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The Utility of Covariance of Combining Ability in Plant Breeding

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Summary. The definition of covariances of half- and full sibs, and hence that of variances of general and specific combining ability with regard to a quantitative character, is extended to take into account the respective covariances between a pair of characters. The interpretation of the dispersion and correlation matrices of general and specific combining ability is discussed by considering a set of single, three- and four-way crosses, made using diallel and line × tester mating systems in *Pennisetum typhoides*. The general implications of the concept of covariance of combining ability in plant breeding are discussed.

Introduction

One of the potent tools for identifying prospective parents and sifting productive hybrids from a set of crosses in F1 generation is the analysis of combining ability (Griffing 1956). The crosses are usually made to conform to a chosen genetic model and field design in order to provide a genetic interpretation of the results obtained on the phenotypic measurements of a quantitative character. The most commonly used designs are diallel and line × tester supplemented by partial diallel and other fractional diallels. With realistic assumptions relevant to plant breeding problems, Griffing (1956) has provided a complete analysis and interpretation of data obtained from a full diallel and its variations. Similar analysis of data from a line × tester design is provided by Kempthorne (1957) and Arunachalam (1974).

The general and specific combining ability effects and variances obtained from a set of F1's would enable a breeder to select desirable parents and crosses for each one of the quantitative components separately, but a majority of the quantitative characters in general, and those related to yield in particular, invariably show varying degrees of association among themselves. Even when the combining ability components are examined for a number of attributes simultaneously, the breeder faces considerable difficulty in judging with confidence the best parents or crosses for a number of yield attributes.

In this paper, the concept of variances of combining ability of a quantitative character is extended logically to covariances between any two characters and its use is demonstrated by an experiment on pearl millet, *Pennisetum typhoides*.

Covariances of General and Specific Combining Ability

The general and specific combining ability variances derive their genetic interpretation from their definition in terms of covariances of half- and full sibs (Kempthorne 1957). It is therefore reasonable to conceive of covariances of half- and full sibs with regard to two quantitative characters in exactly the same way as is done for a single one. The definition of covariances of general and specific combining ability between two characters will follow as a natural extension. It will be apparent that, while the covariance of general combining ability (gca) between two quantitative characters x and y will involve all the additive covariances and interactions involving them, that of specific combining ability (sca) will involve dominance and all epistatic covariances except additive covariance. With an arbitrary inbreeding coefficient F, we can write

$$\mathrm{Cov\ (full\ sibs)} = (1+F/2)\sigma_{xy}(A) + (1+F/2)^2\sigma_{xy}(D) + (1+F/2)^2\sigma_{xy}(AA) + (1+F/2)^3\sigma_{xy}(AD) + \ldots .$$

$$\mathrm{Cov\ (half\text{-}sibs)} = (1+F/4)\sigma_{xy}(A) + (1+F/4)^2\sigma_{xy}(AA) + (1+F/4)^3\sigma_{xy}(AAA) + \ldots\ldots ,$$

where A stands for additive, D for dominance, AD for additive × dominance etc., covariances,

Table 1. Dispersion matrix of general and specific combining ability in *Pennisetum typhoides*

		HH	HT	HE	HY	TT	TE	TY	EE	EY	YY
SC1	g	75.3	26.0	9.3	185.7	37.3	-1.5	-11.9	3.1	29.3	@
	rg	-	0.49	0.61	+	-	-0.14	+	-	+	-
	s	273.5	39.7	35.0	1768.3	125.2	-4.0	295.1	8.2	209.0	26278.7
	rs	-	0.21	0.56	0.38	-	-0.12	0.16	-	0.45	-
SC2	g	20.4	-7.6	4.1	39.6	27.3	-4.4	58.0	1.4	8.1	3159.1
	rg	-	-0.32	0.77	0.16	-	-0.71	0.20	-	0.12	-
	s	194.0	129.5	19.8	1454.7	605.9	19.9	5062.8	5.4	248.6	70119.4
	rs	-	0.38	0.61	0.39	-	0.35	0.78	-	0.40	-
TWC	g	@	29.1	-33.9	428.6	@	20.0	-629.3	@	296.3	@
	rg	-	+	+	+	-	+	+	-	+	-
	s	409.2	-303.4	119.0	-2740.7	368.7	-17.0	5246.8	37.4	-441.5	78100.6
	rs	-	-0.78	0.96	-0.48	-	-0.14	0.98	-	- 0.26	-
FEX	g	276.0	-55.5	13.7	-59.0	@	0.5	-27.1	0.3	-37.7	3386.1
	rg	-	+	=	-0.06	-	+	+	-	=	-
	s	165.2	107.7	3.9	2108.3	399.8	-11.6	2640.0	9.4	214.7	929.7
	rs	-	0.42	0.10	=	-	- 0.19	=	-	=	-

+@ : Not estimable; =: Value greater than one;
rg : Correlation coefficient of gca; rs : Correlation coefficient of sca; g : gca; s : sca

Cov (gca) = Cov(half-sibs) and
Cov (sca) = Cov(full sibs) - 2 Cov(half-sibs).

One can also utilise the correlation coefficients of general and specific combining ability (Griffing, 1956).

The estimation of the covariances in the models mentioned above is quite simple, since the expected values of mean sum of products are similar to those of mean sum of squares (Griffing 1956; Arunachalam 1975). In known systems of mating, such as diallel, partial diallel, triallel, line × tester, triangular and rectangular designs, it is possible to work out the covariances and correlations of general and specific combining abilities between any two metric characters. Since the fixed effects model is more relevant to plant breeding problems and the distribution of the correlation coefficients is unknown, it is not possible to test either the covariances or the correlation coefficients. Despite this difficulty, a dispersion matrix of general and specific combining ability (or a correlation matrix, for that matter) would be a source of additional information to the breeder, as will be shown.

Material

These concepts will be illustrated from a breeding experiment on *Pennisetum typhoides*. Diallel crosses were made using 16 parents providing equal representation to four major sources of diversity -- A, T, W and R. The former two were products, in an advanced generation, of biparental matings and selections from a diallel involving dwarf types; the third was a sample from African germplasm and the fourth resulted from irradiation of chosen material. The F1 and F2 generations were grown during 1974 with a set of 3- and 4-way crosses in their F1 stage. The female parents of 3-way crosses were a set of F1 single crosses and the males were entries selected for a set of ear and plant type characters. Both the male and female parents in the 4-way crosses were F1 single crosses unrelated to each other. A number of quantitative characters related to yield was measured on random samples of five plants per row. Two rows per entry were raised in F2 single crosses, so the sample size was ten plants per F2 entry per replication. The single crosses in F2 and F1 (denoted by SC1 and SC2) were made in a diallel design and the 3- and 4-way crosses (denoted by TWC and FWC) in a line × tester design. All the material was grown in a randomised blocks design in the same experimental environment.

Results

A study of the dispersion and correlation matrices of combining ability (Table 1) revealed that various degrees of association, both desirable and undesirable, existed for combining ability among plant height (H), number of effective tillers (T), ear length (E) and single plant yield (Y). In SC1 and SC2, the estimates of sca covariances were higher than gca for all the characters, as would be found in plant populations needing genetic upgrading. A change in direction in SC2, as compared with SC1, of the covariances of combining ability, for example, cov(sca) between T and E and that between H and T, was of particular interest. The changes in the direction of action were more pronounced for several character combinations in 3-way crosses. They culminated in certain combinations having higher and more desirable cov(gca) than cov(sca) in 4-way crosses, for example in the combinations H - H, H - E and Y - Y. The sample size would appear to be inadequate for 3- and 4-way crosses since some variance components, and hence several correlation coefficients, could not be estimated with reasonable precision.

Scrutiny of the covariances of gca and sca showed that ear length and yield had reinforcing additive gene action in SC1, SC2 and TWC. The combinations, H - Y and T - Y, did not appear to have such gene action. The non-additive gene action, as could be inferred from cov(sca), was variable and was found to act together with additive gene action. This could make straightforward selection a difficult task. The associations between H - E and E - T were also not in the desired direction. A shift in the magnitude and direction of gene action from SC1 was noted in SC2 for all the character pairs.

Discussion

It was evident that major characters related to yield did not show reinforcing epistasis; nor were additive covariances predominant.

The response to selection can be shown to be a function of the breeding values of the selected parents. The gca effect in particular is directly related to the breeding value of the parent (Falconer 1964). However, synergistic action of two or more yield components would be a pre-requisite for upgrading the performance of the derived population. The dispersion matrices of gca and sca would therefore indicate the existence of consonant action of two or more characters, which would help to set the next phase of a breeding programme on a sound footing. In the experiment cited in this paper, for example, the cov(gca) of H with T and Y in FWC and that of H with E in TWC were desirable, while they were undesirable in SC1. Thus a dwarfing gene would pay better dividends in yield for this material when incorporated in FWC and TWC than if incorporated in SC1. This observation could not be made from the variances of gca for H, T, E and Y alone. Examination of the other associations shows the need to tap multiple crosses for ensuring a conformant action of several genes controlling characters related to yield.

Another salient result was the differences observed in SC1 and SC2. Though a sample size twice as large as that used in F1 was used in F2, there would appear to be a lack of consistency in the direction and magnitude of action in the first and second degree components of combining ability. This would set the limitations of extending the combining ability studies to F2 and higher generations in proper perspective, rather than bringing to the fore the value of the desirable segregants made available in F2. The argument here is fairly straightforward, if one recollects the basic assumptions on which the genetic model rests. One powerful reason is that the sample that is scored in F2 of a cross will consist of a large number of genotypes (unknown to the breeder) and the probability that two such samples contain exactly the same genotypes is near zero. This situation does not arise in F1, which is genetically homogeneous when inbred parents are used. Thus, even ignoring the selective elimination that occurs during the sowing of the F2 population, it would be difficult to extend the combining ability studies to F2.

Further, mere phenotypic uniformity may not be adequate for fixing a proper sample size. This gains support from a study of TWC and FWC: the F1 showed a good amount of phenotypic uniformity, but the sample size was not found to be adequate.

It is now known that genetic upgrading results when the forces of natural and artificial selection reinforce each other in the desirable direction. In this context, the covariances of combining ability would provide basic information definitely superior to that given by the variances.

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