3451	a	1.33*	254852*	80	2031	b	1.09ⁿˢ	92944*	87
UFRGS 17	3498	a	0.60*	187202*	82	2499	a	1.52*	61431*	90
UFRGS 18	3506	a	1.02ⁿˢ	140771*	84	1726	b	0.92ⁿˢ	210715*	82
UFRGS 19	3498	a	0.88ⁿˢ	240640*	81	2006	b	0.54*	87976*	87
URS 20	3351	a	1.00ⁿˢ	88521*	87	2028	b	1.11ⁿˢ	95947*	87
URS 21	3497	a	0.78*	450850*	61	2521	a	0.72*	437705*	66
URS 22	3264	a	0.96ⁿˢ	228782*	82	2024	b	0.42*	121743*	86
OR 2	3947	a	1.20*	223471*	82	2523	a	1.26*	91996*	87
OR 3	3799	a	1.20*	188124*	82	2192	a	1.14ⁿˢ	78822*	89
OR 4	3922	a	1.12ⁿˢ	164631*	83	2300	a	1.17ⁿˢ	47172*	90
FAPA 4	3893	a	0.73*	143842*	84	2528	a	1.13ⁿˢ	149356*	84
IAC 7	3171	a	0.81ⁿˢ	159391*	84	2022	b	0.81ⁿˢ	556208*	60

[1] Means not followed by the same letter in columns differ significantly from each other, by the Scott and Knott test at 5% probability.
* significant and ⁿˢ nonsignificant at 5% probability.

by researchers with the goal of analyzing the behavior of genotypes in macro regions (wide adaptability) and also in micro regions (specific adaptability), aiding the choice of parents for artificial crosses in breeding programs, as well as the recommendation of the best genotypes to farmers (Chloupek and Hrstkova 2005; Lin et al. 1986; Kraakman et al. 2004).

Diallel crosses

Diallel crosses represent the best strategy for determining the general (GCA) and specific (SCA) combining ability between putative parents. However, the major barrier for their use is the need of a large number of crosses for evaluation. The interpretation can be affected by the number and quality of data needed to obtain a precise estimate (Burow and Coors 1993). Another point is that an increase in the number of genotypes used in the crosses can preclude the experiment feasibility and increase the difficulty in the analysis.

According to this technique, it is necessary to cross all the selected genotypes (complete diallel) and evaluate their progenies or one can opt for the loss of some genetic information and perform part of the crosses (incomplete diallel). Another limitation is the difficulty in obtaining hybrids due to occurrences of species incompatibility or specific environmental requires. Despite these limitations, this type of analysis provides detailed information regarding the genotypes involved, estimates for parameters useful for the selection of the best parental combinations and an understanding of the genetic effects involved in the targeted characters. The most commonly used techniques are those proposed by: i) Griffing (1956), in that the effects for the

general and specific combining ability between parents are estimated; ii) Gardner and Eberhart (1966), in that the variety and heterosis are evaluated; and iii) Hayman (1954), that provides information regarding the character's basic mechanism of inheritance on the genetic values of the parents used and the selection limit. The Gardner and Eberhart Analyses II and III have recently been revisited with some interesting interpretations (Murray et al. 2003). Furthermore, some software such as DIALLEL-SAS05 (Zhang et al. 2005) is available for helping breeders better design their diallel matings. Some examples of diallel analyses used for the selection of parents are available for wheat (Barbieri et al. 2001), oats (Lorenzeti et al. 2005), common beans (Machado et al. 2002b), maize (Melani and Carena 2005), soybeans (Cruz et al. 1987), and green pepper (Miranda et al. 1998).

In oats, the work of Lorencetti et al. (2005), employing five parents combined with each other in a complete diallel scheme without the reciprocals, adds to the understanding of how this analysis contributes to determining the best parents. In their study, the high individual performance of genotype UPF 16 (168.83 g) was decisive for the increase in the progeny means in those crosses where it appears as one of the parents (Table 2). This resulted in a higher estimate of GCA (35.79), and indicates that the parent was useful for crosses aiming to improve grain yield in oats. The SCA estimates are useful to breeders as a way to promote the selection of hybrid combinations for direct use by farmers in species where heterosis is exploited or for the recommendation of promising specific combinations for the selection of superior recombinants such as those in the present example. Therefore, the major SCA effects observed for the crosses

Table 2. Performance, general (GCA) and specific (SCA) combining ability of five parents and their F₁ hybrids for the character plant grain yield in oats (Lorencetti et al. 2005)

Parents	Plant grain yield (g)						
	UPF 16	UPF 18	UFRGS 7	UFRGS 17	URPel 95-015	Yii+Yij	Yi.
UPF 16	168.83	329.31	202.09	228.11	167.77	1260.94	218.82
UPF 18		93.49	145.09	147.01	135.03	943.42	169.99
UFRGS 7			121.32	191.31	170.71	951.85	166.11
UFRGS 17				107.11	187.57	968.21	172.22
URPel 95-015					133.19	927.46	158.85
Média geral							168.40

General combining ability (GCA)		Specific combining ability (SCA)	
UPF 16	35.79	UPF 16 × UPF 18	134.75
UPF 18	-9.57	UPF 16 × UFRGS 7	6.30
UFRGS 7	-8.37	UPF 16 × UFRGS 17	29.93
UFRGS 17	-6.02	UPF 16 × URPel 95-015	-24.58
URPel 95-015	-11.84	UPF 18 × UFRGS 7	-5.46
-	-	UPF 18 × UFRGS 17	-5.88
-	-	UPF 18 × URPel 95-015	-11.96
-	-	UFRGS 7 × UFRGS 17	37.38
-	-	UFRGS 7 × URPel 95-015	22.50
-	-	UFRGS 17 × URPel 95-015	33.17

UPF 16 × UPF 18, UFRGS 7 × UFRGS 17, and UFRGS 17 × URPel 95-015 reveal that the use of these combinations in breeding programs will produce promising progenies from which superior lines could originate. In general, for plant breeding, hybrid combinations with high SCA and those with at least one parent with high GCA are the most sought after (Paini et al. 1996).

Top Crosses

One of the most efficient procedures for identifying parents with potential use for artificial crosses is the topcross. This procedure rapidly and precisely tests a large number of high performance genotypes (elite lines, such as pure lines, open-pollinated, or synthetic populations) with a common genotype of wide or narrow genetic base, designated tester line. Therefore, it is possible to evaluate the general (GCA) or specific (SCA) combining ability of each genotype against a tester and to estimate the probable outcome of pair-wise combinations of the best genotypes by means of progeny tests.

Two important aspects of the topcross scheme are relevant for estimating parental performance in pairwise combinations: i) the contribution of each parent is directly transferred to the progeny mean ($X_{Parents}$ × $\overline{X}_{Progenies}$), i.e. through additive gene action, and ii) the reliability of the results being obtained is independent of the quantitative or qualitative nature of the data. As a result, it is an efficient technique regardless of the number of genotypes to be tested and its reliability based on the narrow-sense heritability measurements ($h_r^2 = \delta_A^2/\delta_P^2$ where: h_r^2 = narrow-sense heritability, δ_A^2 = additive variance and δ_P^2 = phenotypic variance). Nevertheless, the techniques used in plant breeding often demonstrate points of weakness, as in the case of topcross. The superior pure lines selected by their combining ability with the tester do not always give satisfactory results when crossed with each other, especially when the tester is proper for evaluat-

ing GCA. The positive results are often derived from the complementary addition of genes that may behave distinctively in the progenies obtained from crosses between the elite lines, resulting in poor performances. Therefore, the correlation coefficient (r) between specific crosses involving one parental line and its performance in the test cross is intermediate (r ≤ 0.5), especially when the tester has a broad genetic base. Thus, when a higher stringency is needed on the combining ability tests, the use of a tester with a narrow genetic base can be a favorable alternative to elevate correlation coefficients (r ≤ 0.7) (Allard 1999, Briggs and Knowles 1967). Examples for topcross used in the selection of maize parental genotypes can be found in many articles (Duarte et al. 2003; Gama et al. 1993; Horner et al. 1976; Keller 1949; Mihaljevic et al. 2005; Sawazaki et al. 2000).

Pedigree data

The use of pedigree data as a criterion for studying relationships between genotypes is not new in plant breeding. Malecot's co-ancestry coefficient was the first measure used to evaluate relationships between genotypes (Malecot 1949). This coefficient was defined as the probability that two given alleles would be identical by descent in a genotype product of a given cross. This method is described as an easy and affordable alternative to be used for the selection of parental genotypes and it has been largely employed in genetic distance estimates.

The Malecot's co-ancestry coefficient has been reported in many studies: soybeans (Sneller, 1994), sunflower (Cheres and Knapp 1998), sorghum (Ahnert 1996), cotton (Van Esbroek et al. 1999), rye (Coarce et al. 1996), maize (Smith et al. 1990), and oats (Vieira et al. 2005). In wheat, pedigree data are fairly abundant and favors co-ancestry coefficient estimates (Barbosa Neto et al. 1996; Bertan 2005; Zeven and Schachl 1989; Zeven and Zaven-Hissink 1976). Conversely, depending on the genotype pool, pedigree information is not publicly available and

requires personal contact with breeders or germplasm curators. Therefore, a major barrier for using such a technique is the lack of information at adequate levels for a number of species.

DNA markers

The use of DNA markers in the estimation of genetic distances within and between plant species has grown rapidly in the last decade due to the development of excellent tools for scanning genetic information contained in plant genomes. Many different types of molecular markers are available today, being largely used for measuring genetic distances in many plant species. The main types of markers are: AFLP (amplified fragment length polymorphism), RFLP (restriction fragment length polymorphism), microsatellites, also known as SSRs (simple sequence repeats) and STS-PCR (sequence-tagged sites-polymerase chain reaction) (Dias et al. 2004). RAPD (random amplified polymorphic DNA) have been shown to have low reliability and its use has diminished (Yang et al. 1996). However, to make more precise inferences about the available genotype pool, it is necessary to consider the properties of each marker and the genomic regions they assess.

Examples of molecular-marker used in genetic distance studies are reported for many plant species of agronomic importance (Oliveira et al. 1996; Zimmer et al. 2003, 2006). In wheat, many types of markers have been used (Pinzon-Almanza et al. 2003; Corbellini et al. 2002; Manifesto et al. 2001; Máric et al. 2004). Also, some studies tried to predict hybrid performance and the results showed discrepancies (Kumar 1999). For maize (Boppenmaier et al. 1992) and oats (Moser and Lee 1994), studies have shown that genetic distance can be used to predict the performance of hybrids only for those crosses where the parents belong to the same heterotic group and cannot be extended to crosses between different heterotic groups. A significant correlation between the genetic distance between parents and F[1] performance was found in maize for large genotype samples and large number of markers (Smith et al. 1990). A significant relationship between the parental heterozygosis and hybrid yield was found when the number of inbred lines was increased (Stuber et al. 1992). Hybrid grain yield in maize was correlated with genetic distance based on RAPD markers (Lanza et al. 1997). Conversely, results for wheat (Barbosa Neto et al. 1996) and soybean (Cerna et al. 1997) could not establish any relationship between genetic distance based on RAPD markers and hybrid performance. It should be noted that RAPD markers should not be used for this type of study, due to their low reliability (Yang et al. 1996).

The mapping of genomic regions associated with complex traits, known as quantitative trait loci (QTL), is one of the major goals for breeding programs during the 21st century. Advances in this area have been due to the biotechnology revolution leading to an increase in molecular-marker uses. Currently, there are studies on the genetic mapping of QTL for many traits related to

disease resistance, grain yield, as well as main components of grain yield and other traits of agronomic importance. QTL mapping has been applied to cotton (Lacape et al. 2005), soybeans (Wang et al. 2004), common beans (Faleiro et al. 2003), maize (Sibov et al. 2003), wheat (Börner et al. 2002), barley (Márquez-Cedillo et al. 2001), rice (Zhang et al. 2004), and many other plant species. Mapping results provide us with QTL-associated markers that when used in genetic distance studies within species, should increase the chances of finding distant genotypes carrying complementary genes for important agronomic traits related to the QTL.

Combined morphological and molecular data analysis

Another common strategy used for genetic distance estimates is to combine morphological and molecular data into one analysis (Gower 1971), generating a similarity estimate (index) that ranges from 0 to 1. This technique has been the target of many critics because, in general, the number of data points originating from phenotypic observations is much lower than the ones obtained from molecular markers, resulting in some bias towards the outcome of the molecular analysis (Bertan 2005). The statistical software developed by Gower (1971) does not provide equivalence between the quantitative (phenotypic) and molecular (binary) data when included in different numbers on the combined estimate. Thus, the output reveals a high similarity between the results obtained from the combined analysis and those generated only by molecular data (Bertan 2005). The reduction in the number of RFLP markers to an optimal number was evaluated to determine the variability among a group of maize genotypes (Franco et al. 2001). These comparisons showed that the total variation for the genotypes was obtained with only 15 polymorphic markers, whereas the initial number used was 131. Based on this work, prior selection of polymorphic markers that represent the studied population could potentially be a way to avoid the bias on combined analyses of genetic distance. It has been observed that small distances estimated by molecular markers are consistently associated to small phenotypic distances, while large molecular distances can either be associated with large or small phenotypic distances (Dillmann et al. 1997; Lefebvre et al. 2001). A previous study in our group comparing morphological and molecular markers in wheat (Vieira et al. 2007) showed that among the four most consistent clusters in the AFLP analysis, three were consistent with the distance estimated through morphological characters. Similarity between the distances estimated by these two techniques was evidenced by a moderate but significant correlation (r = 0.47) between genetic distance matrices estimated by means of morphological and AFLP markers.

Genetic distance measures

The major tool used in estimating genetic distances is multivariate analysis. This analysis allows for the possibility of gathering many variables into one analysis. Genetic distance measures based on phenotypic characters are one of the main multivariate techniques used to provide criteria for choosing parents. Genetic distance between genotypes is a way to predict the genetic variability among hybrid combinations (Cruz and Regazzi 2001). However, in addition to genetic distance studies, it is also necessary that the genotypes selected for crosses possess high individual performance, adaptability and stability features for yield. When these requirements are fulfilled, there is a high probability of selecting transgressive genotypes due to the occurrence of heterosis and the action of complementary dominant genes (Carvalho et al. 2001; Carvalho F et al. 2003). High yielding, genetically distant genotypes may represent lines with distinct loci controlling the character and high combining ability.

The downside of evaluations based on the expression of phenotypic characters is the high environmental influence that can reduce the precision of quantitative genetic parameter estimates. Depending on the character and the species evaluated, this problem can be overcome by conducting evaluations in more than one year. The increase in number of years of evaluation makes the estimates more reliable. Therefore, the use of phenotypic characters in genetic distance studies is one of the procedures most used by breeders, because the same type of information is obtained from characterizations, adaptability, stability and yield potential measurements. Examples of efficient uses of multivariate techniques can be found for cotton (Marani and Avieli 1973), oats (Vieira et al. 2005), common beans (Machado et al. 2002a), maize (Boppenmaier et al. 1992) and wheat (Barbosa Neto et al. 1996; Bertan 2005; Máric et al. 2004).

Genetic distance studies, in any plant species, comprise six steps: i) selection of genotypes to be analyzed; ii) data production and formatting; iii) selection of the distance definition or measurement to be used for the estimations; iv) selection of the clustering or plotting procedure to be used; v) analysis of the degree of distortion caused by the clustering/plotting procedure used and vi) interpreting the data (Cruz and Carneiro 2003). For the result of the analysis to be efficient, it is necessary that all the steps be followed rigorously.

The overall distance of Mahalanobis (D^2) and the Euclidean distance are the most used statistical procedures to estimate genetic distances (Cruz and Regazzi 2001). The Mahalanobis distance has some advantages over the Euclidean distance. Mahalanobis distance takes into account the environmental effects and allows for obtaining correlations between characters. This is not the case for the Euclidian distance. However, one limitation of the Mahalanobis procedure is, it requires data from more than one replication to estimate the distance. Once the distance estimates between each genotype pair is obtained, the data are presented in a symmetrical matrix from which the data display

and analysis can be facilitated by the use of a clustering/plotting procedure.

Clustering methods have the goal of separating a pool of observations in many subgroups to obtain homogeneity within and between the formed subgroups. The hierarchical and optimization methods are employed on a large scale by plant breeders. In hierarchical methods, genotypes are grouped by a process that repeats itself at many levels, forming a dendrogram without concern for the number of groups formed. In this case, three distinct forms of clustering may be used on the basis of genotype pair distances (Cruz and Regazzi 1997): i) using the average of distances between all genotype pairs for the formation of each group, named average linkage analysis or UPGMA-Unweighted pair group method with arithmetic mean; ii) using the smallest distance between a pair of genotypes known as single linkage or nearest-neighbor analysis, or iii) using the longer distance between a genotype pair, known as complete linkage or farthest neighbor. However, it is at the discretion of the researcher to adopt the procedure that is most suitable for their data set.

For the optimization methods, groups are established according to a fixed clustering criterion, differing from hierarchical methods due to the fact that clusters are mutually exclusive (Cruz and Regazzi 2001). For the optimization method proposed by Tocher, a criterion of always keeping the average distance within groups smaller than any distance between groups is used (Rao 1952). Another way of displaying distances is through a multidimensional scale, which also requires the use of a distance measure. However, the display is obtained by means of dispersion graphics where the dots represent the genotypes evaluated (NTSYS-pc, 2000).

Tocher's method, dendrogram, and bi-dimensional display of graphics were compared in the evaluation of 19 wheat genotypes recommended for cultivation in Southern Brazil (Bertan, 2005). The analysis of distance was based on 17 phenotypic characters measured in the years 2003 and 2004 in Pelotas, Southern Brazil. The clustering obtained with Tocher's method revealed five groups. Most of the genotypes (13 in total) clustered into one distinct group, which suggested that these genotypes were part of the same heterotic group (Table 3). Agronomic characters distinct from this group are expected for the genotypes CEP29 and ICA2 (group II), BR18 and TB951 (group III), SONORA64 (group IV), and BH1146 (group V), as they formed different groups.

Table 3. Clustering of 19 wheat genotypes using Tocher's method and the overall distance of Mahalanobis (Bertan 2005).

Groups	Genotypes
I	BRS 119, BRS 120, BRS 177, BRS 192, BRS 194, BRS 208, BR 23, BR 35, BRS 49, CEP 24, ICA 1, PF 950354, and RUBI.
II	CEP 29 and ICA 2
III	BR 18 and TB 951
IV	Sonora
V	BH 1146

When the genetic distance was estimated by UPGMA and displayed as a dendrogram (Figure 1), the clustering of genotypes was somewhat similar to Tocher's method, especially regarding the most divergent genotypes. The agreement between these two techniques can be observed when one examines the genotypes present in Tocher's groups II, III, IV, and V (CEP29, ICA2, BR18, TB951, and SONORA). These genotypes were also present in the distant clusters formed by UPGMA, with the exception of BH1146 (Table 3 and Figure 1). However, regarding closer distances, Tocher's clustering leads to the formation of one large cluster, whereas the UPGMA better discriminates the closer genotypes.
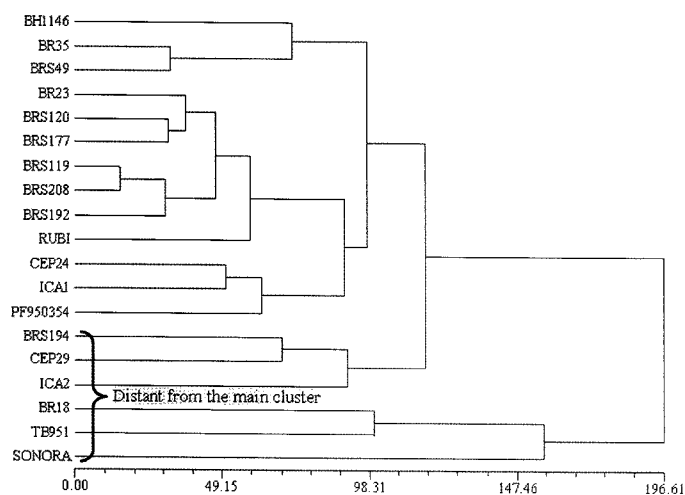
Fig. 1. Dendrogram resulting from the analysis of 19 wheat genotypes (based on 17 phenotypic characters) obtained by UPGMA using the overall distance of Mahalanobis. The cophenetic correlation coefficient (r) is 0.80 (Bertan 2005).

The display of distances on a bi-dimensional plot in the multidimensional scale (MDS) (Figure 2) shows that the longer distance between two genotypes was found between Sonora64 and BH1146, and the results are in agreement with the results from UPGMA and Tocher's analyses (Table 3; Figures 1 and 2). The efficiency of displaying features of Figures 1 and 2 was also estimated using a cophenetic correlation coefficient. The bidimensional scale (r = 0.94) showed a better adjustment between the graphical display and its original matrix, when compared with the UPGMA (r = 0.80) analysis (NTSYS-pc, 2000). However, on the bi-dimensional scale, one needs to be aware that the stress (S) level provoked by the clustering was 14% (Figure 2), a value that is above the suggested limit for acceptance, which is 10% (Kruskal 1964). In general, the clustering procedures compare all genotype pairs through similarity or dissimilarity measures. However, the MDS analysis differs from others because it searches for the best adjustment between the original matrix and the graphical display by means of a regression analysis. The best adjustment is then compared with the original distance by a stress function. Thus, although the

MDS has shown a cophenetic coefficient higher than UPGMA, the stress value slightly above the accepted level suggests that both techniques are equally efficient in preserving the real distances between the genotype pairs evaluated.
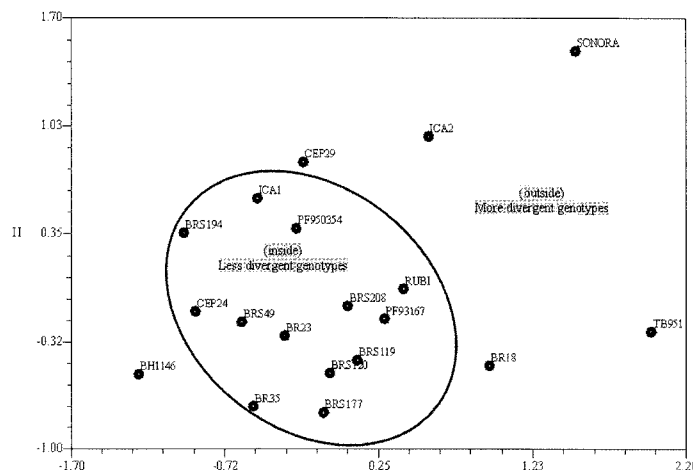

Fig. 2. Bidimensional display (MDS) of 19 wheat genotypes, using the overall distance of Mahalanobis as a measure of genetic distance (based on 17 phenotypic characters). The value for the cophenetic correlation (r) is 0.94 and the stress coefficient (S) = 0.14 (Bertan 2005).

Other display methods are also available to researchers, such as principal components and canonical variables that represent the distance between genotypes using information obtained directly from crosses evaluated, not requiring a distance measure (Cruz and Regazzi 2001). However, these two techniques rely on the majority of contributions being concentrated on the first two components or canonic variables, respectively, in order to have bi- or tri-dimensional plots of distances displayed effectively.

Some scientific papers were taken as the basis to summarize the degree of association (correlation) among the main techniques used as measures of genetic distance. In soybeans (Cox et al. 1985), significant correlations of moderate values were found between isozyme and co-ancestry based estimates (0.48), and morphological characters and co-ancestry-based estimates (0.33). In wheat (Barbosa Neto et al. 1996), low correlation values were found between morphologically based distance and RAPD-based estimates (0.12), morphologically based distance and co-ancestry-based estimates (0.03), and RAPD and co-ancestry-based estimates (-0.01). Also in wheat (Bertan 2005), the use of AFLP markers resulted in genetic distance estimates that were non-significantly correlated with co-ancestry estimates (0.47). A similar scenario was verified for maize (Smith et al. 1990), where genetic distance estimates, based on isozymes, RFLP, and co-ancestry estimates, presented weak correlation coefficient values, but a high correlation was found between RFLP and co-ancestry estimates (0.543).

A detailed study regarding the association among distinct genetic distance measures was described for oats (Vieira et al. 2005). A total of nine commercial genotypes recommended for cultivation in the Southern Region of Brazil were analyzed in experiments with and without fungicide application for disease control. These genotypes were also used for co-ancestry and AFLP-based genetic distance estimates. Among the techniques used, the distances estimated from molecular data (DAFLP) and co-ancestry coefficient analysis (f), were the ones that provided the highest correlation (r = -0.45) (Table 4). The second highest correlation was observed between phenotypic distances comparing plants with and without fungicide application (r = 0.44). This moderate correlation can be attributed to the occurrence of crown rust, considered to be the major disease for the oat crop in Brazil. Among the remaining estimates of genetic distance, no significant correlation was found (Table 4). Thus, the lack of a high correlation is evident when researchers compare different techniques. However, in many cases, statistically significant values are found. The main inferences that justify the results described above have pointed to the properties that each technique has in assessing different genomic regions. Therefore, new studies seeking to increase the association between the different genetic distance estimates will be as successful as their ability to better assess the genome, creating a more representative sample.

Table 4. Correlations between the distance estimates based on AFLP markers (D$_{AFLP}$), phenotypic data with fungicide application (DF$_{cf}$), phenotypic data without fungicide application (DF$_{sf}$), and coancestry coefficient (Vieira et al. 2005).

Groups	(DF$_{cf}$)	(DF$_{sf}$)	(COP)
(D$_{AFLP}$)	-0.13	0.04	-0.45*
(DF$_{cf}$)		0.44*	-0.15
(DF$_{sf}$)			0.06

* significant correlation at 1% error probability.

Final remarks and perspectives

The selection of parents in plant breeding programs is the step that determines the success of future progeny populations. It is at this stage that breeders initiate the selection for a particular plant ideotype that fulfills market demands. Even though recombination may have its role in amplifying the genetic variability of segregating populations, it is the combining ability between two parents and the high performance in agronomic traits that will determine if the offspring will consist of successful elite lines. Considering the lack of information regarding combining ability, studies that point out the relationships among genotypes will be fundamental sources for the scientific research, aiding the breeder in selecting the parents for hybridization. Therefore, phenotypic and DNA marker characterizations, as well as multivariate statistical analyses, are the

key components. Contributions that will improve our ability to determine the most suitable parents for crosses are expected from the biotechnology and bioinformatic tools, making DNA marker and software analyses more accessible to breeders.

Acknowledgments

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