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Additive main effect and multiplicative interaction model for a diallel-cross analysis

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Abstract Diallel mating designs have proved informative in determining the inheritance of quantitative traits of interest to plant breeders. Apart from the well-established analyses of a complete diallel, the two-way factorial data structure of this design lends itself to analysis by the additive-main-effects-and-multiplicative-interaction (AMMI) model. This research article describes the joint application of the AMMI model and Griffing's method 1, model I, to gain insight into the breeding value of inbred lines in a self-pollinated crop such as disomic, hexaploid bread wheat. Data from a multi-environment trial of a complete diallel cross between eight lines adapted to the East African highlands were analyzed to provide an example of this joint analysis. This combined approach identified not only the direction of a cross, i.e. which parent should be male or female, but also which crosses produce offspring showing F_1 heterosis.

Keywords AMMI · Combining ability · Diallel mating design · Parent selection

Introduction

Two types of analysis are commonly used in a diallel cross; a genetical analysis devised by Hayman (1954a,b) and Jinks (1954), and Griffing's (1956) combining ability approach (Hill et al. 1998). The former, which requires the inclusion of the parents, provides information on the genetic architecture of a quantitative character, whereas Griffing's analysis splits the contribution of the parent into general combining ability (GCA), specific combining ability (SCA) and, if reciprocal crosses are made, allows the investigation of reciprocal effects.

A complete diallel cross can also be analyzed by the additive-main-effects-and-multiplicative-interaction (AMMI) model, which is an approach for the analysis of two-way factorial data structures, especially for understanding complex interactions (Gauch 1992). It combines the analysis of variance for the two main factors with a principal component analysis of the residual multiplicative interaction. AMMI can also partition the data into a pattern-rich model and discard the noise-rich residual to gain accuracy (Gauch and Zobel 1996).

The objective of the present research was to demonstrate the advantages of combining the AMMI model with Griffing's method 1, model I, approach for the analysis of a diallel mating design. To illustrate this, a data set, generated from a multi-environment trial of an 8 × 8 complete diallel derived from crosses among bread wheat lines adapted to the East African highlands, was used as an example.

Materials and methods

In a complete diallel the mating of n inbred lines results in n^2 offspring families, of which n are inbred lines and $n(n - 1)$ are F_1s, including their $n(n - 1)/2$ reciprocals. Griffing's (1956) method-1 comprises all n^2 offspring families, while the others (methods 2–4) exclude reciprocals, inbred lines, or both. The additive linear model for method 1, model I (fixed effects), includes the terms indicated in equation (1) for data recorded as plot means (Y_{ijk}) in a randomized complete block design at a single location:

$$Y_{ijk} = \mu + b_k + g_{ij} + \varepsilon_{ijk} \quad i, j = 1, ..., n; k = 1, ..., r \qquad (1)$$

where μ is the population mean, b_k is the effect of the kth block, g_{ij} is the genotypic effect of the ijth cross, and ε is the micro-environmental effect associated with the ijkth plot (Y_{ijk}). In the combining-ability analysis the genotypic effect g_{ij} in equation (1) can be further partitioned as follows:

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Table 1 Analysis of variance for grain yield (g m^{-2}) in an 8 × 8 diallel cross of bread wheat lines

Source of variation	Degrees of freedom	Mean square	$P > F$
Diallel analysis (using cross plot means within environments)			
Environment (E)	6	1 532 738.10	0.001
Blocks/E	7	21 626.56	
Crosses	63	17 940.43	0.001
General combining ability (GCA)	7	80 969.46	0.001
Specific combining ability (SCA)	28	12 211.38	0.001
Reciprocal differences (Rec.)	28	7932.09	0.05
Crosses × E	378	6776.90	0.001
GCA × E	42	19 839.66	0.001
SCA × E	168	5116.71	NS[a]
Rec. × E	168	5166.88	NS
Pooled Error	441	3080.75	
Coefficient of variation (%)		29.3	
Addivie main effects multiplicative interaction model (using cross means per environment)			
Environment	6	766 338.60	0.001
Female (F)	7	25 049.84	0.001
Male (M)	7	21 567.71	0.001
F × M	49	4873.48	0.05
IPCA1	13	7450.99	0.01
IPCA2	11	5377.06	NS
Residual	25	1689.59	NS
Error	378	3888.24	

[a] NS indicates non-significant source of variation

$$g_{ij} = g_i + g_j + s_{ij} + r_{ij} \tag{2}$$

in which g_i and g_j are the general combining-ability (GCA) effects of the ith and jth lines respectively, s_{ij} is the specific combining ability (SCA) of the ijth cross, and r_{ij} is the reciprocal effect associated with this ijthcross. Substitution of equation (2) into equation (1) provides the combining-ability model (of a diallel cross) for any single environment:

$$Y_{ijk} = \mu + b_k + g_i + g_j + s_{ij} + r_{ij} + \varepsilon_{ijk} \tag{3}$$

If the same set of diallel crosses are tested across environments the additive linear model for the combined analysis of variance is:

$$\begin{aligned} Y_{ijkl} = \mu + E_l + b_{k/l} + g_i + g_j + s_{ij} + r_{ij} + (gE)_{il} \\ + (gE)_{jl} + (sE)_{ijl} + (rE)_{ijl} + \varepsilon_{ijkl} \end{aligned} \tag{4}$$

where E_l is the effect of the lth environment and the other new terms are the respective interactions with the environment of the terms defined in equations (1) and (2).

The AMMI model, which can only handle a two-way factorial structure, is

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \Sigma_n \lambda_n \gamma_{in} \delta_{jn} + \rho_{ij} + \varepsilon_{ijk} \tag{5}$$

where α_i and β_j are deviations of the ith and jth parents from the grand mean (i.e. GCA). The multiplicative parameters of this equation are the singular value λ_n for the interaction principal component analysis (IPCA)$_n$, the ith parent eigenvector γ_{in} for the nth axis, and the jth parent eigenvector δ_{jn} for the nth axis. The eigenvectors are scaled as unit vectors and are unit-less, while λ has the units of the specific character being investigated. The recommended scalings for the multiplicative parameters in the AMMI model are $\lambda^{0.5}\gamma_i$ and $\lambda^{0.5}\delta_j$ (Gauch 1992), which, for the analysis of a diallel mating design, are termed the parents' interaction principal component analysis (IPCA) scores. The product of the IPCA scores provides the expected interaction value directly, without needing further multiplication by the singular value. IPCA scores near the origin (0, 0) in the AMMI2 model, or close to the center (0) along the IPCA1 axis in the AMMI1 model, show little multiplicative interaction. The term ρ_{ij} in equation (5) is the residual for the AMMI models when all axes are not used.

From equations (3) and (5) it is clear that $g_i = \alpha_i$ and $g_j = \beta_j$, and $(s_{ij} + r_{ij}) = (\Sigma_n \lambda_n \gamma_{in} \delta_{jn} + \rho_{ij})$, with ε_{ijk} in equation (5) being equal to $[b_k + \varepsilon_{ijk}]$ in equation (3), indicating that the GCA of the parents in a diallel cross are the same as the additive main effects of the AMMI. Unfortunately, the multiplicative interaction plus the AMMI residual cannot be partitioned into SCA and reciprocal differences of the diallel cross.

Multi-environment data sets from a series of bread wheat trials grown in the East African highlands (Wagoire 1997) were used to illustrate the advantage of combining Griffing's and AMMI approaches for the analysis of a diallel cross. For this trial a complete 8 × 8 diallel cross was grown in seven different environments. Within each environment the experimental layout was a randomized complete block design with two replications. Plots comprised two rows of 1.5-m length, with 0.3 m between rows and 0.15 m between plants, (i.e. about 20 plants plot^{-1}). Grain yield was measured on a plot basis and converted to g m^{-2}.

Results and discussion

Environment, crosses and their interaction were all highly significant for grain yield in this multi-environment trial (Table 1). Partitioning the variation among crosses revealed that GCA and SCA effects were highly significant while reciprocal differences were borderline (Table 1). The variance ratio GCA/SCA was 1.4, indicating the importance of additive genetic variation in this material. Furthermore, the GCA effects interacted significantly with environments (Table 1), being most pronounced at the location where the parental genotypes were selected for their wide response to yellow rust (Wagoire et al. 1999), an important disease affecting grain yield in the East African highlands (Wagoire et al. 1998). Clearly the parents of potential cultivars should be selected at the target location. The significant SCA suggested that nonadditive genetic variation affected grain yield in this germplasm. Other studies have also shown the importance of both additive and non-additive gene action in the inheritance of this character (Mishra et al. 1994; Khan et al. 1995; El-Hennawy 1996; Uma-Menon et al. 1996).

Table 2 General combining ability (GCA) and first interaction principal component analysis (IPCA1) for grain yield (g m^{-2}) of eight parental lines used as males (m) or females (f) in a full diallel mating design

Line	GCA	IPCA1$_F$	IPCA1$_M$
Buri	+21.1538	0.0154	0.0626
K. Chiriku	+4.9395	–0.4839	0.4392
Esda/Lira	+17.6092	–0.5115	0.4732
Vee“S”/JUP73/EMU“S”//GJO“S”	+5.9663	0.1167	0.1842
Attila	+12.0556	–0.1500	0.2839
CY8801	–15.1408	0.3798	–0.1601
F60314.76/CN076/7C//KAL/BB/3/PCI“S”/5/CN079	–16.3641	0.0689	–0.3549
CAR853/COC//VEE“S” /3/E7408 PAM“S”/HORK“S”/PF73226	–30.2194	0.5647	–0.5596
Standard error (g_i)	5.2437		
Standard error (g_i–g_j)	7.9200		

The sum of squares due to environments accounted for 71.4% of the total variation for grain yield in the AMMI analysis, whereas 2.7%, 2.3% and 3.7% was explained by the female, male and the male-female interaction respectively (Table 1). The pooled error captured 19.8% of the total variation. The significant IPCA1 explained 28.4% of the male-female interaction, while the non-significant IPCA2 and the residual accounted for 22.2% and 49.4% respectively. Hence, the interpretation of the results from this trial focused on GCA effects and IPCA1.

The highest yielding lines, as determined by their GCA, were those displaying some resistance to yellow rust, namely Buri and Esda/Lira, whereas lines susceptible to this disease had significantly negative GCA effects (Table 2). These results were expected because of the influence of yellow rust on grain yield at some East African highland locations, where yield loss due to yellow rust can amount to 25%. Incorporation of resistance had no extra ‘cost’ in terms of grain yield at a disease-free location, where resistant and susceptible crosses may have similar yields (Wagoire et al. 1998).

According to Gauch and Zobel (1988), one of the main attributes of the AMMI analysis is its ability to improve the predictive accuracy of a yield trial. This requires that the data are subdivided into two sets; the model data and the validation data. The former are used to construct a model, whose predicted values are then compared with the validation data, using, for example, the root mean square difference between the validation data and model-predictions to measure prediction accuracy (Gauch 1992). Unfortunately, as there were only two replicates per environment in this trial, it was not possible to apply this procedure to these results. Nevertheless, these prediction methods may be of interest to those plant breeders who wish to determine the potential of a particular cross in advance. Moreover, Gauch and Zobel (1990) have developed a modified version of the AMMI, which can estimate missing values, using information provided by all observations in a particular trial.

IPCA1 scores for each parent, as male or female, provide additional information. Most of the lines, except Buri, showed contrasting IPCA1 scores when used as male or female (Table 2), confirming the significant reciprocal differences detected by Griffing’s approach. As mentioned earlier, however, the multiplicative interaction will include some non-additive genetic variation due to dominance and epistasis. Both these effects can be a source of better parent heterosis (Jinks and Jones 1958). By combining information from the IPCA1$_F$ and IPCA1$_M$ scores with the GCA values, it is possible to identify those crosses that at least have the potential to produce heterotic offspring. Thus, a selection strategy based on lines that combine a significantly positive GCA value with a high IPCA1 score could be used to exploit heterosis for grain yield in this material. This pinpoints Esda/Lira as a potential parent.

Some justification for this approach comes from previous work on this breeding population, in which F_6 recombinant inbred lines (RIL) were generated by single-seed descent. Hill et al. (2000) reported that crosses between Esda/Lira, as female, and (Vee“S”/JUP73/EMU“S”//GJO“S”), Attila and (CAR853/COC//VEE“S”/3/E7408 PAM“S”/HORK“S”/PF73226), as male, displayed better parent heterosis for grain yield, with the cross to (Vee“S”/JUP73/EMU“S”//GJO“S”) being particularly noteworthy. Buri, the other resistant line with a high GCA value, will contribute mainly additive genes to its offspring because it has low IPCA1 scores and therefore showed little multiplicative interaction in this trial (Table 2). Although the cross to K. Chiriku displayed better parent heterosis, the remaining crosses with Buri as female produced unremarkable offspring. The development of a RIL having Esda/Lira as the female parent appears, therefore, to offer a good prospect for producing cultivars from this breeding population, which are adapted to the rust-prone environments of the East African highlands.

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