Combining ability and heterosis for yield and water use efficiency traits in grounndut - A review

K. John* and P. Raghava Reddy

Regional Agricultural Research Station, S.V.Agricultural College, Tirupati-517502, India. Received: 21-05-2014 Accepted: 26-06-2015

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ABSTRACT

Hybridization followed by selection in segregating generations is the main mode of varietal development in self-pollinated crops like groundnut. Before making crosses, it is important to know which of the parents are going to nick well and yield desirable segregants in terms of yield and other desirable attributes aimed at. There are different mating designs to identify the parents to be included in hybridization programmes. One of the widely used and most informative one is diallel mating design. After identification of parents more suitable to be involved in breeding programme, it is necessary to know the mode of inheritance of the traits to be improved to make wise choice of selection approaches to be followed in segregating generations. Therefore the breeder is constantly needing to determine the potential of additional germplasm as parents, Earlier studies suggest the importance of additive general combining ability (GCA) and non additive (specific combining ability and heterosis) genetic effects in evaluating hybrid performance among parental groundnut lines. The prominent effects on crop plants are reduction in plant growth and changes in various physiological processes. Moisture stress can also adversely influence yield attributes like number of mature pods per plant, 100-pod weight, 100-kernel weight, shelling per cent and harvest index.

Key words: Combining ability, Groundnut, Heterosis, Water use efficiency, Yield.

Groundnut (*Arachis hypogaea* L.) is one of the leading oilseed crops of India and is a rich source of edible oil and protein for human diet. In general, the *per se* performance of parents is not always a true indicator of its potential in hybrid combinations. Combining ability is the relative ability of a genotype to transmit its desirable performance to its crosses. Combining ability analysis is not only the quickest method of understanding the genetic nature of quantitatively inherited characters, but also gives essential information about the selection of parents which in turn throws better segregants. The knowledge of the type of gene action involved in the expression of yield and yield components is essential to choose an appropriate breeding strategy to isolate desirable segregants in the later generations.

Donald (1968) suggested breeding for yield improvement in a particular type of environment by selection for physiological and morphological traits thought to be conducive to high yield in that environment. Wells *et al.* (1991) evaluated physiological changes which resulted in higher yields in groundnut cultivars released in USA. Nageswara Rao (1992) analyzed groundnut production in terms of physiological traits like WUE, photosynthesis and stated that very little progress has been made in identification and exploitation of genetic and physiological traits contributing to yield potential and adaptation. Too often traits are advocated based on theory and there are few attempts to study genetic variability and even fewer to establish their genetic control and heritability, variability, and genetic advance as per cent of mean.

The information on the nature and magnitude of gene action for different quantitative and qualitative traits in any crop species plays a vital role while formulating the efficient breeding programmes. Superior genotypes can be isolated by selection if considerable genetic variation exists within the population. Besides genetic variability, heritability and genetic advance also plays a vital role in the improvement of any character. Moisture stress is an important environmental variable influencing plant growth and yield (Hsiao and Bradford 1983). It affects many aspects of plant growth by modifying their anatomy, morphology, physiology and biochemistry.

Crop physiologists in recent years have identifying physiological traits contributing to superior performance under drought conditions. These include harvest index (HI) (Nageswara Rao *et al.*, 1993), total amount of water transpired (T) and transpiration efficiency (TE) or water use efficiency (WUE) (Wright *et al.*, 1994).

WUE is the ratio of the total drymatter produced per unit of water transpired. Variation in WUE among genotypes of same species was first documented by Briggs

*Corresponding author's e-mail: johnlekhana@rediffmail.com.

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and Shantz (1913) and the possibility of using this as a selection trait in breeding for drought tolerant genotypes has been reported by Tanner and Sinclair (1983). Recent studies have confirmed that substantial genotypic variation for WUE exists in groundnut (Hubick *et al.*, 1986). Wright *et al.* (1988) showed that the genotypic variability for WUE in groundnut ranged from 2.15 to 3.71 g of dry matter per kg of water used. Hebbar (1990) reported a variation from 1.57 to 2.66 g drymatter per kg of water. Wright *et al.* (1993) reported a genotypic variation from 1.8 to 3.7g of dry matter production per kg of water used.

Selection for higher WUE often resulted in decrease in crop growth rates and this was perhaps the most significant setback for further improvement in this trait. This lack of success arises primarily due to strong inter-dependency between transpiration and WUE. Therefore it is essential to identify types where this interdependency is lower.

Water use efficiency is known to increase with decrease in the quantity of water applied without substantial decrease in yield (Hammond and Boote, 1981). Nimitr Vorasoot *et al.* (1988) found WUE to be higher in groundnuts that received lower water regimes at longer irrigation intervals (14 days). Rosario and Fajardo (1988) reported that WUE decreased under water stress in all cultivars of groundnut. Genotypes with greater decrease in stomatal conductance and a minimum change in assimilation rate always show a greater increase in WUE under stress (Hebbar, 1990). Significant positive relation between WUE values obtained in control and stress treatments was also reported by many workers indicating that the G x E is very low for this trait (Wright *et al.*, 1992).

Before actually reviewing the literature on heterosis and combining ability on morphological traits, physiological (water use efficiency traits) and yield attributes related to drought is presented hereunder.

Combining ability: Combining ability refers to the capacity or ability of a genotype to transmit superior performance to its crosses. The value of a parental line depends upon its ability to produce superior hybrids in combination with other parents. Combining ability analysis helps in the evaluation of parents in terms of their genetic value and in the selection of suitable parents for hybridization. The review of literature on gene action governing the inheritance of yields and yield component traits in summarized and presented.

Sprague and Tatum (1942) introduced the concept of combining ability and defined general combining ability (gca) and specific combining ability (sca). The gca refers to the average performance of a line in a set of hybrid combinations. The predominance of gca variance indicates additive gene action which is fixable genetic component. The sca refers to the deviation in the performance of crosses in certain specific combination (worse or better) than what would be expected on the basis of the average performance of the lines involved. The predominance of sca variance indicates non-additive gene action.

Knowledge of the genetic system controlling quantitative characters is essential for the choice of the most effective and efficient selection and breeding procedure. In self-pollinated species, simple genetic models utilizing two factor-mating designs have been used rather extensively to estimate additive and dominance variances on the assumption of negligible epistasis. Genetic models, which can detect and estimate the magnitude of epistatic variation in addition to the additive and dominance variations, are also available. Although, their use has been rather limited in self pollinated species, there is evidence which indicated statistically significant variation attributable to epistatic effects of several economic characters (Stuber and Moll, 1971). Such studies in groundnut are rather limited, it is, therefore, necessary to evaluate the importance of epistasis, in particular the fixable additive by additive type interaction component utilizing varied genetic materials as well as genetic models.

The combining ability analysis gives useful information regarding the nature and magnitude of gene action involved in the expression of quantitative traits (Dhillon, 1975) which helps in selecting appropriate breeding method for crop improvement.

An analysis of combining ability by Mohinder Singh (1983) using 12 parents and 35 F_1 s studies indicated that both additive and non-additive gene actions were important for pod yield, kernel yield per plant and shelling per cent. Further, out of thirty five crosses with high sca effects for pod yield, fifteen crosses showed high specific combining ability effects that involved good x good general combiners. Padma (1983) in a combining ability analysis in groundnut found that additive gene action was important for number of mature pods per plant, pod yield and kernel weight. Khanovkar *et al.* (1984) analysed the data for combining ability in groundnut and observed additive type of gene action in the inheritance of number of pods per plant.

Siva Kumar (1984) observed predominance of additive gene effects for days to 50 per cent flowering, shelling per cent and pod yield. An analysis of combining ability by Habib *et al.* (1985) in 12×12 parent diallel analysis studies indicated that both additive and non-additive gene actions were important for pod yield while additive gene action was important for number of developed and undeveloped pods per plant.

Manoharan *et al.* (1985) in a combining ability analysis reported additive gene action for shelling per cent and pod yield suggesting that improvement in these characters could be achieved through pedigree breeding. He also reported non-additive type of gene action for number of pods per plant. The crosses which have high specific combining ability effects either high x low or low x low combinations. Chandra Reddy (1986) in a 6 x 6 diallel analysis in groundnut reported non-additive gene action for number of mature pods, pod and kernel yield and additive gene action for number of primaries. Ramachandra Reddy (1986) in his studies on combining ability reported that number of primaries, number of pegs, mature pods and pod yield showed non additive type of gene action. Basu *et al.* (1987) in a 8 x 8 diallel analysis for combining ability in groundnut revealed that *gca* variance was higher than the estimated sca variance for traits like number of mature pods per plant, pod yield per plant and shelling per cent, indicating the predominant role of additive gene action for the these traits.

Jagannadha Reddy and Raja Reddy (1987) reported predominance of additive genetic variation for 100-kernel weight. of gene action in the inheritance of pod yield. Nava and Layrisse (1987) in combining ability studies in groundnut observed that additive type of gene action was predominant for pod yield per plant, kernel yield per plant and shelling per cent. Makne and Bhale (1987) in a 10 x 10 diallel combining ability analysis in groundnut showed predominant role of additive gene action in the inheritance of pod yield per plant and non-additive gene action in the inheritance of oil per cent. The *per se* performance of parents was closely associated with their gca effects. The crosses with largest sca effects for pod yield were high x low and low x high general combiners and the sca effects for oil content were generally low in magnitude.

Reddy and Reddy (1988) studied combining ability in a half diallel cross involving five parental lines belonging to Spanish and Valencia botanical types and found that both *gca* and *sca* variances were significant for number of mature pods per plant and shelling per cent, while non-significant for pod yield per plant. The *gca* variance was greater in magnitude than *sca* variance for 100-kernel weight.

Makne and Bhale (1989) analysed the data for combining ability in groundnut and observed importance of both additive and non-additive gene action in the inheritance of pod yield per plant. They also reported a good relationship between *per se* performance and *gca* effects of the parents for all the characters studied.

Seshadri (1990) analysed the data for combining ability in groundnut and observed importance of both additive and non-additive gene action in the inheritance of number of pods per plant in groundnut. Hariprasad (1990) recorded additive gene action in the inheritance of number of mature pods, kernel yield, and pod yield, while nonadditive gene action for number of primaries. Makne (1992) studied 55 F_1 s involving 10 diverse genotypes from different sub-species of groundnut. Variance due to *gca* and *sca* was significant for the characters number of developed pods per plant and harvest index indicating the importance of both additive and non-additive gene action in the inheritance of these characters. Upadhayaya *et al.* (1992) analysed the data for combining ability in groundnut and observed non-additive gene action for kernel yield per plant. Similarly Sateera Banu (1992) also observed the predominance of non-additive gene action for kernel yield per plant and pod yield per plant while additive gene action for number of mature pods per plant.

Bansal et al. (1992) and Skyes and Michaels (1986) in combining ability studies in groundnut observed importance of additive gene action in the inheritance of oil per cent. Contrary to this Reddy and Murthy (1994) reported the importance of both additive and non-additive gene actions in the inheritance of oil per cent. Suresh Kumar (1993) revealed the predominance of non-additive gene action in the inheritance of number of mature pods per plant, harvest index, kernel and pod yields per plant. He also reported importance of both additive and non-additive gene actions for shelling percentage. Varman and Raveendran (1994) in 22 F₁s of 11 x 2 parents showed the predominance of nonadditive gene action in the inheritance of number of pods and pod yield per plant. Both additive and non-additive gene actions were found important in the inheritance of revealed for harvest index, shelling out turn and sound mature kernel per cent.

Nisar Ahmed (1995) reported the importance of non-additive gene action for yield and yield component traits *viz.*, number of pods per plant, number of mature pods per plant and 100-kernel weight. In his studies, both additive and non-additive gene actions were found important in the control of harvest index, whereas additive gene action for shelling percentage. Kalaimani and Thangavelu (1996) revealed the predominance of additive gene action in the inheritance of number of mature pods per plant, shelling per cent, and pod yields per plant in a study of 8 F_1 s for 13 quantitative characters.

Dwivedi et al. (1998) in their combining ability studies recorded significant gca effects for harvest index. Similarly Varman (1998) reported that variance due to gca was higher than sca indicating the predominance of additive gene action in the inheritance of pod weight. Francies and Ramalingam (1999) revealed the predominance of non additive gene action for number of pegs, number of mature pods, pod yield and kernel yield and the role of both additive and non-additive gene action for oil per cent in 24 F, s of inter-specific crosses. Mathur et al. (2000) studied gene action in crosses made by line x tester analysis fashion with four Virginia genotypes and reported the predominance of non-additive gene action in the inheritance of number and weight of mature pods and sound kernel. Parmar et al. (2000) revealed the significance of both gca and sca variance for pod yield, shelling percentage and 100-kernel weight.

Varman (2000) studied combining ability in 30 F_1 s for five traits and reported the predominance of *sca* variance than *gca* variance for number of mature pods, pod yield, shelling out turn and oil content whereas reverse is the true for kernel weight. Ali *et al.* (2001) reported significant role of sca estimates for oil content and pod length, but the magnitude of gca was greater for maturity index and 100seed weight. Nigam *et al.* (2001) reported the importance of additive gene action in the inheritance of specific leaf area and harvest index in all the three crosses he studied. Dasaradha Rami Reddy and Suneetha (2004) reported that higher specific combining ability variance than general combining ability variance for oil per cent and kernel yield per plant. They also observed higher *gca* variance for number of pods per plant, pod yield per plant and harvest index.

Jivani *et al.* (2007) studied the combining ability involving eight diverse groundnut genotypes in one-way diallel for pod yield and its components observed the magnitude of non additive component (specific combining ability sca) was higher than additive for all the six traits in the F_2 generation. Hariprasanna *et al.* (2008) reported that in the F_1 hybrids including reciprocals from a six parent diallel cross along with parents on five quality traits in peanut *viz.* shelling out turn, 100-pod weight, 100-seed weight, count and proportion of sound mature seeds were regulated predominantly by additive gene action suggesting possibility of early generation selection, while non additive gene action also plays an equally important role in the control of seed size.

Sharma and Gupta (2008) studied 45 F_1 s obtained from crossing 10 different lines of groundnut in a diallel fashion. The estimates of gca effects indicated that the parents GG-4, GG-2, GG-5 and GG-20 were good general combiners for pod yield and its componential traits. The crosses GG-5 x ICGV 93462 and GG-20 x ICGV 93462 were best specific combinations for pod yield per plant, kernel yield, days to early flowering and reduced plant height. Jivani *et al.* (2009) in a combining ability study of 8 x 8 diallel set reported significant estimates of gca and sca for all the traits *viz.*, 100-kernel weight, number of pods, sound mature kernel, shelling out turn, kernel yield per plant, pod yield per plant.

Heterosis: Physical manifestation of the beneficial effects of hybridization between diverse parents is usually termed as heterosis and is referred as heterobeltiosis and relative heterosis based on F_1 superiority over better parent and mid parental value respectively. In plant breeding programmes, heterosis is referred to denote the expression of increased vigour of a hybrid over its better parent. Heterosis is a complex biological phenomenon often manifested in the superiority of a hybrid over parental forms according to the rate of development of one or more complex characters (Konarev, 1974).

Positive heterosis over mid parent in 9 F_1 s was recorded by Sridharan and Marappan (1980) for all the nine traits they studied. They reported positive heterosis over the better parent in all the hybrids for number of mature pods, per plant and pod yield. For number of mature pods, heterosis ranged from 23.33% to 87.50% over mid-parent and from 6.22% to 38.40% over better parent. Heterosis for pod yield ranged from 37.44% to 95.33% over mid-parent and from 4.20% to 70.30% over better parent.

Padma (1983) observed positive heterosis for plant height in ten out of eleven crosses. Maximum heterosis was expressed by Valencia x Virginia combination. Virginia x Virginia crosses were both heterotic and high yielding compared to Spanish x Virginia crosses. Arunachalam *et al.* (1984) reported high magnitude of heterosis for yield and its components *viz.*, per cent of mature pods, shelling percentage, pod yield and seed yield in crosses between the parents from intermediate divergence classes than extreme ones. Siva Kumar (1984) reported negative heterosis for height of main axis, days to 50 per cent flowering; 100-kernel weight and pod yield per plant whereas positive heterosis for number of primaries, 100-pod weight and shelling out-turn.

Swe and Branch (1986) reported that crosses of Spanish x runner type parents showed greater heterosis for total pod weight, total pod number and total seed weight whereas negative heterosis was observed for harvest index. Jagannadha Reddy and Raja Reddy (1987) in their studies on heterosis found that the average performance of F_1 hybrids excelled their parental limits for several characters studied. Highest heterosis over mid parent was observed for number of mature pods per plant. The highest percentage of heterosis over better parent was observed for yield and it was low for number of mature pods. Makne and Bhale (1987) in 10 x10 diallel crosses studies observed that most of the crosses showed significant heterosis for pod yield per plant and oil per cent.

Bansal et al. (1993) reported high relative heterosis for seed yield and mature pod number while moderate heterosis for pod yield. Varman and Raveendran (1994) in 22 F₁s of 11 x 2 parents observed high heterobeltiosis for pod yield per plant, shelling per cent, sound mature kernel per cent and number of well filled and mature pods per plant. Varman and Raveendran (1997) reported high levels of heterosis for number of mature pods and pod yield in single crosses while three way crosses exhibited heterotic effects for shelling out turn, pod weight and seed weight. Senthil and Vindhiyavarman (1998) observed positive and significant heterosis for number of mature pods and seed size. Rudraswamy et al. (1999) in F_1 , F_2 and F_3 generation of 6 crosses studied heterosis and inbreeding depression. They reported positive and significant heterosis in F, generation for pod yield. They concluded that heterosis in F₁ generation and inbreeding depression in F_2 and F_3 generations is due to additive gene action. Jayalakshmi *et al.* (2000) reported highest average heterosis over mid parent for kernel yield from 25.52 per cent (ICG 2716 x Tirupati 1) to 73.73 per the

cent (ICG 2716 x ICGV 86031) followed by number of mature pods per plant and root dry mass.

Manivel et al. (2003) reported that Virginia bunch x Virginia bunch crosses were more heterobeltiotic than Spanish bunch x Spanish bunch crosses for late flowering, plant height and number of primary branches while Spanish bunch x Spanish bunch crosses were found more heterotic for early flowering and pod weight per plant than Virginia bunch x Spanish bunch crosses. Parmar et al. (2004) studied 28 crosses for heterosis and reported heterosis for sound mature kernel per cent in 8 crosses, oil per cent in 10 crosses and pod yield in three crosses. Dasaradha Rami Reddy and Suneetha (2004) observed low value of heterosis in general for most of the characters studied in 23 crosses, except number of mature pods per plant. Though heterosis was significant and in desirable direction none of the cross combinations registered more than 25% heterosis either over better parent or standard parent for pod yield per plant.

Jayalakshmi and Reddy (2005) studied heterosis and inbreeding depression in 21 crosses of groundnut. The manifestation of heterosis was of higher order for pod yield, shoot biomass, mature pod number per plant and root dry mass. John and Vasanthi (2006) reported highest heterosis over the better parent (>BP) for pod yield in K-3 x TCGS-150 in F_1 and in F_2 ICGV-91173 x TCGS0150 and kernel yield in K-3 x ICGV-88083 in F_1 and ICGV-991173 x TCGS-150 in F_2 and also reported higher level of heterosis in F_1 and also high inbreeding depression in ICGV-91173 x TCGS-150, ICGV-91173 x ICGV-88083 which suggested the importance of additive gene action in the expression of heterosis in these crosses. Jivani *et al.* (2008) in a diallel analysis using 8 genotypes reported heterosis over mid parent, and better parent and inbreeding depression for all the traits. Non additive gene action with over dominance as indicated by close relationship between heterosis and inbreeding depression was observed for pod yield and its related traits.

CONCLUSION

Combining ability analysis indicated considerable non-additive gene action in the inheritance of majority of the attributes. The non-fixable dominance deviation and epistatic effects are likely to hinder improvement through simple pedigree selection, which is commonly followed in groundnut. Under such situations, breeding procedures have to be amended suitably by postponing the selection to later generations (Baker, 1968). Alternatively internating of the F₂ segregants followed by recurrent selection and pedigree breeding can harness the different kinds of gene - effects. Repeated selection and intermating of segregating materials for two or three cycles, makes it possible to achieve simultaneously improvement in kernel yield and other physiological attributes. Monteverde - Penso and Wyne (1998) suggested that, where hybridization is difficult recurrent selection with minimal crossing followed by single seed descent may be practiced for obtaining better results. Halward et al. (1990) found that recurrent selection was effective for improving both yield and agronomic characters in the broad based groundnut population. For exploitation of such heterosis in future breeding programmes either recurrent selection or diallel selective mating system is to be examined in these crosses. Further, the crosses which recorded high heterosis for pod yield also recorded high inbreeding depression in F, generation indicating importance of non-additive gene action.

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