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Decoding the phenomenon of combining ability for yield and related traits with reference to maize

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Abstract

Knowledge of combining ability of inbred lines is vital for effective exploitation of heterosis for enhancing yield in hybrid breeding programmes. Two types of combining ability analysis *i.e.* general combining ability (GCA) and specific combining (SCA) are reported. While general combining ability governed by additive variance reflects the average performance of parental lines in combination with several other lines, specific combining ability refers to the performance of a specific cross combination involving two parental lines and is the result of non-additive gene action. In the initial phase of breeding programmes, GCA assumes higher importance with, SCA coming into play in later stage of the hybrid development programme, once lines with high GCA are identified and designated to their respective heterotic pools. Lines with high GCA can be used to predict single cross heterosis and therefore it is imperative that heterotic pools with high GCA variance based on combining ability performances are developed. Dissecting the genetic basis of GCA with the help of molecular markers can help to further improve GCA evaluation of the lines for enhancing hybrid development programmes.

Keywords: Combining ability, GCA variance, heterotic pools, hybrid breeding, maize

Introduction

In hybrid breeding programmes identification and selection of elite parents is a pre requisite for producing superior progeny and is the most critical challenge faced by plant breeders (Hallauer, *et al.*, 2010)^[1]. Since grain yield, the primary objective of any breeding programme has low heritability being highly affected by genotype x environment interaction, identification of lines which can serve as parental material for the development of superior hybrids, based on the yield and its contributing traits (Dhillon and Singh, 1978; Singh and Singh, 1984)^[2, 3] becomes a precondition especially in resource limited situations. Inbreds are generally associated with inbreeding depression in allogamous crops resulting in deterioration of vigour and fecundity which can be recovered in a single generation by crossing sufficiently divergent inbred lines which restores the heterozygous balance. However, assessing performance of inbred lines *per se* based on progeny performance is costly and time consuming. Therefore, a breeder must be armed with knowledge of gene action governing performance of lines to be able to identify inbreds with high genetic potential (Fehr, 1987)^[4]. Employing mating schemes designed to analyse combining ability of lines helps to elucidate the nature of gene action governing ability of lines to transmit desirable traits to their progeny and maximize their utility in hybrid development.

What is combining ability?

The concept of combining ability as a measure of gene action was proposed by Sprague and Tatum in 1942 and two types of combining ability *i.e.* General Combining Ability (GCA) and Specific Combining Ability (SCA) are reported. Sprague and Tatum (1942)^[5] defined GCA as the average performance of a genotype in a series of hybrid combinations in that it reflects the breeding value of the parental genotypes and SCA for those cases in which certain hybrid combinations performed better than expected based on the average performances of the parental lines involved in the target cross. Parents showing a high average combining ability in crosses are considered to have good GCA while if their potential to combine well is restricted to a particular cross, they are considered to have good SCA (Reif, *et al.*, 2007; Balestre, *et al.*, 2008; Townsend, *et al.*, 2013)^[6-8].

Gene action governing combining ability

Estimates of the variances in combining ability studies due to GCA and SCA provide an appropriate understanding of the predominant role of additive or non-additive variances of gene. The GCA variance is attributable to additive variance and additive x additive interaction variance while, SCA variance is attributed to dominance variance, additive x additive variance, additive x dominance variance and dominance x dominance variance components (Comstock, and Robinson, 1948) [9]. Gene action is essentially governed by the ratio of GCA to SCA variance where additive gene action is indicated when estimates of GCA / SCA variance component ratio exceeds 1, while non-additive gene action is preponderant when the same component ratio values are less than 1. When the ratio equals 1 it implies presence of both additive and non-additive gene action (Gardner, and Eberhart, 1966; Giffing, 1956; Rink and Hays, 1964) [10-12]. Traits governed by additive gene effects respond to selection while, non-additive gene effects are exploited for hybrid vigour in cross combinations (Dubey, *et al.*, 2009) [13].

Mating designs for combining ability studies

Several mating designs such as top cross (Jenkins and Brunaon, 1932) [14], poly cross (Tysdal *et al.*, 1942) [15], diallel mating (Griffing, 1956) [11], line x tester (Kempthorne, 1957) [16], partial diallel (Kempthorne and Curnow, 1961) [17], triallel and quadriallel (Rawlings and Cockerham, 1962) [18] analyses have been proposed for evaluation of combining ability. Diallel mating designs have been extensively used in combining ability studies to understand the relative contribution of additive and non-additive gene action in controlling the traits of interest from a fixed or random selected set of parental lines in a short period of time (Griffing, 1956; Moterle, *et al.*, 2011) [11, 19]. This system of mating has also been useful in identifying best combiners to increase favourable alleles for improvement of grain yield and other agronomic traits in hybrids.

Gene action governing yield and related traits in maize

Heterosis indicated by superior performance of hybrid progeny in comparison to parents is best exploited in allogamous crops. Maize, one of the world's most produced crops has a long history as a model genetic system and has made major contributions towards the understanding of exploitation of hybrid vigour in breeding programmes (Wallace, *et al.*, 2014) [20]. Using combining ability analysis, it has been shown that of the several yield contributing traits in maize, epistatic gene action is most frequent for ear length, ear width, test weight, number of grain rows and yield. Predominance of additive gene effects for plant height, days to % tasseling and days to % silking (Kumar, *et al.*, 2012; Matin, *et al.*, 2016) [21, 22], while traits such as ear height, days to maturity and grain yield per plant are governed by non-additive gene action (Ramamurthy, 1980; Murthy *et al.*, 1981; Singh and Singh, 1984; Talukder *et al.*, 2016) [23, 24, 3, 25]. Hybrids involving both the parents with high GCA effects indicate that the parental contribution to heterosis is mainly through additive gene action. Johnson and Hayes, (1940) [26] found that for yield and related traits, combinations low x low yielded less than low x high or high x high, although the F₁ crosses between low x high yielded at par with F₁ crosses between high x high. Hull (1952) [27] observed that the mean of the high x high combination may be optimum for exploiting heterosis although the highest specific combination is more likely to occur in high x low crosses. Leng, (1954) [28]

reported that if over dominance is present, the highest degree of heterosis should be found in high x low crosses. Tarutina, *et al.* (1980) [29] reported that heterosis was observed for many characters under different environmental conditions and as a rule, hybrid with the highest percentage of heterosis had a line with high GCA as one of its parents. Vaidya, (1986) [30] also reported that the crosses showing heterosis over check for yield and yield components had at least one good general combiner in their parentage.

Importance of heterotic grouping in combining ability studies

It has also been shown that besides aiding in line selection and exploitation of heterosis, analysis of combining ability also aids in heterotic group classification (Zhang, *et al.*, 2017) [31]. A heterotic group is a group of plant genotypes which may or may not be related and originate from the same or different populations. Genotypes from the same heterotic group show similar behaviour with respect to combining ability and heterosis when crossed with other genotypes from genetically divergent groups (Melchinger, and Gumber, 1998; Ertiro, *et al.*, 2017; Leng *et al.*, 2019) [32, 33, 34]. Assigning the plant genotypes into heterotic groups forms the basis of productive hybrid programs. Most commonly, diallel and line x tester mating schemes have been used in maize for establishing heterotic groups for unknown genotypes (Moreno-Gonzalez, 1988; Ordas, 1991; Vasal *et al.*, 1999; Fan, *et al.*, 2009; Suwarno, *et al.*, 2014) [35-39]. Rojas and Sprague, (1952) [40] stated that based on results of several yield trails it was seen that general combining ability was more important in untested lines but as testing progressed and only the better lines remained, specific combining ability became of greater importance. Since predictors of single cross heterosis between inbred lines increase the efficiency of a hybrid breeding programme (Gissa, *et al.*, 2007) [41] in order to exploit heterosis, it is crucial to recognize and utilize the GCA value of parents along with crosses. Heterotic grouping based on combining ability studies allow exploitation of heterosis (Melchinger, and Gumber, 1998) [32] with establishment of heterotic pools comprising of lines with predominance of GCA variance for early testing. Superior hybrids combinations can be easily predicted from GCA effects in such heterotic groups thereby facilitating easy selection of parental lines (Reif, *et al.*, 2007) [6]. Rojas and Sprague, (1952) [40] stated that based on results of several yield trails it was seen that general combining ability was more important in untested lines but as testing progressed and only the better lines remained, specific combining ability became of greater importance.

Use of molecular markers to facilitate combining ability studies

Molecular markers revealing the genetic basis of QTL (Quantitative Trait Loci) underlying agronomically important traits (Austin, *et al.*, 2000) [42] and dissecting the genetic basis of GCA further, have helped to further improve GCA evaluation of the lines. QTL mapping for GCA was first detected by Gu, (2007) [43] in a maize doubled haploid (DH) population. Lv, *et al.* (2012) [44] discussed the feasibility of QTL mapping for GCA in maize and suggested that mapping loci/genes that govern GCA can be achieved using introgression lines. A number of molecular markers significantly associated with combining ability for yield-related traits in maize are reported. Qi, *et al.*, (2013) [45] identified genetic loci of GCA and SCA for five yield-related

traits under three environments using introgression lines. They detected significant correlations between the number of significant GCA loci and the performance of GCA in the lines under study. Hai, *et al.* (2017) ^[46] generated high-density genetic map and identified 14 QTLs governing GCAs of four yield contributing traits *viz.* ear height, kernel moisture content, kernel ratio and yield per plant for identification of lines with high GCA in two distinct heterotic groups. Zhou, *et al.* (2018) ^[47] identified two QTL hotspots located on chromosomes 5 and 10 in maize governing plant height which can help in identifying ideal plant architecture to directly determine the biomass, planting density, and grain yield in combining ability studies. These and similar studies help to provide a clear picture of the genetic basis of combining ability of several yield and yield regulating components at the molecular level and fast track accumulation of GCA variance for identification of superior hybrid combinations.

Conclusion

Improving grain yield and exploitation of heterosis in allogamous crops such as maize depends primarily on developing ideal hybrids from heterotic pools with high GCA variance which when crossed in various combinations result in high SCA variance depending on degree of divergence. A better understanding of the gene action governing combining ability of divergent lines is therefore an imperative for yield improvement programs through hybrid breeding.

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