

USE OF COMBINING ABILITY, HERITABILITY AND GENETIC ADVANCE IN BREEDING PROGRAMMES

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SUMMARY

The choice of suitable parents for producing desirable hybrids is most important and fundamental step in hybridization programmes since certain combinations produce much superior offspring than others involving apparently equally promising parents. The knowledge about the combining ability effects of the genotypes may help the plant breeder in selecting parents which when crossed would produce more desirable segregates. Biometrical methods like diallel, partial diallel and line x tester may be used for testing the combining ability of parents and their hybrids at an early stage of the programme. Further, estimates of heritability also serve as a useful guide to the plant breeder. If heritability of a character is high than selection would be much easier. But for a character with low heritability, selection will be difficult. The degree of heritability should not be taken as sole criterion while drawing conclusions about the expected genetic gain. Hence, heritability estimates along with expected genetic advance are usually more helpful than heritability value alone.

Key words : Combining ability, heritability, genetic advance, breeding programmes

The choice of parents is the important step in hybridization programme since certain combinations produce much superior offspring than others involving apparently equally promising parents. Thus, any method which would help in choosing desirable parents will be important for the breeder. The mean performance is the simplest biometrical parameter of selecting parents. For instance, when the objective is to improve yield *per se* rather than other bottleneck characters, atleast one of the parents should be high yielding. The reflection of mean performance in the genetic merit of the parent, however, is limited by the presence of genotype x environmental interaction. Most often genetic diversity of parents for the characters needing improvement is considered as an important criteria in choosing parents for any breeding objectives. Among several multivariate statistical methods to measure genetic diversity, distance analysis (D^2 -statistic) is a potent tool (Rao, 1960). Multilocation testing and regression analysis for stability permit to evaluation of average genetic merit of the parents. This kind of approach of selecting parents is applicable to the breeding for adaptability of crop varieties. However, the selection of parents on the basis of combining ability is one of the most commonly used

techniques in almost all crops.

This technique is highly efficient in selection of parents because the productivity of parents in cross combinations and their combining abilities is effectively correlated.

Combining Ability

It is the ability of an individual to transmit its performance to its progeny in crosses. Sprague and Tatum (1942) used the terms, general combining ability (gca) and specific combining ability (sca). The definitions of these terms are as follows : The term general combining ability is used to designate the average performance of a line in a series of cross combinations. The term specific combining ability is used to designate those crosses in which certain combinations do relatively better or worse than would be expected on the basis of the general combining ability.

Estimation of Combining Ability

The general and specific combining abilities can be estimated by some commonly used biometrical

techniques such as diallel, partial diallel and line x tester design.

Statistical Model

Two sets of sampling assumptions can be considered with regard to experimental material—Fixed effect model (model 1) and random effect model (Model II).

- (i) **Fixed effect model or model I :** In model I, the experimental material or parental lines are deliberately chosen. Objective of fixed model is to compare lines or crosses for their own genetic merit. When the analysis of variance based on fixed effect model, one is concerned with comparison of general combining ability effects of actual parents used in the experiment and with comparison of specific combining ability effects of cross combinations.
- (ii) **Random effect model or model II :** In model II, the assumption is that the parent lines are a random sample of large population of lines. In an analysis based on random model, inferences are to be made about the population of lines from which have been sampled. Here variance component is estimated and interpretation is applicable to whole population.

Line x Tester Design

The line x tester design developed by Kempthorne (1957) is used to evaluate lines or inbreds in both self or cross pollinated crops (Table 1). This mating design is basically a top cross (inbred x variety cross) method where several testers are used instead of one, so that the breeder is not only able to obtain information about general combining ability effects but also specific combining ability effects of various cross combinations can be estimated. The procedure is mostly used to screen the germplasm for the choice of better genotypes to directly evolve as commercial varieties or to channelize them into further breeding programmes. In this mating design, a set of inbred lines (l) is crossed in all possible combinations with some broad based genotypes used as testers (t) to produce (lt) full sib progeny families. The crossing programme is exactly similar to North Carolina Design II and similarly, based

on the covariances of half sib (Cov. HS) and full sib (Cov.FS) families. From these covariances between half sibs and full sibs, gca and sca variance components can be estimated.

TABLE 1
Analysis of variance of line x tester design

Item	d. f.	Expected mean square
Lines	l-1	$\sigma^2_e + b\sigma^2_{lt} + bt \sigma^2_l$
Testers	t-1	$\sigma^2_e + b\sigma^2_{lt} + bl \sigma^2_t$
Lines x Testers	(l-1) (t-1)	$\sigma^2_e + b\sigma^2_{lt}$
Error	(r-1) [(l+t+lt)-1]	σ^2_e

Computations of Combining Ability Effects

$$m = \frac{X_{...}}{bt}$$

$$g_i \text{ (line)} = \frac{X_{i..}}{bt} - \frac{X_{...}}{blt}$$

$$g_j \text{ (tester)} = \frac{X_{.j.}}{bl} - \frac{X_{...}}{blt}$$

$$s_{ij} = \frac{X_{ij.}}{b} - \frac{X_{i..}}{bt} + \frac{X_{.j.}}{bl} - \frac{X_{...}}{blt}$$

Where,

- X... is the grand total (total of all crosses)
- Xi.. is the sum of ith line over all testers and all blocks
- X.j. is the sum of the jth tester over all lines and all blocks
- X_(ij) is the sum of ijth cross over blocks

Various standard errors can be calculated as follows :

$$S. E. g_i \text{ (line)} = \sqrt{\frac{\text{Error variance}}{bt}}$$

$$S. E. g_j \text{ (tester)} = \sqrt{\frac{\text{Error variance}}{bl}}$$

$$S. E. s_{ij} = \sqrt{\frac{\text{Error variance}}{b}}$$

$$S. E. (g_i - g_j) (\text{lines}) = \sqrt{\frac{2 \times \text{error variance}}{bt}}$$

$$S.E. (g_j - g_m) (\text{testers}) = \sqrt{\frac{2 \times \text{error variance}}{bl}}$$

$$S.E. (g_{jj} - s_{im}) = \sqrt{\frac{2 \times \text{error variance}}{b}}$$

Diallel Cross

Most extensively used mating design for estimating general and specific combining abilities is diallel crossing system in which in homozygous parents of a set are crossed in all possible combinations to produce n^2 progenies. These n^2 progenies of a diallel table ($n \times n$) can be divided into three groups (i) the n parents, (ii) one set of $n(n-1)/2$ F_1 's and (iii) $n(n-1)/2$ reciprocal F_1 's. Depending upon the inclusion and exclusion of parents and/or reciprocal F_1 's in the analysis, Griffing (1956) suggested four methods :

Method 1: All n^2 progenies are included in the analysis.

Method 2 : Parents and one set of F_1 's are included but reciprocals are excluded i. e. $n(n+1)/2$.

Method 3 : Both sets of F_1 's are included but parents are excluded i. e. $n(n-1)$.

Method 4 : Only one set of F_1 's is included and parents as well as reciprocal F_1 's are excluded i. e. $n(n-1)/2$.

The methods 3 and 4 are suitable to examine the general and specific combining abilities for a specific set of plant material. When it can be assumed that there are no reciprocal cross difference, the method 4 is most appropriate.

In most combining ability analysis in which a chosen set of lines is used. The plant breeders' interest centres on specific combining ability effects for selecting high heterotic F_1 hybrid. In such situation the parents should be excluded. If combining ability is adopted to

select suitable lines for producing synthetic variety and if considerable inbreeding occurs in the species, then it is advisable to include parents. The diallel crossing method 3 or 4 is again most applicable when a random set of lines is used.

Regardless of breeding objectives, most plant breeders are using method 2 (Parents and one set of F_1). This is because the method 2 also allows examination of genetic constitution of parent lines through Hayman's approach (Hayman, 1954).

The use of combining ability analysis, however, has provided very useful information about the combining ability of parents and potential hybrids. But the results of diallel analysis will be reliable only when the material under investigation satisfies the two most critical and unrealistic assumptions of diallel analysis—the absence of epistasis and absence of gene correlation. Methods (consistency of $W_r - V_r$ over arrays and joint regression analysis) are available in the literature (Mather and Jinks, 1982; Singh and Panwar, 2005) to test these assumptions.

Analysis of Diallel Cross Method 2

Item	d. f.	Expected mean squares	MS
Gca	$n-1$	$\sigma^2e + \sigma^2s + (n+2)\sigma^2g$	M_1
Sca	$\frac{1}{2}n(n-1)$	$\sigma^2e + \sigma^2s$	M_2
Error	M	σ^2e	M_3

$$s^2g = \frac{M_1 - M_2}{n+2} = \text{Cov.HS}$$

$$s^2s = M_2 - M_3 = \text{Cov. FS} - 2 \text{Cov. HS}$$

On fixed effect model, the effects may be estimated

$$m = \frac{2}{n(n+1)} Y_{..}$$

$$g_i = \frac{1}{n+2} \left[Y_{i.} + Y_{.i} - \frac{2}{n} Y_{..} \right]$$

$$g_{ij} = Y_{ij} - \frac{1}{n+2} Y_{i.} \left[Y_{.i} + Y_{ij} \right] + \frac{2}{(n+1)(n+2)} Y_{..}$$

Partial Diallel

Although diallel method has several advantages but it has some drawbacks too. The major drawback of this method is that the number of crosses increases tremendously with increase in the number of parents and thus the method puts a limit on the number of parents to be included in the crossing programme. A large number of parents in the diallel not only creates difficulty in attempting a huge number of crosses artificially but also the evaluation of such a large number of crosses under field conditions becomes unmanageable. Therefore, for practical purposes, use of diallel crossing system is limited to the evaluation of diallel progenies produced by crossing a relatively small number of parents. But the inclusion of small number of parents in the diallel programme has two disadvantages (i) The estimate of gca variance will have a large sampling error and (ii) Many potentially superior lines will remain untested. The use of partial or fractional diallel may perhaps greatly help in overcoming the difficulties mentioned above.

Kemphorne and Curnow (1961) described a procedure for sampling the crosses and carried out combining ability analysis. The mating design is called as partial diallel (Table 2). For constructing a partial diallel cross design, it is necessary to know about the symbols 's' and 'k'. The symbol 's' means the number of crosses in which each of n parents is involved and total number of sampled crosses = n x s/2. The symbol k is used to know to crosses in which each of parent will occur and k=(n+1-s)/2. If n=7 and s=4, k will be 2.

The ith parent will be involved in k+i, k+i+1, and k+i-1+s crosses i. e. parent 1 will be included in 1 x 3, 1 x 4, 1 x 5, 1 x 6 crosses and similarly parent 2 will be involved in 2 x 4, 2 x 5, 2 x 6 and 2 x 7 crosses.

$$K = \frac{7+1-4}{2} = 2$$

$$\text{Total crosses sampled} = \frac{n \times s}{2} = \frac{7 \times 4}{2} = 14$$

Here, either n is odd or s is even or vice-versa.

The procedure for sampling for a partial diallel set when n=7 and s=4 (each variety should be crossed 4 times).

Parents	P ₁	P ₂	P ₃	P ₄	P ₅	P ₆	P ₇
P ₁			✓	✓	✓	✓	
P ₂				✓	✓	✓	✓
P ₃					✓	✓	✓
P ₄						✓	✓
P ₅							✓
P ₆							
P ₇							

TABLE 2
Analysis of variance for combining ability in partial diallel

Item	d. f.
Blocks	b-1
Crosses	ns ----- -1 2
Gca	n-1
Sca	ns ----- -n 2
Error	$\left[\begin{matrix} ns \\ \text{-----} -1 \\ 2 \end{matrix} \right] (b-1)$

$$\sigma^2g = \frac{(MS_{gca} - MS_{sca}) (n-1)}{bs (n-2)} = \text{Cov. HS}$$

$$\sigma^2s = \frac{(MS_{gca} - Ms_{error})}{b} = \text{Cov. FS-2 Cov. HS}$$

$$\text{Cov. HS} = \frac{(1+F)}{8} D$$

$$\text{Cov. FS} = \frac{(1+F)D}{4} + \frac{(1+F)^2}{4}$$

Where, F is the inbreeding coefficient.

Heritability may be defined as the proportion of the phenotypic variance attributable to genetic differences i.e. the ratio of genetic variance to the total variance (phenotypic variance) for the trait.

$$\text{Heritability in broad sense (h}^2\text{b)} = \frac{V_g}{V_p}$$

$$= V_g/(V_g+V_e)$$

Whereas V_g , V_p , V_e are the genetic, phenotypic and environmental components of variance, respectively.

$$\text{Heritability in narrow sense (h}^2\text{n)} = \frac{V_A}{V_g+V_e}$$

Heritability in narrow sense expresses fraction of the phenotypic variability attributable to the additive genetic differences (that is, additive variance/phenotypic variance). The heritability in narrow sense, since it is based on the fixable portion of genetic variance, is more important for the plant breeder than the heritability in broad sense. Thus, for obtaining a reliable value of genetic advance, one should use the value of narrow sense heritability rather than that of broad sense heritability.

Heritability can be estimated by three different methods given below :

1. From analysis of variance table of a trial consisting of a large number of genotypes raised in a randomized block design

Here, s_e^2 provides direct estimate of environmental variance, s_g^2 that is, MS genotypes-MS error/ r provides the estimates of genotypic variance and $s_e^2+s_g^2=s_p^2$ (Phenotypic variance). These estimates of components of variance (Table 3) can be used to obtain estimates of heritability in broad sense (s_g^2/s_p^2 if

TABLE 3
Analysis of variance

Item	d. f.	Expected mean square
Replications	$r-1$	$\sigma_e^2 + g\sigma_r^2$
Genotypes	$g-1$	$\sigma_e^2 + r\sigma_g^2$
Error	$(r-1)(g-1)$	σ_e^2

genotypes are heterozygous heritability in narrow sense (s_g^2/s_p^2 if genotypes are homozygous where heritability in broad sense=heritability in narrow sense).

2. Estimation of V_g and V_e from the variances of F_2 , P_1 , P_2 and F_1 generations of a cross

Warner's Method

Warner (1952) suggested a method for estimating heritability using variances of F_2 and backcrosses (BC_1 and BC_2) generation. This method was described by Allard (1960) where the difference $2VF_2 - (V_{BC_1} + V_{BC_2})$ which is equal to $\frac{1}{2}D$, was used to estimate additive genetic variance. The narrow sense heritability in this method is equal to $\frac{1}{2}D/\frac{1}{2}D+H+E$, that is additive genetic variance divided by the phenotypic variance of F_2 . We can also calculate heritability in broad sense by computing average environmental variance using the variances of non-segregating generations (Parents and F_1), that is,

$$E = \frac{V_{P_1} + V_{P_2} + V_{F_1}}{3} \quad (\text{Allard, 1960})$$

If variances of the three generations do not differ significantly from each other and

$$E = \frac{1}{4}V_{P_1} + \frac{1}{4}V_{P_2} + \frac{1}{2}V_{F_1} \quad (\text{Mather and Jinks, 1982})$$

If variance of the F_1 is significantly different from that of parents.

Now, $V_{F_2} - E = \frac{1}{2}D + H$, that is total genetic variances and thus heritability in broad sense will be equal to

$$(\frac{1}{2}D + \frac{1}{4}H)/V_{F_2}$$

3. Parent-off spring regression upon doubling provides as an estimate of heritability. Thus, $h^2=2b$ where, b is the regression of progeny means on parental values.

Genetic advance under selection

Genetic advance under selection which measures the rate of genetic progress due to selection as the deviation between mean genotypic value of the selected families and mean genotypic value of the base population, depends on three things.

1. The amount of genetic variability present in the original base population.
2. The heritability of the character under selection, and
3. The intensity of selection practised by the plant breeder.

The expected genetic advance under selection (G_s) can be calculated with the help of following formula (Allard, 1960).

$$G_s = (K) (sp) (h^2)$$

Where, h^2 is heritability coefficient, sp the phenotypic standard deviation of the base population and K a standardized selection differential. The value of K is constant for a specific selection intensity that is, it would vary only when there is a change in selection intensity. Higher the proportion of selected families or plants to the total number of families/plants tested, smaller will be value of K . For example, for 5 per cent selection intensity the value of K is 2.06, whereas for 20 per cent selection intensity its value is 1.40.

Estimates of heritability serve as a useful guide to the plant breeder. If heritability of a character is high than selection would be much easier. But for a character with low heritability, selection will be difficult due to masking effect of the environment on genotypic effects. Moreover, when dealing with segregating populations, heritability in narrow sense will be more appropriate for estimating reliable value of genetic advance to avoid

higher estimate of G_s while using broad sense heritability while making calculation of G_s . Sometimes, there is absence of a high correspondence between the value of heritability and those of genetic advance because of difference in the magnitude of phenotypic standard deviation. Therefore, genetic advance is considered as a more important parameter than heritability.

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