Bibliographic review

Analysis of the genotype environment interaction in the potato crop (*Solanum tuberosum* L.)

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ABSTRACT

The study of the genotype environment interaction is one of the determining factors in the selection and recommendation of cultivars, which allows to increase the efficiency of the genetic improvement. With the aim of highlighting the importance of the analysis of the genotype environment interaction in the last stage of genetic improvement in potato cultivation, this bibliographic review was carried out, where essential aspects of the crop are collected, such as its taxonomic classification, main characteristics morphological and genetic, as well as elements to take into account for the genetic improvement and analysis of the genotype environment interaction in this crop. It is concluded that knowing the magnitude of the interaction genotype environment for a cultivar in specific environments previously, allows identifying more stable genotypes or with better specific adaptation when making the selection and recommendation of the cultivar in the final stage of genetic improvement.

Keys words: genetic improvement, adaptation, stability, selection

INTRODUCTION

Solanum tuberosum L. (Family Solanaceae, Petota Section) [(1, 2)] comes from wild species found north of Lake Titicaca, southern Peru [(3)]. It is one of the most important food crops spread worldwide [(4)]. As regards production and nutritional importance, the potato occupies the fourth place after rice, wheat and corn [5]. The annual world production is approximately 377 million tons and covers around 19 million hectares for an average yield of 19.5 tha^{-1} [6]. The need to meet the demand for food worldwide is increasing every day, in that sense, the use of crop breeding is essential and becomes an alternative to achieve productive demands [7].

In Cuba, the potato occupies the first place among the roots and tubers and is planted every year around 6'600 ha in six provinces (Artemisa, Mayabeque, Matanzas, Cienfuegos, Villa Clara and Ciego de Ávila) with an average yield between 18 and 25 t ha^{-1} and an annual production between 200,000 and 300,000 t. Due to the large planting extensions and the preferences of consumers towards the crop, it is considered one of the most important food [8].

In the final stage of genetic improvement, the study of the Genotype x Environment interaction is a matter of relevance, since it is one of the determining factors in the selection and recommendation of cultivars [9].

The Genotype x Environment interaction highlights the importance of the environmental effect on adaptation and varietal behavior. Their study helps increase the efficiency of improvement [10].

Knowing the magnitude of the Genotype X Environment interaction allows assessing the stability of the cultivars in the range of environments in which they want to be introduced, as well as the productive potentials and limitations of these in the localities [11].

Based on the above, the objective of this work is to deepen some aspects of the genotype environment interaction in the genetic improvement of the potato crop (*Solanum tuberosum* L.).

Potato Biology

Taxonomic classification and morphological characteristics of the potato

Potato (*Solanum tuberosum* L), as Table 1 shows, belongs to the Solanaceae family. It is an herbaceous, dicotyledonous plant, equipped with an aerial and other underground system of rhizomatous nature from which the tubers originate [12]. The potato plant according to the varieties has an erect or semi-right growth. The tubers are modified stems and constitute the reserve organs of the plant; they vary in size, shape and skin color and mass. The buds or eyes of the mature tuber remain dormant (dormancy) until they develop a stolen from which a new plant originates. The leaves are compound and the flower is bisexual. The ripe fruit is a berry usually dark green and contains the seeds, called botanical seeds, to differentiate them from the tuber-seed [13].

Table 1. Taxonomic classification of *Solanum tuberosum* L. (Modified from [1,2]

Kingdom	Plantae
Division	Magnoliophyta
Class	Magnoliopsida
Subclass	Asteridae
Family	Solanaceae
Gender	Solanum
Subgenre	Potatoe
Section	Petota
Series	Tuberosa

Potato genetic characteristics

The cultivated potato *S. tuberosum* ssp *tuberosum*, as well as *S. tuberosum* ssp *andigena* are autotetraploid (2n = 4x = 48 chromosomes). In this way, the transmission of the attributes from parents to children involves a tetrasomic inheritance, where chromosomes segregate and bias linkage estimates. An autotetraploid has four sets of homologous chromosomes with a pair of alleles: A (dominant) and a (recessive), located in a locus along the chromosome; three kinds of gametes can be formed after meiosis: AA, Aa and aa being the same diploids [14,15]. After fertilization it is possible to obtain five different types of genotypes with these two alleles: quadruples (AAAA), triptychs (AAAa), duplices (AAaa), symplices (Aaaa) and nulliplices (aaaa). From the above explained it is clear that by the tetrasomic inheritance it can be expected in the progeny that the highest proportion of phenotypes present the dominant gene while a small proportion would be of aaaa genotypes [15].

The diversity of a tetraploid loci results in a maximum heterozygosity with six first-order, four second-order and one third-order dominance interactions. A trialleic loci has three first-order interactions, two second-order interactions, while a dialectic loci has only one first-order interaction and an allelic monkey does not have intralocus interactions [16].

Diploids (2n = 2x = 24 chromosomes) comprise the majority of cultivated wild species, indicating a disomic inheritance. In this way, the study of inheritance and the combination of specific genes is easier than the previous one, therefore, population improvement is more efficient, but greater performance and adaptability at the tetraploid level is expected [17].

A phenotype has measurable characteristics by individuals in a population. Some traits are known to be inherited in a Mendelian way. This means that they are not relatively affected by the environment, they are inherited by segregation of alleles by a simple locus. They are simple genes whose phenotype can be given in a small number of discrete forms. In a diploid organism a simple locus can be represented by the same or different alleles called homozygous and heterozygous. Examples: The P locus with two P and p alleles, the PP and pp genotypes are homozygous, the heterozygous genotypes produce two types of P and p gametes in equal proportion due to meiotic segregation (Table 2) [18].

Table 2. Gametes produced by diploid genotypes

Diploid Genotypes	Gametes	Genotypes
PP	all (P)	Homozygous
Pp	all (p)	Homozygous
Pp	(P) and (p)	Heterozygous

In the case of Complete Dominance, the recessive allele can be expressed only in the homozygous state. The dominant allele is expressed both in the homozygous and the heterozygous state, therefore, each genotype will have its phenotype as stated above. With three genotypes, six different combinations can be performed [18].

Tetrasomic inheritance presents advantages and disadvantages for genetic improvement over disomic inheritance. According to the currently accepted theory of potato heterosis, interactions within and between locuses are very important for performance determination [19].

In diploids the maximum number of different alleles per locus is two and only an interallelic A1A2 interaction is possible, that is, a single heterogeneous form, while in a polysomaltetraploid, with a maximum possible number of four different alleles per locus can exist 11 interactions per locus [20].

The interactions can be tetralelic (A1, A2, A3 and A4); trialélica (A1A1, A2 and A3); dialectic (A1A1A2A2, A1A1A1A2) or mono-allelic (A1A1A1A1). The tetrasomic level is considered of higher productivity than the disomic level, since it harbors more genetic diversity per locus, therefore it will have greater possibilities of heterotic responses [21].

Experimental data obtained in potatoes and other natural tetrasomictetraploids (alfalfa) and induced (autotetraploid corn and rye), argue that the theory of tetrasomic inheritance is more complex than disomic inheritance. Therefore, numerous progenies are required to perform any genetic study. For example, if you consider a locus with two alleles, A and a. In one diploid three genotypes are possible: AA, Aa and aa, in contrast, in a tetraploid five genotypes are possible: AAAA (quadruplex), AAAa (triplex), AAaa (duplex), Aaaa (simplexo) and aaaa (nuliplex). Consequently, segregation in diploids can occur as a result of single genotype mating, Aa, while in tetraploids it can occur by mating three genotypes, AAAa, AAaa, Aaaa [22].

When a heterozygous individual is self-fertilized for a locus, the probability of obtaining recessive homozygous offspring is ¼ in diploids and 1/36 in duplex tetraploids. In addition, phenomena such as incomplete dominance and double reduction can increase the complexity of tetrasomic inheritance compared to dysomic. This complexity can be a real obstacle when it is desired to recover certain recombinant genotypes in the offspring, especially for characters controlled by origins, such as yield or resistance to some diseases [22].

Potato genetic improvement

The optimal improvement plan is one capable of maximizing the possibilities offered by the species to be improved [23]. Well-directed genetic manipulation has opened the doors to exploit much more rapidly (few generations) the great attributes of wild species [24].

Plant genetic improvement can contribute by improving the degree of sustainability of agricultural production systems, by developing genotypes adapted to new environmental requirements and new demands of the consumer market [25].

The central objective of any program to improve a crop of economic importance is the release of more productive cultivars, resistant to the most dissimilar conditions of commercial exploitation [26].

The progress of the improvement depends on the genetic systems and the selection methods available, when the characteristics are inherited in a dominant gene in a single dose and when the presence of such genes is a complete protection against a disease or a clear reaction defined, or on the contrary if this protection or clear reaction of the plant does not exist or in the absence of the gene, progress in the improvement can be made quickly. The process of improvement is much slower when the genetic system is polygenic and the reaction of the plants is intermediate (27).

At present, in many countries, work is being done to improve the potato, with the traditional way as a fundamental way, and in turn work and research in new ways that make this work safer and more dynamic (28).

Generate potato cultivars that meet the demand of farmers, merchants, industrialists and consumers in general and that have attributes of precocity, higher yield, culinary quality and resistance to The main biotic and abiotic factors that affect the potato are the most important objectives of the genetic improvement of the potato (5).

The fact that the potato is autotetraploid and that the environment has a strong effect on its development, makes it very difficult to determine the inheritance of many of its characters. Some characteristics are determined by a single dominant gene, while others are governed by a polygenic system (4).

Genotype-environment interaction

The study of genotype-environment interaction (IGA) is a topic of relevance in the final stage of genetic improvement, being one of the determining factors in the selection and recommendation of cultivars (9).

In this last stage, work is generally carried out within several environments, with experimental differences where the so-called IGA is an important component of phenotypic variability (29) and determines a differentiated behavior of genotypes (30).

When the contribution of the environment represents a high proportion of the phenotypic value, the effect of the selection is reduced and the progress of the improvement is slow, reducing the correlation between the phenotype and the genotype (31).

In this way, the IGA can be defined as the relative differential behavior that genotypes show when they are subjected to different environments; or expressed in other terms, it is the inability of a genotype to respond similarly when planted in different environments, this interaction reduces the association between genotypic and phenotypic values and forces plant breeders to consider the stability or adaptability of materials (32). The IGA is a characteristic that will be evaluated in the outstanding genotypes with the purpose of selecting those with less interaction in the region of interest and whose response in performance is increased as conditions improve [33].

Therefore, for the determination of IGA, genotypes must be evaluated in different locations, years and even times [34].

The term "locality" indicates spatial variation, while environment is a general term that includes all the conditions under which plants grow, and can encompass places, years, management practices or a combination of these factors. Commonly each place / year is considered a separate environment. The IGA shows the importance of the environmental effect in adaptation and varietal behavior. Their study helps increase the efficiency of improvement. It is important that the trials cover a representative range of environmental conditions (spatial and temporal variation) to determine genotypic responses [10].

To assess the agronomic behavior of the cultivars generated, it is necessary to measure the relative stability of the genotypes submitted to all the predominant environments in a potential adaptation region. In addition, the concepts of adaptability and stability must be integrated to define the behavior of genotypes evaluated through contrasting environments [35].

These two terms are of great importance when addressing this issue. First of all stability is defined as uniform behavior and predictable over time (semesters or years) or agronomic practices of a certain genotype in a given location [32], or in other words refers to the ability of genotypes to show highly predictable behavior based on environmental stimulation [35]. Second, adaptability is the uniform and predictable behavior of a particular genotype across different locations [32], or the ability of genotypes to advantageously take advantage of environmental stimuli [35]. Other researchers use the terms as synonyms [32].

Knowing the magnitude of the IGA allows to evaluate the stability of the cultivars in the range of environments in which they want to be introduced and also the productive potentials and limitations of these in the localities [11].

In Cuba, the importance of such interaction in different crops has been discussed [36,29,37], which is why it is currently common in the selective process and has been replicated in its two main senses: spatial and temporal; however, this is always limited by the problems of cost and operability when executed centrally by the research centers [30].

In the case of the potato that basically its reproduction is asexual (many individuals with the same genotype (clones) can be produced and planted) effects can be observed in different environmental conditions, observing marked effects of the environment on the phenotypic expression of these, being due work to reduce the environmental effect by using appropriate experimental designs (28).

There are several methodologies that are used to determine the IGA, including univariate and multivariate methods (38). Taking into account the terms of stability and adaptability as synonyms, there are methodologies based on analysis of variance, for these, several methods have been proposed, but always with some difficulty (32). However, Wrike in 1962 proposed the ecovalence method (32,28) based on the IGAs, which are distributed among the genotypes: those with low participation in the value of the IGA are considered stable and with a small ecovalence, opposite for those with great participation (32). There are also the methodologies based on the regression. These include the method proposed by Finlay and Wilkinson in 1963 (32,28), where a regression analysis of the performance of each variety is performed on the environmental index of each locality, in order to estimate the stability of the genotypes . In 1966, Eberhart and Russell modified this proposal by incorporating deviations from the regression line as a second stability criterion (32). This is also known as the stability method (28). The plant improver looks for high yield varieties, with a regression coefficient close to 1 and regression deviations as small as possible (32).

However, at present, multivariate methods are very useful tools for data analysis and especially for improvement (28). One of the most widely used multivariate methods is the Main Additive Effects and Multiplicative Interactions (AMMI) method, since the effects of genotypes and the environment are considered additive and linear, which allows it to be study by analysis procedures of variance, while the IGA has multiplicative effects that can be explained through principal component analysis (ACP) (39).

These models aim to explain the interaction associated with a bifactorial ANOVA, from a simultaneous representation of rows (genotypes) and columns (environments) and give the possibility to study the degree of stability of genotypes, when tested in different environments (40).

In addition, it can be useful for the identification of genotypes of high productivity and adaptability, zoning of crops for purposes of regional recommendation and selection of evaluation locations (41).

Also, they are effective for various purposes such as understanding genotype-environment interaction, which includes classifying environments, improving accuracy in estimated performance, which increases the probability of successful selection of genotypes with high yields, estimate missing data, increase the flexibility and efficiency of experimental designs (42).

This method allows to represent the results from the Biplot model, from the decomposition of the genotype-environment interaction into values and vectors, allowing simultaneous representations of individuals and variables, where the variables can be years, localities or both at the same time, and in this way the most stable genotypes can be identified (43). In this way the markers of genotypes and environments will be joined in a two-dimensional plane. To obtain the so-called "markers" it is necessary to multiply the singular value λ to the results of the genotype vectors (ug) and / or the environment (ve) (44).

The Biplot model is a tool that has increased its popularity among plant breeders and other agricultural researchers and is widely used in the evaluation of cultivars and in the investigation of mega-environments, since it allows us to examine through the IGA, the ability to discriminate and the representativeness of the test environments, as a convenient measure of defining homogeneous mega-environments (45). Mega-environment is the set of environments where some cultivars perform similarly and differently from the response obtained in other environments or sets of environments (42).

Principal Component Analysis (ACP) has been the most widely used multivariate statistical technique in the classification of environments, due to its ability to reduce the original variables sufficiently well correlated in a few factors or uncorrelated components, capable of explaining, in to a large extent, the variability of the original sample (46).

In the ACP the values of the axes describe the response patterns of the genotypes, by means of a sensitivity index, the positive values describe the genotypes with the best performance in high performance environments, and the opposite occurs with the negative scores. A value of zero or close to this corresponds to a genotype with medium sensitivity. When in the ACP a genotype has a value close to zero, the interaction is small; when both ACP values have the same sign, their interaction is positive; If they are different, it is negative [47].

CONCLUSIONS

Knowing the magnitude of the Genotype X Environment interaction for a crop in specific environments beforehand, allows to identify more stable genotypes or with better specific adaptation when making the selection and recommendation of the cultivar in the final stage of genetic improvement. In addition, their knowledge provides tools to increase the yield of crop sowing campaigns, since the locations where there was greater stability or adaptation depending on the objective being pursued can be exploited more efficiently.

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