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Principles for Griffing's combining ability analysis

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Abstract

Griffing's diallel analysis is used in plant improvement programs to identify superior parents for crossing and for characterizing general, specific, and reciprocal effects. Eight different model/method combinations are commonly used in the analysis. The accuracy of the analysis is improved by using the appropriate model and method. In many instances, Model One with Method Three or Four is the most appropriate for obtaining unbiased estimates of combining abilities and gene action. The effective use of Griffing's analysis and the influence of several factors on this analysis are discussed. A personal computer program on this analysis is also made available to interested readers.

Introduction

The choice of parents for developing plant breeding populations can be difficult. Available resources, program objectives, and the genetic nature of the characters of interest will affect the final decision. In the decision-making process, the experienced plant geneticist may rely on the outcome of various biometrical evaluations.

Griffing's biometrical analysis (Griffing, 1956) has been widely used to aid plant geneticists in the selection of parents for hybridization (Williams & Windham, 1988; Krueger, Weinman & Gabelman, 1989; Arabi *et al.*, 1990). In most instances, the analysis provides reliable information on the combining ability of parents, i.e., the potential of parents to produce superior progenies following hybridization, and the magnitude of additive and non-additive gene action. Griffing's analysis is not hindered by the requirements of numerous genetic assumptions (Christie & Shattuck, 1992) and interpretations from this evaluation are usually straightforward. However, several important factors must be considered when using the analysis. A survey of the current literature indicates that these factors are at times overlooked and may lead to erroneous conclusions. In this paper, we describe Griffing's analysis and present information for its effective use. In addition, since the computations of this analysis can be laborious and time consuming, we offer, to interested scientists and educators, at no charge, a personal computer program for Griffing's analysis.

Models and methods

Griffing's analysis was originally developed for both plant and animal research to explore main effects (general combining ability, GCA) and interactions (specific combining ability, SCA). The analysis considers varieties (v) or genotypes grown randomly in a randomized block (b) experimental design based on the model:

$$x_{ijkl} = \mu + v_{ij} + b_k + (bv)_{ijk} + e_{ijkl}$$

where μ = population mean, v_{ij} = effect for the ijth genotype, b_k = the kth block effect, $(bv)_{ijk}$ the interaction between the ijth genotype and kth block, and e_{ijkl} = the environmental effect for the ijklth individual.

Varietal effects are explained in terms of general and specific combining ability effects and occasionally reciprocal effects as shown:

$$V_{ij} = g_i + g_j + s_{ij} + r_{ij}$$

where g_i = GCA of the ith inbred parent, g_j = GCA of the jth inbred parent, s_{ij} is the SCA effect for the cross between the jth and kth parents, and r_{ij} is the reciprocal effect for the ith and jth parents.

Reciprocal effects reflect differences in the values of the reciprocal crosses and can be positive or negative depending on the direction/calculation of the effects. GCA effects refer to the average performance of the progeny of an individual when mated with a series of genotypes. A parent with a GCA of 0 has an average combining ability and depending on the index used, parents with positive or negative GCA values perform above or below average. SCA expresses the performance of the progeny from a cross between two parents based on the average performance of the parents involved. SCA effects are either positive of negative. GCA is attributed to additive gene action and SCA to non-additive effects.

Griffing considered four models involving genotypes and block effects. The genotypes and blocks were either constant, random, or combinations of both as follows: Model One, or the fixed effect model, where the variety and block effects are constant; Model Two, or random model, where the genotype and block effects are random; Mixed Model Three where the genotype effects are constant and the block effects are random; and Mixed Model Four where the genotype effects are random and the block effects are constant.

Four diallel crossing methods were presented by Griffing and are shown in Table 1. These crossing schemes involved different combinations of parents, F_1s and reciprocals. Thus, Griffing's analysis produced 16 different model/method combinations.

Discussion

Although Griffing's analysis was originally presented using inbred parents, this analysis can be used on parents with varying inbreeding coefficients (F). In practice, the objectives of the analysis, the biology of the evaluated species, and the preference of the plant geneticist will determine if inbred parents are used for the analysis. For example, in some cross pollinating species, such as alfalfa, inbreeding can result in the death of plants, and the narrowing of the germplasm base. Thus, combining ability studies are usually performed on non-inbred parents or parents partially inbred for only one generation. If non-inbred parents are used to estimate population variances, the variance interpretations should be adjusted for the F value (Becker, 1985). When parental inbreeding is not a problem and the objectives of the analysis are to identify progeny of

Table 1. The required number of genotypes for Griffing's analysis for X parents

Method	Evaluated genotypes	Genotypes number	X = 5	X = 10	X = 20
			Genotypes to examine		
One	Parents, F_1, and reciprocal crosses	x^2	25	100	400
Two	Parents and F_1 generation	$\frac{x(x+1)}{2}$	15	55	210
Three	F_1 and reciprocal crosses	$x(x-1)$	20	90	380
Four	F_1 generation	$\frac{x(x-1)}{2}$	10	45	190

parental combinations with a high degree of F_1 uniformity and to maximize the number and expression of heterozygous combinations, then a parental F value of 1.0 or near 1.0 may be preferred. It should be noted that in early generation ($F < 0.75$) parental line testing for combining ability, appropriate tester(s) rather than diallel crossing schemes should be used.

Significant variety/genotype differences must be present before conducting Griffing's analysis. The analysis of variance (ANOVA) can be used to test for genotypic differences. Transforming data sets for Griffing's analysis, unlike for the ANOVA (Keith-Smith, 1976), is rarely practiced (Quimio & Zapata, 1990; Widstrom, Bondari & McMillian, 1992) and usually not necessary. Data transformation would not be expected to substantially change the parental or cross combination rank performances but may alter the GCA/SCA ratio. A systematic procedure for choosing the appropriate transformation for genetic data has been discussed (Kerbusch, Van der Staay, & Hendriks, 1981) and a computer program on transformation selection has been developed (Crusio, 1990).

The program objectives and parental sampling procedures will determine the most appropriate model to use. Models One and Two are most commonly used in Griffing's analysis; thus, we will limit our discussion to these models. If the parents are deliberately selected, then Model One is appropriate and inferences should be restricted to the set of parents evaluated. For example, this model is used for testing promising inbred lines for combining ability to identify the most promising parents for developing hybrids and open-pollinated populations. Model Two is suitable when the evaluated parents are used as a sample to obtain information on the population from which they were selected. When using Model Two with inbred lines, the evaluated parents must be from a population of non-selected inbred lines originally derived from a random mating population in equilibrium. In plant improvement programs, this requirement may be difficult to satisfy. Furthermore, the number of parents sampled must be large enough to insure that reliable variance estimates are obtained. The minimal number of parents necessary to achieve this may well exceed 8-10 parents (Hayman, 1960; Pederson, 1971; Hayward, 1979). Unfortunately, as diallels increase in size, they become laborious and costly to manage. It is for these reasons that some researchers have argued that Model One is the most appropriate for Griffing's analysis (Baker, 1978).

The method selected can affect data interpretations. When the trait of interest is affected when parents are inbred and combining ability effects, progeny performance predictions or genetic variances are required, Method Three or Four is appropriate. Unlike Methods One and Two, Methods Three and Four do not include the parental performance in the analysis. Inclusion of inbred parents into the calculations can bias the GCA and SCA mean squares and variances (Kalloo, Singh & Bhutani, 1974; Hayes & Paroda, 1974; Weber, 1976). In most instances, the GCA and SCA variances are noticeably inflated and the GCA/SCA mean square and variance ratios are underestimated. These problems are accentuated when large performance differences exist between one or more of the inbred parents and their progeny. Furthermore, when parents are included in the array calculations, the SCA effects tend to be associated with the mean performances of parents and can fail to reflect the true value of certain hybrid combinations. In these instances, the values of hybrids *per se* may offer more useful information than the SCA effect values (Kalloo, Singh & Bhutani, 1974).

Methods One and Three were developed to detect reciprocal effects in plants arising from cytoplasmic differences and/or cytoplasmic-genic relationships. Although reciprocal effects are often ignored in plant improvement programs, attention to this factor has been occasionally warranted during parental selection (Krueger, Weinman & Gabelman, 1989; Widstrom, Bondari & McMillian, 1992). The inclusion of parents in Method One will not influence the reciprocal estimates, but may cause an inflation of the GCA and SCA mean squares and biases in the GCA and SCA variances and the GCA/SCA variance ratio. The information provided by a complete diallel analysis (Method One) represents the parental set accurately only when parental inbreeding depression is not important. Thus, Method Three is the most suitable choice when the evaluated trait is influenced by parental inbreeding depression and reciprocal differences between crosses are anticipated.

F_1 data are normally analyzed in Griffing's analysis, but data from the F_2 and backcross generations have also been used (Gill *et al.*, 1977; Patil &

Chopde, 1981; Borojevic, 1990). GCA effects for certain characteristics have shown consistency when analyzed over several generations; in other instances the parental GCA rank performances between generations have been inconsistent (Snijders, 1990). F_1 heterosis predictions based on the extrapolation of specific effects recorded in other generations than the F_1 should be approached with caution. The presence of epistasis involving additive effects in segregating generations can bias the magnitude and repeatability of SCA effects (Bhullar, Gill & Khehra, 1979).

GCA and SCA can interact with the environment and cause changes in parental combining abilities over the environments (Matzinger, Sprague & Cockerham, 1959; Hayes & Paroda, 1974; Holbrook, 1990; Singh *et al.*, 1992). To obtain precise combining ability estimates, it may be necessary to evaluate parents in more than one environment. Singh (1973) extended the use of Griffing's analysis to assess GCA and SCA over several environments. When the diallel is conducted in only one environment, plant geneticists should attempt to match the diallel with the environment of interest.

Computer program

We offer a user-friendly personal computer software program to perform the four methods in Griffing's analysis. Different data sets can be easily and rapidly analyzed for interpretation, which should facilitate research and educational objectives. The software program is written in basic and can be used on any IBM-compatible computer equipped with Dos 3.3 or above. The program is compatible with both laser and dot matrix printers and can evaluate a maximum of ten parents and ten blocks/replications. The program calculates variety/genotypic and block/replication differences from a randomized block experimental design using the ANOVA. Mean values, general, specific, and reciprocal effects along with the GCA, SCA, and reciprocals mean squares and F values are next calculated. Results of the analysis are automatically saved on the program diskette and the user can view the results on the monitor or request a print-out. Adequate instructions on the use of this program are provided in the tutorial section of this program.

To obtain this program, send a self-addressed diskette mailer with an IBM-compatible formatted diskette to B. Christie.

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