Comunicata Scientiae 3(2): 76-83, 2012

Review Article

Genetic parameters and variability in soybean genotypes

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Abstract

Several genetic breeding programs contributed to the development of soybean cultivars with high yield and adapted to different Brazilian edaphoclimatic conditions. However, the continuous progress of genetic breeding of this specie depends on the genetic variability and application of genetic parameters informations which helps a more efficient selection process.There are many multivariated technical approaches to study the variability among soybean groups, such as dissimilarity measures, cluster analysis, principal components and canonical variables. The heritability estimation, genetic gain and genetic correlations are important parameters which permit the breeder to choose the best improvement strategy.

Keywords: *Glycine max*, genetic divergence, multivariate analysis

Parâmetros genéticos e variabilidade em genótipos de soja

Resumo

Vários programas de melhoramento genético contribuíram para o desenvolvimento de cultivares de soja com alto rendimento e adaptados às diferentes condições edafoclimáticas Brazileiras. No entanto, o progresso contínuo de melhoramento genético desta espécie depende da variabilidade genética e da aplicação de informações sobre parâmetros genéticos que corroborem com o processo. Há muitas abordagens técnicas multivariadas para estudar a variabilidade entre os grupos de soja, tais como as medidas de dissimilaridade, análise de agrupamento, componentes principais e variáveis canônicas. A estimativa de herdabilidade, ganho genético e correlações genéticas são importantes parâmetros que permitem ao criador a escolhada melhor estratégia de melhoramento.

Palavras-chave: *Glycine max,* divergência genética, análise multivariada

Received: 11 May 2012
Accepted: 25 June 2012

Introduction

The soybean [*Glycine max* (L.) Merrill] is the one of the most important vegetal food source in the world; it is due to the high oil (20%) and protein (40%) content. This vegetal specie had the higher expansion of cultivated area in recent years, turning Brazil into the second in production and exportation of this legume in the world, with a crop production of 66.7 millions of harvested tons in 2009/2010, surpassed only by the USA (Conab, 2010).

Part of brazilian success in the soybean culture is attributed to soaring scientific and technical efforts, whereas the objective has always been the constant release of new cultivars of high yield, large adaptation and resistance to major diseases (Empresa Brazileira de Pesquisa Agropecuária, 2008).

Although the Brazilian germoplasm presents a close genetic base, what brings some difficulties to breeding programs as, e.g., the low variability of genes involved with diseases resistance, turning it possible the eminent reach of a productivity limit (Mulato, 2009).

The knowledge on phenotypic variability components, which results from the interaction between the genetic effects and environment, is of outstanding importance while choosing breeding methods, places to conduct the yield tests, repetition number and the selection gain prediction.The environmental variations may mask those from genetic nature. Therefore, the higher the variability due to environmental effects in relation of total variability is, the harder an effective selection of superior genotypes will be (Borém & Miranda, 2009).

The analysis of genetic divergence through multivariate techniques makes it possible the simultaneous avaliation of various characters and permits several inferences to be made based on a data set. These techniques are able to generate important information to maintenance of genetic resources, in the germplasm banks simplification andnucleus collections formation (Arriel et al., 2006), beyond assisting traits descriptors choosing that best representsgenetic diversity (Fonseca & Silva, 1999).To breeding programs, the multivariate approaches available may be used, mainly, forthe identification of potential genitors to crossings with higher heterotic effect (Karasawa et al., 2005).

Among the most used multivariate techniques, there are: dissimilarity analysis, obtained with Euclidean distance, widespread distance of Mahalanobis; principal components analysis; canonical variables; and cluster methods, such as: Tocher, UPGMA (Unweighted Pair Group Method with Arithmetic Mean), nearest /farthest neighbors.

Thus, the obtention of estimatives of genetic and phenotypic parameters, like heritability, correlations, expected gains from selection and genetic divergence studies have fundamental importance in geneticbreeding programs, since they enable the decision-making related to the most appropriated methods to conduct the segregant populations, to the characters which should be selected in initial and advanced steps of the program and also concerning the weight attributed to each trait, separately or combined (Farias, 2008).

This review aims to gather information on techniques and methodologies that a breeding program can use for planning and conducting crosses on segregating populations.

Development

Genetic Divergence

The analysis of genetic divergence is destinated to the identification of appropriate genitors in order to obtain hibrids with higher heterotic effect, which provide more segregation in recombinations, possibiliting the transgressives emergence (Cruz & Carneiro, 2006). Genetic resources are used as genetic variation sources to desirable characters and needed to plant breeding (Rodriguez et al., 1999). To estimate the phenotypic diversity among subsamples from a germplasm bank, it is necessary to characterize and evaluate themas forimportant traits for crop (Bueno et al., 2001).

Studies about genetic variability of soybean have demonstrated that Brazilian germplasm has a close genetic base, being originated from few ancestor lineages, which may explain the recurrent similarity between two or more cultivars at the moment of crop protection deposit. Thus, the identification of distinct genotypes isa usefull tool to guide genetic improvement programs.

According to Bonetti (1983), about 70% of cultivars developed inRio Grande do Sul, in the1960s, came from American cultivars: Hill, Hood or both. Using the coefficient of parentage, Hiromoto & Vello (1986) determined the genetic base of this soybean germplasm and reported that 100% of genetic content of Brazilian cultivars, during those years, have been originated from 26 ancestors, among which, eleven Asiatic lineages contributed with more than 90%. Four ancestors, with major contribution to Brazilian soybean germplasm, are the same that contributed to those produced in the south of the USA, that also have a close genetic base (Gizlice et al., 1994).

In a research envolving 90 elite adapted cultivars to different brazilian environments, Miranda et al. (2007) have estimated the coefficient of parentage and they have reported that the effective size is reduced (11 and 13), supporting, this way, the high similarity degree of Brazilian cultivars.

Evaluating genealogies of 444 Brazilian cultivars clustered by release period before 1971 until 2009, Wysmierski (2010) found 14 parental contributing with more than 90% of genetic base of Brazilian cultivars. The author comments the increase of ancestors number with time elapsing, but the four main ancestors were the same in all periods and their contribution were more concentrated, of 46.60% (before 1971) to 57.59% (period of 2001-2009), indicating the narrowing of genetic base.

Hytenet al. (2006), measuring the genetic divergence between four soybean populations, concluded that during the crop domestication, about 50% of all diversity from materials and 81% of rare alleles were lost, what has led to around 60% of allele frequence changes.

The geographic origin might interfere inthe genetic divergence between genotypes. Mulatoet al. (2010)have evaluated79 soybean subsamples from different world regions as for their genetic diversity and they have found a high genetic diversity among the selected subsamples; five (05) groups and several subgroups have been discovered, besides a moderate relationship between genetic divergence and geographic subsamples origin has been observed.

The estimation of genetic diversity may be donethrough genetic markers, and the classification can be organized as morphological and molecular ones (Colombari Filho, 2009). Some characteristics promote differences among genotypes being, eventually, reproduced accurately during progenies and used to correlate toother interesting traits.

Multivariate analyzes are techniques which evaluates numerous informations based on collected or measured data, set for different genotypes. Among the multivariate analyzes, the cluster method stands out by the adoption of some criteria as for optimization and hierarchy (Cruz et al., 2004).

The cluster method depends onthe use of a dissimilarity measurement previously estimated (Cruz et al., 2004), among which Euclidean distance and Mahalanobis' widespread distance can be found. The last one is a measurement obtained byquantitative data, with repetition, employed in studies of divergence in different crops (Mulato et al., 2010).

The employment of multivariate analyzes starting from measures of dissimilarity makes the probability of superior genotypes recuperation at segregant generations higher, mainly, when the crossing is made between superior and genetically distinct individuals (Carvalho et al., 2003).

Among the most widely used methods for optimization, Tocher's method uses the criterion of the establishment of groups, so that, the average distance intragroups is always less than any other distance between the groups. The hierarchical methods involve the creation of a hierarchical agglomerative division or in the form of a dendrogram, theseobservations are combined step by step and there are notpredefined numbers of groups to be formed. The single linkage method or nearest neighbor, the complete linkage or farthest neighbor and average linkage between groups (UPGMA) methods are examples of hierarchical ones (Cruz, 2008).

The Tocher's method allows mutually exclusivegroup formation, while hierarchical methods present a big possibility of number of groups, what makes necessary a researcher's decision as for the adoption of the group that best represents the expected clustering structure, based on his own data set (Bertan et al., 2006). According to Cruz et al. (2004), the stablishment of a visual exam of linkage where agreat level of changes occur makes group boundaries possible

The Tocher's clustering is normally used together with UPGMA, revealing correspondence tothe allocation of elements in the groups (Arriel et al., 2006). The concordance with Tocher's clustering persists, several times, using another hierarchical clustering or multivariate techniques.

The UPGMA clustering methoduses the average of distances between every genotype pair to form each group. It is adopted inlarge scales in plant breeding, in representation of distances in multivariated studies, presenting advantages if related to other hierarchical methods (Bertan et al., 2006).

Koga et al. (2008) used multivariate analyzes to detail the infective cycles of *Phakopsora pachyrhizi*(Syd. & P. Syd.) in soybean genotypes, with stablishment of groups with more promising genotypes to use as a genetic source against rust. Several other authors have also used multivariated analyzes to characterize soybean lineages and to determine the genetic diversity through many characters(Araújo&Velo, 2010; Bharadwaj et al., 2009; Azevedo et al., 2004; Mulato et al., 2010; Priolli et al., 2010).

Estimation of Genetic and Phenotypic Parameters

The study and knowledge on quantitative characters represent the primary interest for plant breeding, since the beginning of soybean genetic researches, looking for more efficient breeding methods (Farias, 2008).

The genetic parameters usually studied refer to genetic variances in its addictive and non-addictive components, to heritability coefficient (*lato* and *stricto sensu*), and tothe interactions between genetic and environmental effects and genetic correlations among these characters (Silveira, 2007).

The estimationof components variability in the populations andhow much of its amount is due to genetic differences are fundamental to every breeding program, allowing theknowledge onthe genetic control of the trait and this population potential to selection (Ramalho & Pinto, 2008). According to Silveira (2007), these estimationencourages the decision-making related to the appropriated characters, which should be selected at starting and advanced steps of an improvement program, and it helps to determine each weight should be attributed to each character, separately or combined.

The estimation of genetic parametes allows researchers to obtain information onthe type of genic action that controls the characters under study,provides the basis for the assessment of breeding programs and the improving of population, and also helps developing new methods for breeding (Contreras, 1990).

Among the most influent genetic parameters to the breeder, some can be cited: 1) additive genetic variance, which results in predominant effects from additive alleles, in other words, represents a fraction of heritable genetic variance; 2) genetic variance due to dominance deviation (or dominant variance), results from intra-allelic interaction of gens in segregant loci, so, from the combination of alleles of each genotype; 3) epistatic genetic variance, results from the intra-allelic interaction of two or more segregant loci and it can be divided in additive x additive, additive x dominant, dominant x dominant, for two loci and divided in additive x additive x additive, etc., for three or more loci;4) variance of environmental x genotypes interaction; 5) genetic correlations between quantitative characters of breeding importance to crop in particular (Gardner, 1963).

In the selection process it is important to know the nature and magnitude of gene effects that control a character. In the presence of the additive variance, the selection is easy, as an individual or group of superior individuals, to produce a higher offspring (Ramalho & Pinto, 2008). The additive genetic value is indicative of the number of desirable alleles into the selection unit (Cruz & Regazzi, 1997; Falconer, 1987).

Heritability

The heritability (h^2) is one of the genetic parameters, which most contribute to the breeder work. It provides the proportion of total phenotypic variance that is attributed to genetic causes. Thus, it measures the reliability of the phenotypic value as an indicator of the genotypic value (Ramalho et al., 1993). Thereby, it expresses the confidence of the phenotypic value as a guide to the genetic value, therefore, it takes part into almost all the formulas related to breeding methods, and many practical decisions about procedures depend on its magnitude, as wella as theselection of strategies for a particular character in the population (Falconer, 1987).

Jacquard (1983) presented 3 principles to define the heritability: (1) as measure of similarity between parent and son, (2) genetic portion at lato sensu and (3) genetic portion at stricto sensu. But the heritability does not typifythe character, not being a fixed value, ranging in function of population and character in the study (Ramalho et al., 1993).

It is possible to estimate two types of heritability: lato sensu (ha) and stricto sensu (hr). Concerning lato sensu, the heritability can be defined as the ratio between the genotypic variance and phenotypic variance, while, the stricto sensu one is defined as the ratio between additive genetic variance and phenotypic variance. Thus, the difference is in the numerator of these fractions (Ramalho & Pinto, 2008; Falconer & Mackay, 1996; Allard, 1971).

The heritability coefficient (h^2) can range from 0 to 1. When $h^2 = 1$, it means that phenotype is completely determined by genotype, not suffering environmental influence. Being $h^2 = 0$, the character variability does not have genetic origin (Allard, 1971).

The estimation of heritability might range with the characteristic, the method to estimation, the populational variability, the inbreeding level, the size of sample evaluated, the number and type of environment considered, the type of portion and the precision at the experimental conduction and data collection (Borém & Miranda, 2009).

Characters with high heritability allow more success in selection, so that the chance of obtaining superior progenies with selected individuals is larger. This way, breeders use, several times, indirect selection to obtain more gains with characters with low heritability, selecting correlated characters (Castro, 2008).

The main characteristics of interest in the genetic breeding of soybean are quantitative, thus they are very influenced by environment. The yield is a noteworthy character, sinceit presents low heritability (20 – 30%), what can be attributed to the purely quantitative behavior, in function of a large number of loci that controls it, that permitsagreatenvironmental influence and, consequently, a reduction of relationship between the genetic and phenotypic variances. Many works corroborate with this low heritability: Castro (2008) has evaluated the heritage of grain yield and soybean yield components, in Piracicaba city (SP) and he has found a heritability of 16% to this character. Costa et al. (2008) have made estimatives of heritability in early generations of biparental soybean crosses and they have obtained a heritability of 45%. Carvalho et al. (2009) have found a heritability of 52.8%. Other values were found with some variation: 59.09% (Silva, 2008), 19% (Farias, 2008), 76.08% (Silveira, 2007), 12 to 59% (Vieira, 2009) and of 53% (Medeiros, 2009).

Expected gain with selection

The estimation of genetic gain with selection is an important parameter to a breeder;it shows how the population will gain in relation to their performance before the selection is practiced.

Besides heritability, the estimative of gain is important to genetic inferences. A essential aspect of majority of breeding programs is the selection inside a base-population, composed by genetically variable individuals and the use of the selected material to obtain of new populations, it should be made the comparision of the new population with the base-populations. To this, it is necessary to determine the progress achieved with the selection, which depends on the amount of genetic variability of the base-population and the magnitude of the effects that it masks (environmental components and interaction) (Silveira et al., 2006). When data set of base-population is not available, the expected gain is estimated according tothe selection, in other words, to what will probably occur tonext generation, using the avaiable components of variance.

The most important factors that interfer, directly or indirectly, in the gain with selection, according to Vencovsky & Barriga (1992) are: selection intensity, genetic properties of population and the environmental conditions. The gain is directly related with the selection differential, dependingon thedifference of selected group average and the original population average. This way, the quantitative characters, e.g., grain yield, present aproximately a normal distribution; a major selection differential is obtained when a minor number of superior units are selected (progenies or individuals). Therefore, the greater the selective pressure is, the higher the differential will be. So, a high selective pressure implies a higher risk of drastic reduction on genetic variability, which may compromise the gain in successive cycles. The more heterogeneous a population is, the greaterthe chances of gain with selection will be, since it is based on genetic differences (Farias, 2008).

The possibility of prediction by determined selection strategy is one of the main contributions of quantitative genetic to the breeding. Based on this information, it is possible to guide, in amost effective way, the breeding program, predicting the success of the selection scheme adopted and determining, scientifically, which techniques can be more effective (Cruz et al., 2004).

The gain with selection will reduce time, due, mainly, to the continuous use of the same germplasm on hybridization. However, in recent years, this situation has been improved, since new cultivars are released and an addition to gains in the improvement of agronomic traits for the correction of quantitative traits isachieved, corresponding to relative gains in grain yield (Colombari Filho, 2009).

Overall, the various characters of economic interest are correlated, what makes it possible the occurance of changes in other ones, provided by a selection. However, when this genetic correlation is favorable, it is possible to gain to one character through indirect selection on other characters associated.

The efficiency ofearly test from estimates of expected responses to the selection of progeny derived from $F_2$and F_4plants in Piracicaba-SPwas evaluated by Carvalho et al. (2009), who have used selection intensities of 40 and 50% and have obtained answers to grain yield of 6.75 and 5.59% (F_2 generation) and of 10.96 and 9.08% (F_4 generation), respectively.

Another way to estimate the expected gain with selection is through the indexes use stablished to optimal combination of diverse characters, allowing to efficiently carry out the simultaneous selection of multiple characters. When compared with direct selection, many studies have presented relatively near or higher results, between the two methods. Generally, the gain on the main character is reduced but this reduction is offsetted by an increase in favorable distribution of gains in other important agronomic traits. Thus, different alternative indexes correspond to different selection and gains (Barbaro, 2006).

Mouraet al. (2008) assessing 176 F_6 lineages of soybeaninLondrina city-PR, in order to observe soybean cyst nematode (race 1); have estimated the genetic parameters and obtained gains with selection ranging of 16.65 to 23.99 %.

Correlation between characters and path analysis

The correlation is a measure of intensity of linear association between two variables or a measure of joint variation degree, which can be positive or negative. Information oncorrelation between characters are extremelyimportant, because they permit the breeder to know what happens with a character when another, to which the first is correlated, is selected (Ramalho et al., 1993).

In plant breeding, the knowledge on correlation between characters becomes much more important when the selection of an specific character is harder, due to its low heritability and/ or measure and identification difficulties (Cruzet al., 2004).

Phenotypic, genetic and environmental correlations can be estimated. The correlation estimated based with directly measured data set is the phenotypic. It has two causes genetics and environmental.The main cause of genetic correlation is pleiotropism, ie, property by which a gene influences two or more characters.The linkage disequilibrium is also cause of genetic correlation; however, it is transient, occurring mainly in populations originating from divergent crosses (Falconer, 1987).

The environment is the cause of correlations between characters influenced by the same environmental variations. Negative estimatives of environmental correlation indicates that environment favores a character in detriment of another one, and a positive estimation indicates the benefits or losses of both concerning environmental variation (Cruz et al., 2004).

The correlation coefficients are adimensional and their absolute value does not pass by a unit, no matter if it is a positive or a negative one; the coefficient of correlation equals zero shows a non linear relation between the two variables and the existence of a relation or dependence between them.

The correlation values depend on the genetic base of the population that is being evaluated as for determined characters, showing a range to positive and negative estimatives, proportioning indicatives of the way a selection of a character can affect all the others (Heiko, 2001).

According to Lopes et al. (2002), although it can be possible to add levels of statistical significance for the phenotypic and genetic correlations, there is a tendency among plant breeders to value the sign (positive and negative) and the magnitude of the values applied in the interpretation of the correlations. Thus, it is common to observe values estimatives below -0.5 and above 0.5.

Traits whose heritability is higher, allow greater success in the selection, so that the chance of obtaining superior progenies with selected individuals is higher. For this reason, breeders may adopt the use of indirect selection for quantitative traits with low heritability, a selection through correlated characters.

Although the correlations are of great important in breeding, they can conduce to wrong selection strategies if used inappropriately, since their estimatives do not express a direct relation of cause and effect, as estimated by path analyzes.

Path analysis is the breakdown of correlations in the direct and indirect effects of independent characters and explanatory variable on a basic main variable, whose estimatives are obtained by regression equations, in which the variables are previously determined (Wright, 1921; 1923; Li, 2001).

The success of path analysis is, basically, the formula of causeeffectrelation between the variables. Besides, the breakdown of correlations depends on the studied characters, what is normally stablished by previous knowledge accumulated by the breeder, on their importance and, if it is possible, the inter-relation expressed by path diagrams (Cruz et al., 2004).

A common problem in path analysis studies is the multicolinearityoccurence, ie, inter-relation at explanatory variables. A high multicolinearity condition conduces to inconsistent estimatives of coefficient of regression and overestimates the direct effects of explanatory variables as for the answer variable. Some strategies have been adopted to soften the adverse effects of multicolinearity, such as variable elimination and ridge analysis (Carvalho, 1995; Bizeti et al., 2004).

Ina recent study developed by Alcântara Neto et al. (2011), concerning path analysis, it was possible to conclude that the number of seed pods per plant in soybean crops is the component of yield that presents the greater direct effect on the dried yield materia ; the total grain production per plant plays an important role as for dried material yield, while the height of first seed pod has shown a low effect of cause-relation in the study of variables.

As orientation for breeding programs, the quantitation of indirect effects of selection for a character is fundamental to the obtention of genetic material which assemblesa set of favorable attributes, allowing the progress in the character to occurafter the selection of another one.

Iqbal et al. (2010) have assessed the correlation among 9 agronomic traits in nineteen different soybean genotypes, and they have observed a positive correlation as for grain yield in all studied characters, except for the height of plant at flowering. The oil content trait presented a positive and significant correlation with yield, weight of 100 seeds and days to mature. The number of nodes per plant was significantly negative if correlated to grain yield trait.

Conclusions

Studies involving genetic divergence combinedwithestimatesofgeneticparametersare important to delineate the breeding programs and to define selection strategies that results on higher genetic gains.

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