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Bibliographic review

Analysis of the genotype environment interaction in the of soybean crop (*Glycine max* (L) Merrill)

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ABSTRACT

The differentiated behavior of the varieties in different environments is what is known as genotype-environment interaction (GxE). A very important aspect when the selection and destination environments are different. This is the fundamental problem of the genetic improvement of plants. Direct selection in the destination environment has always been more effective, since it allows to improve the specific adaptation of the varieties in the environment where they will grow. Thus, cultivars and crops express their greatest potential. The definition of the cultivar with better adaptation and its interaction with dates of cultivation has the greatest benefits. It makes possible better preparation to manage the effects of climate change, which favors the selection of materials on farms. This bibliographical review was carried out with the objective of highlighting the importance of the genotype-environment interaction analysis in the genetic improvement program in the soybean crop, where essential aspects of the crop are addressed, such as its taxonomic classification, main morphological characteristics and genetics, applied biotechnology for genetic improvement, as well as elements to take into account for the genetic improvement and analysis of the genotype environment interaction in this crop. In addition, basic concepts such as adaptability and stability are discussed. It is concluded that the genotype environment interaction in the improvement programs has a determining influence on the new cultivar obtaining and more stable genotypes and with better specific adaptation at the time of making the selection and that the development of strategies that integrate the traditional plant breeding with modern molecular techniques they enhance the program of genetic improvement of the crops.

Key words: genetic improvement, selection, adaptability, stability

INTRODUCTION

From Asian origin, the cultivated soybean, *Glycine max* (L) Merrill, is native to northern and central China (1). It is known that it arrived in Cuba in 1904 from the United States and it was planted at the Santiago de las Vegas Agronomic Station in Havana, today the Institute for Fundamental Research in Tropical Agriculture (INIFAT) (2).

From the oilseeds that are produced worldwide, soybeans occupy the first place in terms of production, and consumption with more than 50 % in each of these concepts, in relation to the rest of oilseeds, due to its great diversity of uses, derived from its high protein content and oil quality (3). On average, dry grain contains 20 % oil and 40 % protein (4). The main by-products obtained from soy are oil for human consumption, and flour used as a protein ingredient in balanced feed for domestic animals (mainly pigs and poultry). Furthermore, oil represents an option for the production of biodiesel (3). Soy protein contains all essential amino acids for humans, and it is the only protein of plant origin with a quality, valued by the score of its amino acids, of 100 %, comparable to proteins of animal origin, although it is limiting in an amino acid (methionine), so it is important that it be combined with a cereal (rice, quinoa, oats) or with animal protein to be able to form a good quality of protein (4,5). Soy represents 56 % of the total production of oilseeds grown worldwide, with Brazil, the United States and Argentina being the main producers and exporters in the world (6).

The South American country, which is the largest exporter, estimates that it will harvest around 123 million metric tons of oilseeds in the 2019-2020 season, surpassing its northern rival's harvest of 112.9 million (6). At the moment, world soybean production amounts to 354.5 million tons, 5.2 % (17.8 million tons) more than in the 2017/18 season (7), covering a total of 127 million hectares sown for an average yield per hectare of 2.8 tons (8). Part of these increases has been possible today, by using genetic engineering added to conventional practices as one more tool to improve or modify crops with the aim of obtaining higher yields and guaranteeing world food security (9).

There are a series of management practices that, although they should not be taken as a recipe, serve to meet the objective of a crop adequate establishment, which will allow maximum growth during the critical period and the most appropriate use of available resources. The environment defines the growth and development of the crop, and therefore the productive response of the chosen maturity group (10). Genotype-Environment interaction (GxE) is an extremely common phenomenon, fundamentally when evaluating: stability, specific and general adaptations of cultivars in a given environment, in which it is intended to be introduced, as well as the productive potentials and limitations of these in the localities (11). The maximum expression of the productive potential of the environment and the cultivar is achieved with a correct management of the crop that contemplates the choice of cultivars based on their yield and adaptation (12).

In these considerations, the objective of this work is to highlight the influence of the genotype-environment interaction in the soybean crop (*Glycine max* (L.) Merrill).

Taxonomy and morphological characteristics of the crop

Glycine max (L.) Merrill, as shown in Table 1, belongs to the Fabaceae (Leguminosae) family. It is an annual herbaceous plant, whose productive cycle ranges from three to seven months and a wingspan of 40 to 100 cm depending on the cultivar (13). The plant's air system; leaves, stems and pods are pubescent, varying the color of the beautiful ones from blond to brown more or less greyish. The leaves are alternate, trifoliate, green in vegetative state and turn yellow-brown at maturity, the stem is erect and branched (14). The flower is perfect (hermaphrodite), it is found in axillary racemose inflorescences in variable numbers, it is yellowish-white or purple, depending on the cultivar. The fruit is a pod dehiscent by both sutures, flattened, pubescent, with a length of 2 to 7 cm and a diameter between 1 to 2.5 cm, green in color when immature, which turns yellow, gray or black when ripe. Each fruit contains two to three rounded seeds, with a diameter of 5 to 10 mm (15). The root system is pivotal and can reach a depth of 15-30 cm, it is also capable of nodulation in symbiosis with bacteria of the genus *Rizobium* (16).

Table 1. Taxonomic classification of soybean crop (17)

Domain	Eukarya
Kingdom	Plantae
Division	Magnoliophyta
Class	Magnoliopsida
Subclass	Rosidae
Order	Fabales
Family	Fabaceae
Subfamily	Faboideae
Gender	*Glycine*
Species	*Glycine max* (L.) Merrill

Genetic characteristics of soy

G. max, as well as its ancestor *Glycine soybean* Sieb-Zucc have a chromosomal endowment 2n=2x=40 so they are diploid with two sets of homologous chromosomes with a pair of alleles per chromosome, where the transmission of characters from the parents to the offspring are of disomic inheritance (18).

The soybean genome (William 82) deciphered by a group of scientists from almost twenty research institutes, show that the DNA of this plant contains in its 20 pairs of chromosomes around 46.430 high-confidence protein coding genes, made up of something more than 1.100 million base pairs or nucleotides. With the genome sequenced, the scientific community today also has access to information on more than 20.000 species of legumes and can explore the extraordinary evolutionary innovation represented by symbiotic nitrogen fixation (18,19). Various studies with molecular markers indicate that cultivated soybeans present low levels of diversity due to the reduced genetic base from which most of the genetic improvement programs for soybeans in the world have started (20). Genetic information is the essential foundation of current crop improvement programs. Accurate information is required for effective monitoring of genomic variations, mapping of important trait *loci*, and discovery of new alleles (21) where wild germplasm constitutes a significant proportion of the genetic resources of the main crop species (22,23). The high-quality reference genome of wild soybeans is a crucial tool for use in such studies, because it increases the precision of the genetic analysis of populations (21).

During the domestication of the crop, hereditary changes have occurred that are being revealed by gene mapping and genome analysis, which has resulted in accessions from different geographic areas showing high genetic diversity (24). A striking feature of the soybean genome is that 57 % of the genomic sequence occurs in low-recombination, repeat-rich heterochromatic regions surrounding the centromeres. The average genetic-physical distance relationship is 1 cM by 197 kb in euchromatic regions, and 1 cM by 3.5 Mb in heterochromatic regions (24,25). The 93 % of recombination occurs in the euchromatic genomic region rich in low-repeating genes, which only represents 43 % of the genome. However, 21.6 % of the high-confidence genes are found in the repeat-rich regions in the chromosomal centers (25).

Genetic improvement of soy

The genetic improvement of plants is based on a complete understanding and application of the principles of genetics. It also requires knowledge of the factors that affect cultivar adaptation. The most important characters can be modified to a greater extent by the environment. This also leads to the fact that it is not possible to draw, with sufficient certainty, conclusions about the genotypic foundations of a trait from its phenotypic expression: $s_p^2 = s_G^2 + s_A^2 + s_{GA}^2$, the phenotype is equal to the Environment Genotype and the GxE Interaction. This has the consequence that different genotypes achieve the same yields by modifications (10,12).

The overwhelming majority of agricultural products that we know and use are not the result of plant natural evolution but of the human manipulation. The purpose of genetic improvement in crops is to enhance plants in relation to their environment and achieve a higher yield of their edible or usable fruits to satisfy their needs, in addition to contributing to the sustainability of agricultural production systems, through the development of genotypes adapted to new environmental requirements and new consumer market demands (26).

The use of methods for the genetic improvement of the soybean crop is the most economical and environmentally safe control to obtain highly productive cultivars under adverse conditions (obtain genetic gain for the yield and other characteristics associated with it in the environment). Self-pollinating species are generally bred by two methods, mutation induction and artificial hybridization, although the introduction of new varieties is not considered a breeding method, it leads to higher production yields (27). By improving the genetics of crops, the cost per ton produced is reduced and resistance to pests and diseases is achieved, while increasing the yields and quality of the grains (27,28).

The central objective of any program for the improvement of an economically important crop is the release of more productive cultivars, resistant to the most dissimilar conditions of commercial exploitation. It is estimated that the contribution of genetic improvement to increasing crop yields in general is around 50 % (29).

Genetic improvement programs in soybean cultivation focus mainly on the yield of seeds with high protein content and cultivars with genetic resistance to biotic and abiotic factors (28). These improvement programs have made a significant contribution to the productive improvement of soybeans, the yield from 1969 to 2010 increased at a rate of 28 kg ha year and it is estimated that 70 % of this increase was due to genetics (26).

Applied biotechnology for the genetic improvement of soybeans

In a broad sense, modern agro-biotechnology comprises two large areas known as "genetic engineering" and "selection assisted by molecular markers", whose complementation broadens the possibility of generating important qualitative and quantitative innovations for the crop. Genetic engineering results in transformed plants from the incorporation of genes that encode the expression of new characteristics for the species (30). The transfer of genes from one organism to another is a natural process that creates variations in biological traits. This fact underlies all attempts to improve species of agricultural importance, either through traditional breeding or through molecular biology techniques. Current methods, which allow a gene to be transferred from one organism to another, involve the same basic scientific processes that are applied in the crossing of species that allow farmers to carefully select and introduce beneficial traits to their crops (31).

In the case of genetic engineering it is the obtaining of varieties that produce the toxin of the bacterium called *Bacillus thuringiensis*. The transferred gene, called “Cry”, is known as “Bt gene”b (30). The events that contain it have genes that amplify the expression of the toxin, making it more efficient in the control of soybean worms, with a production up to 1000 times more than the synthesis encoded by the original bacterial gene (31). Another case is that of the varieties resistant to glyphosate, the transformation event "A 40-3-2" developed by the company Monsanto in the USA contains the CP4-EPSPS gene that intervenes in metabolic pathways, giving plants resistance to the herbicide (31). At the disposal of the breeding companies, it made possible the creation of the well-known “RR varieties” that quickly took over almost 100% of the cultivated area (30,31).

A large number of transgenic varieties are in the development stage. Genes have been transferred that increase yield, provide resistance to biotic factors (fungi, bacteria, viruses, nematodes, insects), abiotic factors (drought, heat, cold, salinity), tolerate other herbicidal molecules or present a nutritional and energy balance that prioritizes the presence of valuable amino acids and fatty acids (32). In 2018 in the United States, 9 biotechnological events were approved, 3 correspond to soybeans, 4 to corn, one to potatoes and another to alfalfa. Meanwhile, 2 events were approved in 2017, one of them also corresponds to soy; there were 6 in 2016, half were soybeans, and 5 were approved in 2015, of which three were oilseed (32).

Assisted selection is very useful in breeding. Markers are DNA sequences whose expression is identified at the molecular level and have a known location in the genome. By linking genes of interest with a molecular marker, it is possible to select carrier varieties with a higher probability of success than in traditional selection (31).

The ISAAA (International Service for the Acquisition of Agro-biotechnological Applications) has published the report on the growth of transgenic crops in the world 2018, and this document highlights that 26 countries have cultivated 191.7 million hectares of modified products genetically. The report points out that the four main biotech crops, corn, soybeans, rapeseed and cotton, have been the ones with the greatest presence in the 26 countries, being the leading soybean with a total of 95.9 million hectares, representing an increase of 2 % compared to 2017 data. The most widely used technology is herbicide tolerant soybeans (33).

In soybeans, biotechnology has played and will continue to play a valuable role in public and private breeding programs. Based on the availability and combination of conventional and molecular technologies, a substantial increase in the rate of genetic gain can be predicted for economically important traits in the next decade (34).

Conventional breeding strategies are still very important for the genetic improvement of crops. However, the cultivation of soybeans is still a great challenge, because it is self-reproducing and the genetic diversity of the cultivars currently used is quite narrow. Most of the soybean genotypes used today are derived from common ancestors, limiting breeding strategies to produce more genetically improved soybean cultivars (33,34).

Genotype-environment interaction

The first concern when starting a breeding program is to define whether the objective is the development of cultivars in a wide spectrum of environments or the development of a cultivar highly adapted to specific environments (35).

Plants can adjust to variations in their environment due to the plasticity shown by their genotypes, where the contribution of the environment represents a high proportion of the phenotypic value, the selection effect is reduced and the improvement progress is slow, decreasing the correlation between phenotype and genotype and makes it difficult to appreciate the genetic potential of cultivars. The productive potential of the environment can condition the compensation expressed by the crop in growth and yield, where the compensation capacity through its plasticity translates into stability in grain yield (35,36).

The genotype environment interaction (GxE) arises as a result of changes in the ordering of cultivars as the environment changes and complicates the cultivar evaluation and recommendation process (35).

Studies on GxE are very useful in crop genetic improvement programs, because the genotype responds differently to different environments, so this interaction effects are not statistically additive (37). In this last stage of the breeding program, work is generally carried out within several environments, with experimental differences where the so-called GxE is an important component of phenotypic variability (38). In this way it is affirmed that the phenotypic expression (F) of the different characters is dependent on the genotype (G), environment (E) and GxE (35).

Therefore, GxE refers to the differential behavior of genotypes through variable environmental conditions, frequently described as the inconsistency of behavior between genotypes from one environment to another, and when this occurs in a large proportion, it reduces the genetic progress of selection (39).

The new genotype formation requires genetic material evaluation in different environments and the measurement of the genotype-environment interaction, which gives an idea about the phenotypic stability of genotypes in the face of environmental fluctuations (40). Phenotypic stability refers to the constant behavior without variation of a genotype through all the environments where it is evaluated, regardless of the conditions that are favorable or not for the culture (35).

For the analysis of GxE and stability, several statistical procedures have been used including univariate and multivariate methods. The most widely used multivariate method is the Principal Additive Effects and Multiplicative Interactions (AMMI) method, considering that the effects of genotypes and the environment are additive and linear. This statistical method not only allows estimating stability, but also to evaluate localities and as a consequence classify environments (41). Another parameter that is also analyzed within the GxE is adaptability, which is nothing more than the ability to take advantage of environmental variations, where the ecotype is capable of exhibiting highly predictable behavior even with environmental variations (35).

Statistical methodology to determine the GxE

Analysis of variance (ANOVA): the sources of variation depend on the number of locations and times under study. It provides information on the relative stability for individual genotypes, the sources of variation are divided into main effects and their respective interactions.

Regression analysis and principal components (PCA): a regression analysis of the yield of each variety is carried out on the environmental index of each locality, in order to estimate the stability of the genotypes. A stable variety is considered when the regression coefficient is equal to or close to 1.

Environmental index: it is nothing more than the yield potential of each locality, it is the difference between the average yield of the varieties in the locality and the variety average in all the localities in which the evaluation was carried out (35).

The method of additive main effects and multiplicative interactions (AMMI): allows evaluating the effects of GxE interactions simultaneously by means of a graphical representation in multivariate scatter diagrams. This last method combines the ANOVA and PCA techniques. The model assumes additive components for the main effects of the genotypes and multiplicative components for the interaction (35,42). A variety is considered stable when it shows a regression coefficient close to 1 and the sum of its deviations close to zero (42).

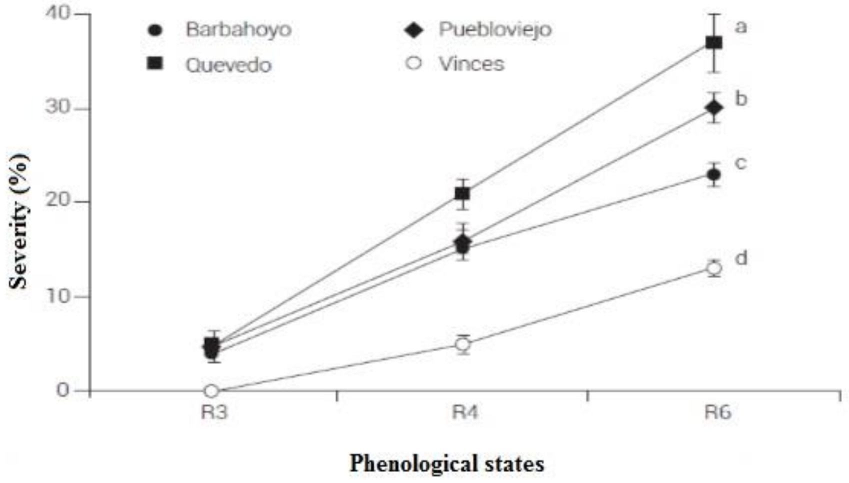
In a genetic improvement program, multi-environmental trials are usually conducted to evaluate genotypes and gain precision in the selection of those with the best performance for a given environment. In soybeans, these breeding programs aim to develop high-yielding cultivars with the widest possible adaptation to simplify cultivar choice and seed production procedures (43).

Although a particular soybean cultivar is grown in a defined area depending on the maturity group to which it belongs, within each area there are very different agro-ecological conditions. From this fact derives the need for a cultivar to spread in the market, it has to maintain a good yield in environment range in which it is grown. This strategy involves conducting repeated trials in space and time, and subsequently evaluating them together (44).

Seven soybean genotypes were studied, So ITAV 1, So ITAV 2, So ITAV 3, So ITAV 4, So ITAV 5, So ITAV 6 and So ITAV 7 developed at the University of Guayaquil, Ecuador, and a commercial variety to know its adaptability and phenotypic stability, grain productivity and resistance to Asian rust (Phakopsora pachyrhizi). In the 2015, 2016 and 2017 seasons, eight trials were planted in representative environments of Los Ríos province, Ecuador, under a randomized complete block experimental design with four replications. Agronomic characteristics of the plant and yield and its components were evaluated, to which an analysis of variance and multiple comparisons of means were carried out by the Tukey test ($p \leq 0.05$). Additionally, the association between performance components was studied using Pearson correlations and linear regression. The additive main effects and multiplicative interaction model (AMMI model) was used to evaluate genetic stability.

Main results

The INIAP-308 variety obtained the lowest loading height (12.02 cm) and plant height (53.25 cm), with averages of all genotypes of 16.15 and 68.89 cm, respectively. Likewise, the INIAP-308 variety, with 41.13 d, was the earliest genotype. However, this same variety reached (111.63 d) in the R8 phenological state later (Figure 1) (42).

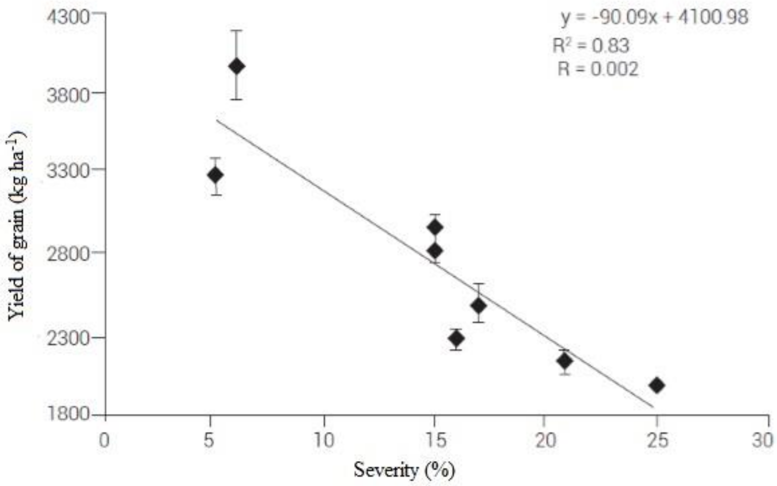


Taken from Revista Fitotecnia Mexicana

Figure 1. Average severity of Asian rust of eight soybean genotypes in phenological states R3 to R6 in four environments of the Ecuadorian coast, in the years 2015 to 2017

The number of grains per pods and grain yield were statistically different between genotypes. The So ITAV 7 line, with 2.72, obtained the highest number of grains per pod.

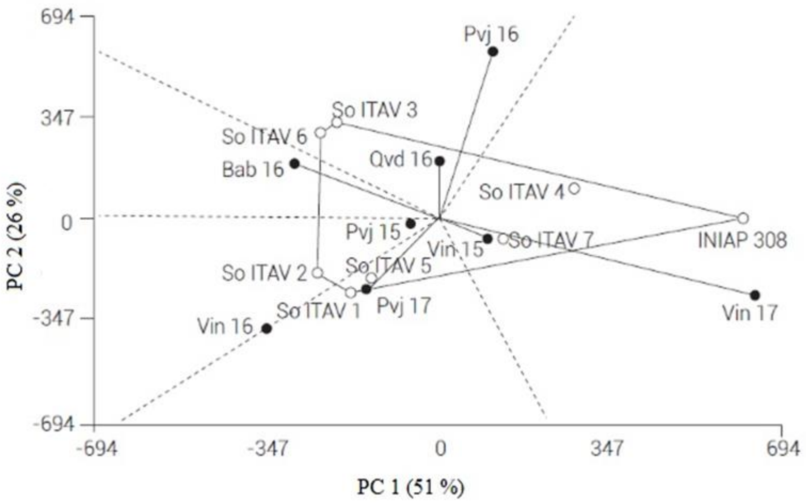
The grain yield of this genotype (2917.25 kg ha^{-1}) was similar to the rest of the lines, but statistically higher than the control commercial variety INIAP-308 (2594.50 kg ha^{-1}) (Figure 2) (42).



Taken from Revista Fitotecnia Mexicana

Figure 2. Regression between the severity of Asian rust and the yield of eight soybeans, using the average of all localities studied during the 2015 to 2017 seasons

The So ITAV 7 line obtained the highest grain yield and stability. Regarding the environments, Vinces season 2017 was the most variable, and Puebloviejo season 2015 recorded the least variation. The Babahoyo season 2016 and Vinces season 2017 environments registered the greatest differences. The soybean genotypes established in the Vinces locality showed the least severity of Asian rust, compared to other localities (Figure 3) (42).



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Environments Vin15, vin 16, Vin 17, Pvj 15, Pvj 16, Pvj 17, Bab16, Qvd 16 = Vinces 2015, Vinces 2016, Vinces 2017, Puebloviejo 2015, Puebloviejo 2016, Puebloviejo 2017, Babahoyo 2016, Quevedo 2016

Figure 3. Representation of genotypes and environments with respect to the first two axes of principal components of the AMMI model for grain yield in eight environments of the Ecuadorian coast, between the years 2015 to 2017

CONCLUSIONS

- This study showed the determining influence of the genotype-environment interaction in the improvement programs to obtain new cultivars and genotypes that are more stable and with better specific adaptation when making the selection and that the development of strategies that integrate traditional plant breeding with modern molecular techniques they favor the genetic improvement program of crops.
- Knowing the role of this interaction, allows increasing the crop yield and the environments and localities where greater stability and adaptation are present can be exploited more efficiently.

RECOMMENDATIONS

Check the influence of the GxE interaction in the improvement programs as well as the implementation of modern molecular techniques that favor the genetic improvement program of crops.

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