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Review

Genetic adaptability of inheritance of resistance to biotic and abiotic stress level on crop: Role of epistasis

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Several studies that attempt to identify the genetic basis of quantitative traits ignore the presence of epistatic effects and theirs role in plant genetic adaptability. Epistasis has been detected in the inheritance of many quantitative traits on crop. Moreover, generation means analysis of several traits assessed in diverse environmental conditions revealed that the mode of inheritance of each trait varied with the biotic or abiotic stress level. With less stress level, only additive and dominance effects was found significant. In contrast with moderate and higher stress level, epistatic effect was induced. Thus, a relationship was found between the complexity of model of inheritance and stress level. When the biotic or abiotic stress increases, epistasis effect was solicited and the more the stress increase, the amplitude of epistasis was more important and the model of inheritance was more complicated. This result was showed for resistance to 15 isolates of *Septoria tritici* in durum wheat with different levels of aggressiveness; for resistance to six isolates of *Phytophthora nicotianae* in pepper and for resistance to five salt concentrations at germination stage in durum wheat. Indeed, the generic effects of environment on genetic model of inheritance complicate the procedure of amelioration of quantitative traits. Hence, it is becoming evident that plant genetically expressed differences when operated in wide range of environments, and epistasis play a crucial role in genetic adeptness. The best way of crop breeding must therefore be investigated in each special environment.

Key words: Epistasis, quantitative traits, genetic adaptation, environment.

INTRODUCTION

There is limited knowledge on the importance of epistasis on inheritance of quantitative traits on crops and theirs role in plant genetic adeptness. The mechanisms implicated in the control of quantitative traits is so complicated and dependent upon many factors, the genetic background of the genotype, the environmental effects and genotype by environment interaction (Lynch and Walsh, 1998). Interactions among loci or between genes and environmental factors make a substantial contributions to variation in complex traits. Nonetheless, many studies that attempt to identify the genetic basis of quantitative traits ignore the possibility that loci interaction (Carlborg and Haley, 2004). In quantitative genetics, inheritance of quantitative traits is based on a model simple and restrictive, where several parameters such as epistatic effects are assumed negligible (Phillips, 1998).

In contrast, epistasis is common in gene systems that determine quantitative traits, it is also a major problem in studies of these traits because it complicates the interpretation of genetic experiments and makes predictions difficult (Viana, 2000). The importance of epistasis is not well understood, and its contribution to quantitative variation was once considered to be small (Crow, 1987). Thus, the genotypic component of an individual is not only dependent upon the genes at the loci of interest, but also with the genetic interaction and the rest of the genetic background. Recently, epistatic effects were considered as important for complex traits by many researchers (Checa et al., 2006; Aruna and Nigam, 2009; Dashti et al., 2010; Kumar and Prakash 2011; Toledo et al., 2011; Hussain et al., 2011; Paul et al., 2011).

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Epistasis has substantial impacts on evolution, particularly in the rate of adaptation (Chou et al., 2011). The future of agricultural productivity and sustainability depends on the ability of crop plants (field crops) to grow and be productive in response to changing environments.

Adaptability is defined as the ability of a crop (or variety) to respond positively to changes in agricultural conditions (Chloupek and Hrstkova, 2005). Adaptation to stresses like cold, drought or diseases are among the most central problems in the world trying to grapple with food security (Ulukan, 2008). Genotype by environment interaction (GE) has been reported in numerous studies under several designations, e.g. different response patterns, adaptation, or stability of genotypes (Voltas et al., 2002). Genetic adaptation may be accompanied by a phenotypic variation and in this case it is detected in the form of interaction between genotype and environment. However, the number of gene solicited and theirs interactions can change from an environment to another without touching the phenotypic variance of the trait assessed. In this last case, there is a considerable lack of information, and no study has been interested to this type of genetic adaptation. Plant genetic adaptability is of primary importance in many aspects of genomic research and is a special priority in the study of major crops grown in a wide range of environments (Saranga et al., 2001). Plants provide unique opportunities to study the mechanism basis and evolutionary processes of adaptation to diverse environmental conditions (Anderson et al., 2011).

However, inheritance could not be understood solely by examining the action of individual genes (Phillips, 2008). Adaptation is generally a quantitative complex feature of an organism, involving many traits such as developmental, behavioral, morphological (adventitious or tap root system), physiological (accumulation of some chemical compounds), reproductive (prolonged seed viability), etc. (Gould, 2002). Significant progress has been made toward linking phenotype and genotype for a number of plant traits and genes. Quantitative traits are affected by many genes that act singly and in interaction with each other (Reif et al*.,* 2009). The objective of this study was to provide the importance of epistatic effects in inheritance of quantitative traits and their role in plant genetic adaptability to the biotic and abiotic stress levels.

WHY EPISTASTIC EFFECTS ARE NEGLECTED OR CONSIDERED NONEXISTENT

Poor tradition

Epistasis has long had two different definitions depending on the context in which it is discussed. The classical definition describes an allele at one locus completely masking the effect of an allele at a second locus (Mendelian viewpoint). In quantitative genetics, epistasis encompasses a wide range of interactions and can be extended to more than two loci. These two definitions coexist because they are typically applied to different types of study populations and different types of traits (Aylor and Zeng, 2008). According to Lukens and Doebley (1999), the inheritance of quantitative traits is based usually on the additive model that is highly simplified and restrictive. Indeed, quantitative traits are controlled not only by several genes with individual effects (additive effects) but also by interactions between genes (epistasis) and between genes and environment. However, the majority of geneticists are only interested to classical epistasis based in Mendelian viewpoint (Phillips, 2008). How genes combine to determine the phenotype of a quantitative character? The simplest case is to admit that the genes are expressed individually, but in reality genetic interactions are present (Hill et al*.,* 2008).

Extensive works in inheritance of qualitative traits had highlighted the importance of classical epistasis at a ‘locus-by-locus’ level. Many authors have admitted that genes contribute additively (Morton, 1974; Rao et al., 1976, 1979) and others have considered the non-additive effect is due to dominance effects (Jinks and Fulker, 1970; Jinks and Eaves, 1974; Rao et al., 1982). Although, the advent of molecular markers in 1980 has opened new perspectives for the identification of loci involved in the variation of quantitative traits (QTL), however, these approaches are focused in the individual QTLs effects and genetic interactions are ignored or considered negligible

Complexity of model and lack of methods of investigation

Genetics quantitative is largely influenced by the additive theory (Wagner et al., 1998). Epistatic effects are not involved in genetic studies for the theoretical complexity of the statistical studies by introducing the epistatic component (Viana, 2000). Until recently, empirical work on this fundamental issue has been limited partly because of the absence of reliable quantitative genetic approaches for quantifying epistasis (Whitlock et al., 1995; Fenster et al., 1997). The presence of this component leads to an over-parameterization and identification of the parameters of model becomes complicated. According to Viana (2000, 2005), the components of epistatic effects are not usually estimated in genetic studies due to lack of investigative methods, except those based on Generation Means Analysis (Mather and Jinks, 1974) and “Triple Test Cross” analysis (Kearsey and Jinks, 1968) and the high number of generations to be produced and assessed.

Importance of epistasis in inheritance of quantitative traits

Based in several studies realized in our laboratory, we found that epistatic is a crucial component in inheritance of quantitative traits. Generation means analysis of several quantitative traits assessed for 10 years on three crops (*Triticum durum*, *Avena* sp. and *Capsicum annuum*) revealed the importance of epistatic compared to additive and dominance genetic effects. For resistance to yellowberry in durum wheat Bnejdi and El Gazzeh (2008) showed the rejection of the additive dominance model and the epistatic model was found appropriate for all cases. For resistance to *Phytophtora nicotianae* in pepper, the epistatic model was revealed as adequate for all combinations cross-isolates (Bnejdi et al., 2009). For resistance to *Puccinia coronata* in oats (Bnejdi et al., 2010a), inheritance of this traits revealed that the digenic epistatic model with maternal effects was found adequate for all combination cross-isolate. Also, for grain protein content in durum wheat, the additive dominance and the digenic epistatic models were found adequate in three cases and five cases, respectively (Bnejdi and El Gazzah, 2010). Recent studies suggest that epistatic effects are present for resistance to pests or diseases in many species. Examples are wheat and Fusarium head blight (Waldron et al., 2008), sesame and powdery mildew (Rao et al., 2011), common bean and Fusarium root rot (Mukankusi et al., 2011), barley and Fusarium head blight (Flavio et al., 2003), maize and common smut (Namayandeh et al., 2011). Using molecular markers, Lin et al. (2000) reported the existence of epistatic interactions between three QTLs controlling heading date in rice.

Epistasis and genetic adaptability to the level of biotic and abiotic stress

One of the major topics of discussion is the effect of biotic and abiotic stress levels (aggressiveness of isolates or salt concentration) in the determination of the expression of genes and their interactions. Based in extensive works realized in our laboratory, inheritance of the majority of the quantitative trait was not stable as considered by many geneticists and can change with the stress levels. Thus, the contribution of individual genes effects and their interactions on phenotypic expression were largely dependent upon the environmental conditions. The model of inheritance was simple to complicated, depending upon environmental constraints. With low stress levels, plant solicits only the individual gene effects (additive and dominance effect). While with moderate and higher stress levels, epistasis was induced and a relationship was found between genetic interaction and stress levels. Examples are: for resistance to different salt treatments (50, 75, 100, 150 and 200 mmol) at germination stage in durum wheat (Bnejdi et al., 2011a). Generation means analysis indicated that, with low salinity level (50 and 75 mmol/L), only additive and dominance effects were implicated in the genetic control of this trait. For moderate salinity level (100 and 150 mmol/L) in the two crosses, genetic interactions were solicited and the digenic epistatic model was sufficient to explain variation in generation means. However, for the 200 mmol/L treatment, none of these models explained the variations in generation means and probably, higher order interactions or genes linkage were solicited.

Li et al. (2000, 2001) report significant micro-geographical genetic differentiation of populations of *Triticum dicoccoides* (wild emmer wheat) in response to water and aridity stresses. Similar result was showed for inheritance of resistance to *S. tritici* in durum wheat (Bnejdi et al., 2011b). Generation mean analysis revealed that the mode of inheritance was dependent upon the aggressiveness level of isolates. With less aggressive isolates, only additive and dominance effects were implicated in the genetic control and epistasis was not induced. However, with moderately aggressive isolates the genetic interaction effects were introduced and the digenic epistatic model was found appropriate, thus indicating that epistasis was an integral component. For isolates with a greater aggressiveness level, none of the models explained the variations in generation means, and probably higher order genetic interactions or linkage effects were present. The relationship between aggressiveness level and the complexity of the model of inheritance was reported for resistance to salt at germination stage in durum, for resistance to *P. nicotianae* in pepper and for resistance to *S. tritici* in durum wheat (Bnejdi et al., 2011a,b, 2010b).

The variation of the model of inheritance from simple to complicated with stress level indicate that the expression of genes and their interactions was not stable and was site-dependant. Li et al. (1999) found that microclimatic selection appears to play an important role in DNA differentiation as well as in protein polymorphism. Recently, Ouiza et al. (2010) reported that the accumulation of proline increase with the intensity of salinity. Khattak et al. (2001) showed that the genes controlling seed yield per plant, and 1000 seed weight in mungbean are sensitive to the environment. Similar results were also found by Braam et al. (1996), who reported that the regulation and functions of the Arabidopsis TCH genes were dependent upon environmental stress.

The exploitation of epistasis is of great importance to plant breeders (Parvez et al., 2007). Epistasis of the additive x additive type could be exploited in a breeding program with the additive component, since it can be fixed by selection. Therefore, the exploitation of the additive x dominance and dominance x dominance types of interactions require the maintenance of heterozygosity. Kaczamarek et al. (2002) reported that heterozygote populations are more adaptable than homozygote populations to varied environmental conditions. Maintaining production under conditions of climate and environmental change will require the breeding of new crop varieties better adapted to these conditions.

CONCLUSION

It is clear that the genetic background play a significant role in the adaptation of organism to diverse environmental constraints, but the genetic mechanism is still ambiguous. The first challenge is to reject the concept of a character inherited additively, which is based on an idea that is not correct: a simple addition of individual genes effects. The idea of building a character of biological effects by simple addition is contrary to everything we know about the complexity of organism. It is important to point out that most models of inheritance are simple allusions of the complex genetic phenomena. Epistasis is a significant component in the inheritance of quantitative characters, no matter how it is designed; biologists are facing the reality of complexity of genetic systems. The second point of interest arising from comparisons of genetic models of our study is the high incidence of epistasis effects. Epistasis was preponderant than additive and dominance effects in inheritance of all majority of quantitative traits. The final point of interest arising from the result showed that the inheritance of quantitative traits is very complicated and depends in great part upon the constraint of environmental effects.

Quantitative genetical analysis has been traditionally hampered not only by the assumption of absence of epistasis, but also by the variation of the model of inheritance with the environmental conditions. Another similarity among the models reported in this study is the common occurrence of relationship between epistasis and environmental stress. Therefore, to obtain credible information on inheritance of any quantitative trait assessed in wide range of environments, genetic adaptability should be considered in the genetic analysis. More also, breeding program should be planned in such a way that selection of new genotypes with the desired genetic adaptability to environmental constraints is achieved. Epistatic seems to play a significant role in the adaptation of plants and was solicited only in presence of stresses. In favourable environment (absence of biotic or abiotic stress), selection would be simpler because only additive and dominance effects are implicated.

However, the genetic mechanism will not be stable when plant is grown in presence of stresses. For the cultivars designed for exploitation in a wide environmental condition, selection under stress is suggested for the stability of cultivars. Therefore, the maintenance of heterozygosity can give two advantages; the exploitation of epistatic effects and adaptability to varied environmental conditions. Successful methods will be those that can map-up the gene to form superior gene combinations interacting in a favorable manner and at the same time maintain heterozygosity. Although heterosis is widely used in breeding, but the genetic basis has not been elucidated. The postulate of additive and dominance effects is not sufficient to explain this biological phenomenon and epistasis seems to play a significant role in the manifestation of heterosis. Exploitation of epistasis could be realized throughout vigor hybrid (heterosis) or marker-assisted selection schemes.

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