



International Journal of
**Plant Breeding
and Genetics**

ISSN 1819-3595



Academic
Journals Inc.

www.academicjournals.com

Implications of Epistasis in Maize Breeding

¹Parvez A. Sofi, ¹A.G. Rather and ²M.Z.K. Warsi

¹Division of Plant Breeding and Genetics, SKUAST-K, Shalimar, 191121, J and K, India

²GBPUA&T, Pantnagar, Uttarakhand, India

Abstract: Epistasis was thought to be absent in the inheritance of most of the traits of economic worth such as yield, but there is growing enthusiasm and evidence that it is an integral part of genetic architecture of quantitative traits. Epistasis, when present, causes bias in the estimation of important genetic parameters resulting in erroneous estimates of expected gain under selection. This hampers the efficiency of breeding programmes aimed at exploitation of various components of genetic variance such as additive and dominance. The effect of epistasis on genetic variance components is all the more important in view of the fact that none of the mating designs developed so far ensures that epistasis if present does not influence the estimates of genetic components. A number of studies in maize have established the fact that epistasis has a significant role in trait expression but, as of now, all the genetic models to test and estimate it precisely are elusive. Recent studies with molecular markers have clearly revealed that epistasis has a significant role in inheritance of quantitative traits as well as plant growth and development. It would thus be logical to search for epistasis and optimize its use in the development of promising cultivars for target environments rather than attributing it to left over variance after additive and dominance effects are accounted for.

Key words: Maize, epistasis, genetic components, additive-dominance model, inbred line, hybrid

INTRODUCTION

Maize (*Zea mays* L.) is an important crop from plant breeder's point of view. In fact some of the basic and important concepts, that have revolutionized the science of plant breeding have evolved from research on maize. These concepts have been later on found to be equally applicable to other crops as well. The important concepts of combining ability and heterosis, which are of practical consideration to a plant breeder, have been developed in maize (Shull, 1908; Rickey, 1927). Maize owing to its wide genetic variability and enormous biological diversity is referred to as *Drosophilla* of plant kingdom. Most of the important aspects of quantitative traits have been elucidated by research on this crop. A large number of genetic principles underlying such variation of metric traits have been crystallised in maize and later on applied to other crops with equal success. A reasonable proportion of breeding procedures currently employed in crop species, have been conceptualized and developed in a systematic manner in maize breeding. Maize breeding has become one of the success stories, especially with the consolidation of knowledge on various genetic parameters using the principles of quantitative genetics. Infact, maize has witnessed greater practical applicability of most breeding methodologies than any other crop owing to its superb genetic variability and enormous biological diversity. As such a large number of studies have been carried out in maize to characterize the genetic architecture of yield and quality traits for establishing a framework for successful application of various crop improvement

Corresponding Author: Parvez A. Sofi, Division of Plant Breeding and Genetics, SKUAST-K, Shalimar, 191121, J and K, India

methodologies. Thus quantitative genetics has made significant contribution to genetic improvement of maize. However, as Lewontin (1977) pointed out that beyond the generalization that phenotype is the manifestation of genotype expressed in environment, little is known about the architecture of quantitative traits in terms of the number of loci conditioning a trait, the number of alleles segregating per locus, the allelic frequencies, effect of allelic substitutions, the linkage relationship among loci, the non-allelic interactions and expression and regulation of genes.

The characterization of genetic components using appropriate mating designs and field experimentation is imperative as it helps in estimation and partitioning of various components, which eventually determine the applicability and success of breeding procedures. Fisher (1918) and Wright (1922) provided the basic framework for characterizing and partitioning genetic variance into physically assignable components. Dickerson (1963), Dudley and Moll (1969) and Mather and Jinks (1971) outlined the following components of genetic variance, which are of practical consideration in crop improvement programmes.

- Additive genetic variance associated with the average effects of individual genes. It measures the breeding value of genotypes and is always fixable through selection.
- Dominance variance associated with intra-allelic interactions of genes at segregating loci and measures breeding behaviour of alleles in heterozygotes. It is of practical application in heterosis breeding.
- Epistatic variances associated with inter-allelic (non-allelic) interaction of genes at two or more segregating loci. Epistasis involving additive effects is fixable and as such exploited in intra-population improvement. Other epistatic effects are used in hybrid breeding.
- Relative dominance, which is the ratio of dominance variance to additive genetic variance, decides the appropriate breeding strategy to be employed for seeking improvement in a quantitative trait. The values less or more than unity indicate over-dominance, unit values indicate complete dominance while as negative values or values approaching zero indicate absence of dominance.
- Genotype x environment interaction, a component which causes bias in estimation of additive and dominance components. Thus relative importance of these components from single environment experiment is of little practical value (Comstock and Moll, 1963).

Cockerham (1954) and Kempthorne (1955) partitioned the non-allelic interaction into digenic (additive x additive, additive x dominance and dominance x dominance) for a two locus model and trigenic and higher order interactions by including the additional loci. From a plant breeding point of view, only additive x additive epistasis accounts for the breeding value of a population whereas the remaining components are non-fixable components. Cockerham (1961) and Dudley and Moll (1969) illustrated the interpretations and implications of different components of genetic variance in plant breeding programmes. They further elaborated the utility of various mating and environmental designs for the estimation of the genetic components. Thus one factor design is sufficient for detection of genetic variability. A two factor design separates additive and dominance variance (assuming epistasis to be absent) whereas for estimation of epistasis, complex designs or combination of designs is required.

A large array of biometrical procedures has been developed for relative estimation of genetic components. Although, most of these procedures estimate only additive and dominance genetic variance assuming epistasis to be absent but practically it is not possible to isolate epistasis and quantitative traits. The general conclusion, thus, has been that as the number of genes conditioning a quantitative trait increases, it is reasonable to predict greater interactions among those genes. Eta-Ndu and Openshaw (1999) were of the opinion that failure to include epistatic in estimation causes bias in estimates of genetic components and therefore the expected gain from selection. The magnitude of bias

depends upon the relative values of epistasis effects, comparatively to deviations d and h type of prevailing epistasis and direction of dominance. The existence of a large array of interactions in a polygenic system cause over-estimation or under-estimation of heritability estimates (narrow sense), thereby introducing an additional bias in predicted gains from selection. In fact most such genetic models suffer from same basic deficiencies. Kearsey and Jinks (1968) pointed out that three difficulties are encountered while attempting to estimate additive, dominance and environmental components of quantitative traits based on second degree statistics.

- Non-allelic interactions are assumed to be absent although valid test to show its absence is seldom provided by most of the designs.
- The estimates of dominance variances are associated with larger standard errors as compared to additive variances and
- Estimates of additive and dominance variances are differentially influenced by linkage, gene distribution and environment.

The basic framework of the genetic architecture of a crop is elucidated by the nature and extent of gene action for yield and its attributes. It has been established beyond doubt that breeding procedures are dictated by action, interaction and linkage relationships of genes conditioning a quantitative trait. Maize being a major food crop has been extensively studied for gene action. Sprague and Tatum (1942) and Comstock and Robinson (1952) were the first to attempt the partitioning of genetic variance into physically assignable components in maize. Hallauer and Miranda (1988) reviewed and summarized variance component studies in maize. The general conclusion from these studies is that in most maize populations, additive component for grain yield is usually 2-4 times large than dominance component. Dominance variance is important in maize populations and is often significant, but usually smaller than additive variance. These results are often interpreted as implying that additive gene action is of primary importance for grain yield and that grain yield is conditioned by genes with partial to complete dominance.

EPISTASIS

Epistasis remains one of the most complex aspects of quantitative genetics, which hinders reliable estimation of experimental results. Mendelian genetics provided basis for epistasis for qualitative traits but statistical approaches in quantitative genetics have ignored it or assumed to be of little importance. Fisher (1918) was first to outline a procedure, which could partition non-allelic interaction into various components. Cockerham (1954) and Kempthorne (1954) further partitioned epistatic variance into additive \times additive, additive \times dominance and dominance \times dominance. In determining the importance of epistasis, it is appropriate to inquire as to where such gene action is expected to occur with greatest frequency. It has been generally assumed that epistasis must be important portion of genetic variance in maize and that such non-allelic gene action would eventually be a major factor in explanation of heterosis exhibited in this species (Robinson, 1996).

Maize breeders have put in a lot of experimental efforts to detect the presence or absence of epistasis in inheritance of complex polygenic traits. Earlier studies of Eberhart *et al.* (1966), Chi *et al.* (1969) and Silva and Hallauer (1975) indicated that epistasis was not significant component of genetic variability in maize. This was largely due to basic assumption in early variance component studies that epistasis was unimportant for grain yield. This assumption was required because the number of covariance of relatives was not available for estimation of epistasis and because the epistatic models are difficult to handle mathematically. Hallauer and Miranda (1988) have provided an excellent review of studies for estimating epistasis in maize. The general conclusions have been that studies based on generation mean analysis have reported significant epistasis while as studies based on variances

(covariances of relatives) have reported non-significant epistatic effects. Similarly studies with open pollinating varieties generally have shown additive effects as more important while as for elite inbred lines dominance and epistatic effects are more important than additive effects.

Jinks (1955), Bauman (1959) and Sprague *et al.* (1962) were early workers to report importance of epistatic effects. Two earliest attempts to estimate epistatic variances in maize populations were reported by Eberhart *et al.* (1966) and Silva and Hallauer (1975). In both cases progenies developed by design I and II were evaluated. The parents were non-inbreds ($F = 0$) for design I and inbreds ($F = 1$) for design II matings. Due to inherent limitations in the genetic models used, both the studies were unable to obtain realistic estimates of digenic epistasis. In fact, the study of Silva and Hallauer (1975) revealed that additive-dominance model accounted for 99% of total genetic variation for grain yield.

Chi *et al.* (1969) used complex mating design in Reid yellow dent open pollinated variety using least square analysis and found no evidence of epistasis and almost all the genetic variation was accounted for by additive-dominance model. Similarly, Wright *et al.* (1971) used diallel using 60 inbred lines developed from Kurg Yellow dent maize variety and detected significant epistasis although it accounted for only 0.27% of genetic variation whereas additive and error component accounted for 94%. Stuber and Moll (1973) observed significant epistatic effects for grain yield in single, double and three-way crosses developed from selected and non-selected populations.

Xing *et al.* (1990) studied three endosperm traits using TTC and concluded that significant epistasis was present for all the traits. Studies of Eta-Ndu and Openshaw (1999), using a modified TTC, revealed that both epistasis and linkage disequilibrium for yield were detected in both populations studied. Jung *et al.* (1994) conducted genetic analysis of two crosses viz., DE811ASR×DE811 and DE811ASR×LH132 and found significant additive×dominance effects in both crosses. Lamkey *et al.* (1995) studied inheritance of yield and other traits in an elite maize hybrid between two dent inbred lines B73 and B84. Epistasis was reported as an important component of for grain yield accounting for 21% of variation among generation means. Wolf and Hallauer (1977) conducted a modified TTC in maize by crossing 100 unselected F_2 plants to two inbred lines B73 and M017 and their F_1 and evaluated test-cross progenies over three locations. They reported that epistasis was significant for ear length, number of rows ear⁻¹, ear height and flowering traits. They further reported that additive×dominance and dominance×dominance effects were significant for grain yield. Frank and Hallauer (1997) used generation means analysis for studying inheritance of twin ear trait in maize and reported that additive and dominance variance accounted for 94% of total genetic variation that epistasis was relatively unimportant.

Eta-Ndu and Openshaw (1999) used TTC to analyse importance of epistasis in two maize hybrids A679 × W× 6005 and 679 × FR902 by crossing their F_{2s} to parents as well as F_1 . There was evidence of epistasis in both populations but there was no association between epistasis and test cross yields of F_3 and backcrosses. Studies of Zhang *et al.* (2000) on 19 quantitative traits of improved maize population NEAU-2 revealed that epistasis was important for most of traits except grain yield and its component traits for which additive component was 85-92%.

Has *et al.* (2000) studied three way crosses between early and late maize inbreds and significant influence of epistasis on grain yield was reported. Singh and Khalidi (2001) used seven broad based varieties J603, Diara, Tarum, MDR-1, EBR, EVA602 and EVA605 along with their progenies i.e., selfs and crosses. Analysis of test cross data revealed that epistasis and linkage disequilibrium contributed significantly to total genetic variation upto the tune of 42-54%. The magnitude of epistasis exceeded additive and dominance components for all component traits but the largest influence was on number of rows ear⁻¹. Similarly Hinze and Lamkey (2003) conducted modified generation means analysis using P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 . Out of 40 tests cross progeny sets studied, five resulted in significant epistatic effect for grain yield. Yu and Bernardo (2004), however, observed that epistasis was not detected for any of the traits studied.

Mihaljevic *et al.* (2005) conducted generation means analysis to assess the importance of epistasis for grain yield and grain moisture in flint maize inbreds and found that generation means did not differ significantly from each other indicating thereby that epistasis was negligible in its net effect. Similar procedure used by Azizi *et al.* (2006) with inbreds B73, Mo17 and K74 found significant epistasis for most of the traits. They further reported that epistasis interacted with planting density more than additive and dominance components. Parvez Sofi (2006) using TTC, reported significant epistasis for grain yield and its components in maize.

The success of genetic enhancement of any trait of interest, in a crop improvement programme relies heavily on the availability of necessary genetic variation and its manipulation to develop suitable cultivars. In fact plant breeding aims at improving plant architecture for traits of economic and agronomic worth through the management of genetic variability. A greater proportion of such traits are governed by a large number of genes with smaller contributions to the trait resulting in continuous rather than discrete variation (Liu, 1998). The analysis of such a variation, designated as quantitative variation and its potential genetic basis is of prime importance to a plant breeder (Asins, 2002). Based on the concept given by Fisher (1918) for understanding the nature of quantitative traits, the genetics of such traits was studied by simple statistical techniques (means, variance, covariance's, heritabilities etc.) with the assumption that there are several segregating loci in a population, which share individual allelic contributions, being slight relative to environmental contribution. Even on such a minimalistic or black box concept, considerable progress could be achieved in advancing our knowledge of quantitative traits. Substantial theoretical and empirical progress has also been made on several aspects such as genetic architecture, heritability, direct and correlated response to selection and subsequently optimising the breeding methodologies for improving upon a crop species (Kearsey, 2002). Despite these and other advancements, the actual pattern of inheritance of quantitative traits continues to remain a moving target for geneticists and plant breeders. Even though there has been growing enthusiasm about newer biometrical and molecular tools, there is no disagreement either that our knowledge on various aspects of quantitative traits is far from adequate due to complex action, interaction and linkage relationship of genes governing such traits. The studies on genetic architecture of quantitative traits mainly unravel the relative importance of genetic components of variation primarily the additive, dominance and epistatic components controlling such traits. Epistasis is the interaction of alleles at different loci, thus a form of non-additive gene action. This departure from additivity renders the predictability procedures unreliable. The type of gene action governing a trait is very important in decision making regarding the breeding method and type of cultivars (inbred, hybrid, population) together with interpretation of results from quantitative genetic experiments. Pioneering work by prominent experimenters in the area particularly Sprague, Comstock, Robinson, Cockerham and others resulted in the development of mating schemes designed to estimate genetic variance components (Hallauer and Miranda, 1988). Earlier studies in maize revealed that epistasis was not an important component of genetic variation and that the variation was mainly accounted for by additive gene effects followed by dominance (Eberhart *et al.*, 1966; Chi *et al.*, 1969; Silva and Hallauer *et al.*, 1975). However, various other studies have concluded that epistasis was an integral component of genetic variation (Jinks, 1955; Bauman, 1959; Sprague *et al.*, 1962; Darrah and Hallauer, 1972; Lamkey *et al.*, 1995; Wolf and Hallauer, 1997; Eta-Ndu and Openshaw, 1999; Zhang *et al.*, 2004; Fan *et al.*, 2005; Khan and McNeilly, 2005).

Although epistasis is common and not occasional in genetic systems that determine quantitative traits, its estimation is unusual in genetic studies due to the limitations in methodology as in case of triple test cross, the high number of generations to be produced and assessed (Viana, 2000) and mainly because only one type of progeny: half-sib, full-sib or inbred families are commonly included in such experiments. The biometrical techniques developed for detection of epistasis have mainly involved the generation means analysis (Mather and Jinks, 1971) that permits estimation of linear components of

genotypic means and Triple Test Cross (TTC) analysis (Kearsey and Jinks, 1968) that permits testing the existence of epistasis. TTC (Triple test cross) analysis provides unambiguous test for the presence of epistasis regardless of gene frequencies, degree of inbreeding and linkage relationships. TTC has been accepted as a powerful design furnishing independent and equally precise estimates of additive and dominance components of genetic variation in the event of non-detection of epistasis. The design has wide applicability as it can be used to investigate both segregating and non-segregating populations arising from different generations such as F_2 , backcross and homozygous lines.

Presence of epistasis in maize inbreds should not significantly affect commercial maize breeding programmes (Lamkey *et al.*, 1995). This is because inbreeding is carried out simultaneously with hybrid evaluations and favourable epistatic gene combinations can ultimately be fixed in the inbreds, having good specific combining ability. Development of source populations by crossing related inbreds or inbreds from same heterotic patterns or recycling the elite inbred lines to form new source populations will help maintain and accumulate favourable epistatic gene combinations, especially linked ones (Wolf and Hallauer, 1997). In fact, the presence of positive epistatic effects may significantly contribute to expression of heterosis. Studies in maize have indicated dispersion of dominant alleles coupled with complementary epistasis to be the major components of heterosis (Chahal *et al.*, 1991).

For polygenic traits like yield that are of prime importance, from improvement point of view to plant breeders, the influence of epistasis is generally quantified in terms of statistical parameters as interaction of pairs of loci i.e., [i j] type (homozygote x homozygote) and [j + l] type (homozygote x heterozygote and heterozygote x heterozygote) at digenic level. The exploitation of [i type] is mainly through development of inbred lines whereas; latter type is mainly through hybrid breeding. However, all types of epistasis can be utilised for intra as well as inter-population improvement programmes. The utilisation of [i] type epistasis is relatively tedious and depends largely on development of completely homozygous lines. So far, we are yet to establish principles of a selection theory, which would help us, identify superior genotypes with high level of additive x additive epistasis during early segregating generations. The situation is further complicated by the fact that, in presence of large epistatic component, selection has to be done by evaluating large number of families besides delaying the process to later generations, where appreciable amount of homozygosity has been attained.

Tabano and Bernardo (2005) reported inadequacy of additive-dominance model in maize and concluded that non-additive gene effects including epistasis are very important in development of inbred lines and help maintain genetic variation in small populations. However, so far, there is no proven evidence regarding the nature of epistatic bias on estimation of genetic components. Moreover, there is no conclusive evidence regarding the effect of epistasis on the expression of quantitative traits. It would therefore be rational to emphasize that epistasis, whenever present, imitates additive and dominance components in a way that their separate estimation become difficult. Thus estimates of additive and dominance components by existing genetic models contain a portion of epistatic variance in a way that does not impair their prediction power (Chahal *et al.*, 1991).

IMPLICATIONS IN MAIZE BREEDING

One of the greatest implications of epistasis is that the estimation of genetic components with methods assuming no epistasis is generally biased and as such may cause significantly ambiguous estimates of important genetic parameters such as heritability and eventually the expected genetic gain which ultimately translates into wrong choice of selection strategies and wastage of resources. The effect of epistasis on genetic variance components is all the more important in view of the fact that none of the mating designs developed so far ensures that epistasis if present does not influence the estimates of genetic components.

All systems of selection are fruitful if the gene action is entirely additive. With the inclusion of dominance, the picture is not so clear as the degree of dominance is important. If a substantial number of loci exhibit over-dominance, then it is imperative to use a strategy that will lead to a heterozygous genotype. The inclusion of epistasis makes the picture even less clear. Selection schemes such as mass and family selection are effective with additive interaction (Kojima, 1959), but are ineffective with additive \times dominance and dominance \times dominance interactions. The preponderance of additive genetic variance for yield and its component traits signifies the effectiveness of intra population improvement methods in upgrading the genetic potential of the target population but the existence of significant epistasis precludes fruitful results in immediate generations and as such the selection process has to be delayed until substantial homozygosity is achieved particularly in the development of inbred lines. Reciprocal Recurrent selection, on the other hand, would be an ideal breeding strategy for exploitation of both additive and non-additive gene effects (Popi and Kannenberg, 2001). In fact such a strategy will not only increase the frequency of favourable alleles but also maintain the genetic variation without reaching a dead end (Doerksen *et al.*, 2003). However, the implication of epistasis in such population improvement programmes is two folds, i.e., through its direct contribution to the development of superior populations and indirectly through its effect on predicted response to selection. The realized response to selection through a particular breeding strategy as described may be far from its expected values if only additive-dominance model is assumed with no consideration to epistasis. There is also no substantial loss in the additive genetic variance in short term as reported by Guzman and Lamkey (2000). They observed that there was no significant decrease in additive variation probably due to compensation by epistasis after 5 cycles of recurrent selection.

Presence of significant variation attributable to epistasis has considerable bearing on development of hybrids and their evaluation procedures. Since, in recent times, greater focus has been laid on the development of single crosses and modified three-way crosses, the need for development of improved techniques to predict double cross performances has declined. Epistatic gene complexes may occupy significant role in single cross performances. The production of three-way and double crosses provides an opportunity for genetic recombination in parental single crosses by disrupting such gene complexes which not only provides for evaluation of prediction procedures but also assessment of significance of epistatic effects in performance of single cross. Stuber *et al.* (1973) opined that in case of cross combinations strongly influenced by epistasis, the evaluation procedure becomes more tedious, including the need for actual testing of double and three-way crosses. In order to develop hybrid oriented populations inbreeding tolerance is assuming vital importance. Therefore recycling of elite lines has been widely used by the maize breeders to develop productive and vigorous parental lines. However, as already stated, the fixation of favorable epistatic combinations in parental lines contributes profoundly to the superior performance of single cross hybrids. Occasionally such crosses do not yield promising lines upon recycling. This is particularly due to the fact that these favorable epistatic combinations of genes get dissipated upon segregation and recombination. One suggested alternative would be to have at least one backcross to the better parent to maintain/recover the favorable epistatic gene combinations (Wolf and Hallauer, 1997). Cach *et al.* (2005) were of the opinion that significance of epistatic variance justifies the production of inbred parental lines to fix allelic combinations in the production of hybrid cultivars.

One of the potential aspects of the presence of significant epistasis, which is of practical consideration to plant breeders, is their ability to produce novel phenotypes that can perform beyond expectations. In fact New World cottons are a striking example of practical utilization of epistatic effects. However, despite a great opportunity which epistasis offers to plant breeders, its utilization for crop improvement is greatly hampered by its unpredictable nature, lack of adequate theoretical understanding and procedural inadequacies for its estimation. Stuber *et al.* (1996) in his classical study

on genetic basis of heterosis in maize observed epistasis to be of minor importance in hybrid performances. However, Cockerham and Zeng (1996) analyzed the same data using orthogonal contrasts and detected significant A×A, A×D and D×D interactions for grain yield. The advent of molecular markers and QTL analysis has greatly facilitated the dissection of quantitative traits in finer details in terms of action, interaction and linkage relationships of genes governing them. In fact most of the present studies involving genetic analysis of quantitative traits are being carried out using molecular markers by assessing the relationship between the genome heterozygosity and phenotypic performance. One of the classical studies recently was conducted by Wagner *et al.* (2006) for elucidating gene action in the maize hybrid B73 × Mo17 using microarrays. The most common mode of action was additive but several hundred genes exhibited non-additive gene action including dominance, over-dominance and epistasis. Such studies based on expression levels of various genes governing quantitative traits and the variability in levels of expression in parents and hybrids could help unravel the genetic factors underlying several important aspects of maize breeding such as heterosis and inbreeding depression.

A number of studies in maize have established the fact that epistasis has a significant role in trait expression but, as of now, all the genetic models to test and estimate it precisely are elusive. The reason for this statement has to do with the very nature of quantitative genetic models themselves, that is, all estimates of gene action and gene effects have been averaged over the whole genome. Estimates of individual loci have been impossible and there is most likely a distribution of gene action and effects influencing a given quantitative trait. Determining the nature of distribution could be very important in the design of breeding programmes to capitalize on the types of gene action that may exist for a trait. Therefore, recognising the inadequacy of present genetic and statistical models, it would be better to switch over to approaches where genotypes are known (Templeton, 2000). Recent studies with molecular markers have clearly revealed that epistasis has a significant role in inheritance of quantitative traits as well as plant growth and development (Yu *et al.*, 1997; Li *et al.*, 1997). It would thus be logical to search for epistasis and optimise its use in the development of promising cultivars for target environments rather than attributing it to left over variance after additive and dominance effects are accounted for.

REFERENCES

- Asins, M.J., 2002. Present and future QTL analysis in plant breeding. *Plant Breed.*, 121: 281-286.
- Azizi, F., A.M. Rezai and G. Saeidi, 2006. Generation mean analysis to estimate genetic parameters for different traits in two crosses of corn. *J. Agric. Sci. Technol.*, 8: 112-117.
- Bauman, L.F., 1959. Evidence of non-allelic interaction in determining yield, ear height and kernel row number in corn. *Agron. J.*, 51: 531-534.
- Cach, N., J. Perez, J. Lewis, F. Calle, N. Morante and H. Ceballos, 2005. Epistasis in expression of relevant traits in cassava for sub humid conditions. *J. Heredity*, 96: 586-592.
- Chahal, G.S., T.H. Singh and D.S. Virk, 1991. Measurement and Utilization of non-allelic interaction in plant breeding. *Crop Improv. Soc. India, PAU.*, pp: 63.
- Chi, K.R., S.A. Eberhart and S.A. Penny, 1969. Covariances among relatives in a maize variety. *Genetics*, 63: 511-520.
- Cockerham, C.C., 1954. An extension of concept of partitioning hereditary variances for analysis of covariances among relatives, when epistasis is present. *Genetics*, 39: 859-882.
- Cockerham, C.C., 1961. Implications of genetic variances in a hybrid breeding programme. *Crop Sci.*, 1: 47-52.
- Cockerham, C. and Z. Zeng, 1996. Design III with marker loci. *Genetics*, 143: 437-456.

- Comstock, R.E. and H.F. Robinson, 1952. Estimation of Average Dominance of Genes. In: Heterosis, Gowen J.W. (Ed.), pp: 494-516.
- Comstock, R.E. and R.H. Moll, 1963. G x E interaction. In: Statistical Genetics and Plant Breeding. Hanson, W. and H.F. Robinson (Eds.), pp: 164-196.
- Darrah, L.L. and A.R. Hallauer, 1972. Genetic effects estimated from generation means in four diallel sets of maize inbreds. *Crop Sci.*, 12: 615-621.
- Dickerson, G.E., 1963. Biometrical Interpretation of Genetic Parameters of a Population. In: Statistical Genetics and Plant Breeding. Hanson, W. and H.F. Robinson (Eds.), pp: 95-107.
- Doerksen, T., L. Kannenberg and L. Lee, 2003. Effect of recurrent selection on combining ability in maize breeding populations. *Crop Sci.*, 43: 1652-1658.
- Dudley, J.W. and R.H. Moll, 1969. Interpretation and use of estimates of heritability and genetic variances in plant breeding. *Crop Sci.*, 9: 257-261.
- Eberhart, S.A., R.H. Moll, H.F. Robinson and C.C. Cockerham, 1966. Epistatic and other variances in two varieties of maize. *Crop Sci.*, 6: 275-280.
- Eta-Ndu, T. and S.J. Openshaw, 1999. Epistasis for grain yield in two F₂ populations of maize. *Crop Sci.*, 39: 346-352.
- Fan, Q., K. Yang and S. Qiao, 2005. Analysis of genetics of four kernel traits in maize. *China J. Agric. Sci.*, 18: 378-381
- Fisher, R.A., 1918. The correlation between relatives on the supposition of Mendalian inheritance. *Trans. Royal Soc. London*, 52: 399-433.
- Frank, T.E. and A.R. Hallauer, 1994. Generation mean analysis of twin ear trait in maize. *J. Heredity*, 88: 469-474.
- Guzman, P. and K.R. Lamkey, 2000. Effective population size and genetic variability in BSII maize population. *Crop Sci.*, 40: 1370-1378.
- Hallauer, A.R. and J.B. Miranda, 1988. Quantitative genetics in maize breeding. Iowa State College Press, Ames, pp: 434.
- Has, I., I. Cabulea and V. Has, 2000. Epistasis in threeway crosses involving early and late inbreds of maize. *Roman. Agric. Res.*, 13: 1-18.
- Hinze, L.L. and K.R. Lamkey, 2003. Absence of epistasis for grain yield in elite maize hybrids. *Crop Sci.*, 43: 46-56.
- Jinks, J.L., 1955. A survey of genetical basis of heterosis in variety of diallel crosses. *Heredity*, 9: 223-238.
- Jung, M., T. Weldekidan, D. Schaff, A. Paterson, S. Twigey and J. Hank, 1994. Generation mean analysis and QTL mapping of anthracnose stalk rot resistance in maize. *Theor. Applied Genet.*, 89: 413-418.
- Kearsey, M.J. and J.L. Jinks, 1968. A general method of detecting additive, dominance and epistatic variation for metric traits. I, Theory, *Heredity*, 23: 403-409.
- Kearsey, M.J., 2002. QTL. Analysis-Problems and Possible Solutions. In: Quantitative Genetics, Genomics and Plant Breeding. Kang, M.S. (Ed.), CABI Publishers, pp: 45-57.
- Kempthorne, O., 1954. The correlation between relatives random mating population. *Proc. Roy. Soc. Edinburg*, 143: 103-113.
- Kempthorne, O., 1955. The theoretical values of correlation between relatives in random mating populations. *Genetics*, 40: 153-167.
- Khan, A. and T. McNielly, 2005. Triple test cross analysis for salinity tolerance based on seedling root length in maize. *Breed. Sci.*, 55: 321-325.
- Kojima, K., 1959. Role of epistasis and overdominance instability of equalibra with selection. *Proc. Nation. Academy Sci.*, 45: 984-989.

- Lamkey, K.R., J.C. Bruce and A.E. Mekhinger, 1995. Epistasis in an elite maize hybrid and choke of generation for inbred line development. *Crop Sci.*, 35: 1272-1281.
- Lewontin, R.C., 1977. Adaptation of populations to varying environments. *CSH Symposium on Quantitative Biol.*, 22: 395-408.
- Li, Z., S. Pinson, W. Park, A. Paterson and J. Stansel, 1997. Epistasis for three grain yield components in rice. *Genetics*, 145: 453-465.
- Liu, B.H., 1998. *Statistical Genomics: Linkage Mapping and QTL. Analysis.* CRC. Press, USA., pp: 1-11.
- Lonnquist, J.H., C. Cota and C.O. Gardener, 1966. Effects of Mass Selection and Thermal Neutron Irradiation on Genetic Variances in a Variety of Corn. *Crop Sci.*, 6: 330-332.
- Mather, K. and J.L. Jinks, 1971. *Biometrical Genetics.* Chapman and Hall, London, pp: 376.
- Mihaljevic, R., H.F. Utz and A.H. Melchinger, 2005. No evidence of epistasis and per se performance of elite European flint maize inbreds from generation mean and QTL analysis. *Crop Sci.*, 45: 2605-2613.
- Parvez, S., 2006. Genetic architecture for yield and its components in maize. Ph.D Thesis, Submitted to SKUAST-K, Shalimar, J and K, India, pp: 201.
- Popi, J. and L. Kannenberg, 2001. Response to selection over 15 years of HOPE maize breeding system. *Maydica*, 46: 93-103.
- Rickey, F.D., 1927. Convergent improvement of selfed lines of corn. *Am. Natural.*, 61: 430-449.
- Robinson, H.F., 1996. Quantitative genetics in relation to breeding on centennial Mendelism. *Indian J. Genet. Plant Breed.*, 26: 171-187.
- Shull, G.H., 1908. The composition of a field of maize. *Rep. Am. Breeders Assoc.*, 5: 51-59.
- Silva, J.C. and A.R. Hallauer, 1975. Estimation of epistatic variances in Iowa stiff stalk synthetic maize. *J. Heredity*, 66: 290-296.
- Singh, R.D. and G.A. Khalidi, 2001. Role of epistasis in expression of yield and yield components in synthesized population in maize. In: *Hundred of Post-Mendelian Genetics and Plant Breeding Retrospect and Prospects*, pp: 291.
- Sprague, G.F. and L.A. Tatum, 1942. General V/S Specific combining ability in a single cross of corn. *J. Am. Soc. Agron.*, 34: 923-932.
- Sprague, G.F., W.A. Russel, L.H. Penny, T.W. Horner and W.D. Hanson, 1962. Effect of epistasis on grain yield in maize. *Crop Sci.*, Z: 205-208.
- Stuber, C.W., R.H. Moll and W.D. Hanson, 1966. Genetic variances and interrelationship of six traits in hybrid populations of maize. *Crop Sci.*, 5: 455-458.
- Stuber, C.W. and R.H. Moll, 1973. Epistasis in maize. II. Comparison of selected with unselected population. *Genetics*, 67: 137-144.
- Tabano, A. and R. Bernardo, 2005. Genetic variation in maize breeding populations with different number of parents. *Crop Sci.*, 45: 2301-2306.
- Templeton, R., 2000. Epistasis and Complex Traits. In: *Epistasis and Evolutionary Process.* Wolf, J.B. (Ed.), Oxford University Press, NY., pp: 41-57.
- Viana, J.M., 2000. Components of variation of polygenic system with digenic epistasis. *Genet. Molecul. Biol.*, 23: 883-892.
- Wagner, R.A., J. Yi, R. DeCook, L. Borsuk, D. Nettleton and P. Schnable, 2006. All possible modes of gene action are observed in global comparison of gene action in a maize F₁ hybrid and its inbred parents. *Proc. Nat. Acad. Sci.*, 103: 6805-6810.
- Wolf, D.P. and A.R. Hallauer, 1997. Triple test cross analysis to detect epistasis in maize. *Crop Sci.*, 37: 763-770.

- Wright, S., 1922. The effects of Inbreeding and Cross Breeding in Guinea Pigs. USDA Bull. No. 1121, pp: 352.
- Wright, J.A., A.R. Hallauer, L.H. Penny and S.A. Eberhart, 1971. Estimating genetic variances in maize by use of single and three way crosses among unselected inbred lines. *Crop Sci.*, 11: 690-695.
- Xing, L.Q., S.B. Kong and L.X. Han, 1990. Inheritance of modifiers of opaque-2 gene in maize. II. A study of 3 endosperm traits by triple test cross. *Acta-Agricultural Universitatis-Pekinesis*, 16: 33-38.
- Yu, S.B., J. Li, C. Xu, Y. Tan, Y. Gao, X. Li, Q. Zhang and M.S. Maroof, 1997. Importance of epistasis as genetic basis of heterosis in elite rice hybrid. *Proc. Nat. Acad. Sci.*, 94: 9226-9231.
- Yu, J. and R. Bernardo, 2004. Changes in genetic variances during advanced cycle breeding in maize. *Crop Sci.*, 44: 405-410.
- Zhang, X., Y. Jun, Y. Zhang, H. Chang, Z. Wang, X.F. Zhang, Y.L. Zhang, H.Z. Chang and Z.H. Wang, 2000. Genetic analysis of quantitative traits in improved maize population of NEAU 2. *Scientia Agricultura, Sinka*, 33: 105-112.
- Zhang, X., Y. Chen, L. Wu, R. Guo, G. Bai, L. Ku and H.B. Wang, 2004. Analysis of gene effects of ear traits of temperate x tropical crosses in maize. *J. Henan Agricultural University*, 38: 365-369.