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Relationships among analytical methods used to study genotypic variation and genotype-by-environment interaction in plant breeding multi-environment experiments

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Abstract Following the recognition of the importance of dealing with the effects of genotype-by-environment ($G \times E$) interaction in multi-environment testing of genotypes in plant breeding programs, there has been substantial development in the area of analytical methodology to quantify and describe these interactions. Three major areas where there have been developments are the analysis of variance, indirect selection, and pattern analysis methodologies. This has resulted in a wide range of analytical methods each with their own advocates. There is little doubt that the development of these methodologies has greatly contributed to an enhanced understanding of the magnitude and form of $G \times E$ interactions and our ability to quantify their presence in a multi-environment experiment. However, our understanding of the environmental and physiological bases of the nature of $G \times E$ interactions in plant breeding has not improved commensurably with the availability of these methodologies. This may in part be due to concentration on the statistical aspects of the analytical methodologies rather than on the complementary resolution of the biological basis of the differences in genotypic adaptation observed in plant breeding experiments. There are clear relationships between many of the analytical methodologies used for studying genotypic variation and $G \times E$ interaction in plant breeding experiments. However, from the numerous discussions on the relative merits of alternative ways of analysing $G \times E$ interactions which can be found in the literature, these relationships do not appear to be widely appreciated. This paper outlines the relevant theoretical relationships between the analysis of variance, indirect selection and pattern analysis methodologies, and their practical implications for the plant breeder interested in assessing the effects of $G \times E$ interaction on the response to selection. The variance components estimated from the combined analysis of variance can be used to judge the relative magnitude of genotypic and $G \times E$ interaction variance. Where concern is on the effect of lack of correlation among environments, the $G \times E$ interaction component can be partitioned into a component due to heterogeneity of genotypic variance among environments and another due to the lack of correlation among environments. In addition, the pooled genetic correlation among all environments can be estimated as the intraclass correlation from the variance components of the combined analysis of variance. Where $G \times E$ interaction accounts for a large proportion of the variation among genotypes, the individual genetic correlations between environments could be investigated rather than the pooled genetic correlation. Indirect selection theory can be applied to the case where the same character is measured on the same genotypes in different environments. Where there are no correlations of error effects among environments, the phenotypic correlation between environments may be used to investigate indirect response to selection. Pattern analysis (classification and ordination) methods based on standardised data can be used to summarise the relationships among environments in terms of the scope to exploit indirect selection. With the availability of this range of analytical methodology, it is now possible to investigate the results of more comprehensive experiments which attempt to understand the nature of differences in genotypic adaptation. Hence a greater focus of interest on understanding the causes of the interaction can be achieved.

Key words $G \times E$ interaction · Analysis of variance · Indirect selection · Pattern analysis

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Introduction

When conducting multi-environment trials (METs), plant breeders commonly observe that genotypes change in their relative performance across test environ-

ments. This phenomenon, referred to as genotype-by-environment ($G \times E$) interaction, can take on many forms (Haldane 1947; Allard and Bradshaw 1964). When investigating the form of $G \times E$ interactions, it is worthwhile distinguishing between interaction due to heterogeneity of genotypic variance among environments (Lefkovitch 1990) and that due to the lack of correlation of genotypic performance among environments (Dickerson 1962; Cockerham 1963; Shorter and Mungomery 1981), particularly where the latter results in re-ranking of genotypes across environments (Haldane 1947; Baker 1988b, c, 1990). Eisemann et al. (1990) emphasised that it is that part of $G \times E$ interaction which leads to re-ranking which impedes response to selection as it can change the composition of the select and reject groups across environments.

Following the early documentation of the presence and form of $G \times E$ interactions (Haldane 1947; Comstock and Moll 1963; Allard and Bradshaw 1964), there has been considerable research on their impact in plant breeding. The focus on $G \times E$ interactions as a component of plant adaptation is largely a consequence of the uncertainty they introduce into the process of selection among genotypes, particularly where this is based on their phenotypic performance in a relatively small sample of environments taken from the target population of environments. Comstock and Moll (1963) gave a comprehensive overview of the impact of $G \times E$ interactions on the study of differences in genotypic adaptation. They emphasised the flux between the genotypic and $G \times E$ interaction components of variance and the dependence of this upon the way in which the target population of environments was sampled. More recently, Nyquist (1991) has extended the discussions of Comstock and Moll (1963) to consider the impact of $G \times E$ interactions on the estimation of heritability and the prediction of response to selection.

The majority of research on $G \times E$ interactions to-date has concentrated upon the development of analytical methodologies for quantifying their magnitude, characterising their form, and the development of strategies to select among genotypes based on the use of predominantly biometrical methods. There are a number of reviews of these analytical methods which are worth consulting (Freeman 1973, 1990; Hill 1975; Westcott 1986; Baker, 1988a; Crossa 1990; DeLacy and Cooper 1990; Basford et al. 1991; Cooper et al. 1993c). Many others have focussed on discussing the merits, or lack of merit, of one or two methods (Finlay and Wilkinson 1963; Byth et al. 1976; Fox and Rosielle 1982; Crossa et al. 1991; Zobel 1990; Bull et al. 1992). Alternatively, some workers have attempted to define the environmental causes and physiological basis of the $G \times E$ interactions (Baker 1988b; Eisemann et al. 1990; Lawn and Imrie 1991, 1993; Shorter et al. 1991).

In the study of $G \times E$ interactions, most papers concentrate on using only one or two of the available analytical methods without discussing their inter-relations. The analysis of variance has been widely used to partition total phenotypic variation into components due to genotype, $G \times E$ interaction, and error (micro-environmental variation) (Gardner 1963; Baker 1969; Moll and Stuber 1974; Brennan and Byth 1979; DeLacy et al. 1990b; Nyquist 1991). The relative sizes of the variance components are frequently used to quantify the magnitude of $G \times E$ interactions. Where the ratio of $G \times E$ interaction to genotypic variation is high, $G \times E$ interaction is considered to present the plant breeder with a problem where the objective is selection among genotypes.

Falconer (1952, 1989) argued that the genetic correlation between environments can be used to quantify the importance of $G \times E$ interactions. As the genetic correlation decreases, $G \times E$ interaction has a stronger influence and it is argued that different genetic systems become more important for adaptation in the two environments. Many workers have adopted this approach and studied the impact of $G \times E$ interactions as a case of indirect selection (Yamada 1962; Atlin and Frey 1989, 1990; Shaw 1989; Itoh and Yamada 1990; Cooper et al. 1993a, b). However, as the number of environments sampled in METs increases, the number of pairwise comparisons between environments increases exponentially. To deal with this problem many workers have used pattern analysis (classification and ordination) methodology to summarise the relationships among the environments on the way in which they discriminate among the genotypes. Pattern analysis uses a complementary relationship between the similarity (required by ordination procedures) and dissimilarity (required by hierarchical classification procedures) measures derived by Gower (1966, 1967) to provide a companion classification and ordination analyses of the same data. These companion analyses highlight different aspects of the same data. DeLacy and Cooper (1990) and DeLacy et al. (1990a) presented some of these relationships for the analysis of MET data.

Classification analysis results in the definition of groups of environments (Horner and Frey 1957; Abou-El-Fittouh et al. 1969; Fox and Rosielle 1982; Ivory et al. 1991; Cooper et al. 1993b). The investigation then proceeds by studying $G \times E$ interaction among the groups of environments rather than individual environments. This reduces the number of comparisons which require consideration. To summarise the discrimination among genotypes for the groups of environments a two-way classification can be conducted (Byth et al. 1976) by superimposing the results of the independent classification of genotypes and environments. Truncating the classifications of genotypes and environments at some level (DeLacy 1981) allows the investigation of the among- and within-group partition of the genotypic and $G \times E$ interaction variation. A response plot based on group means can be constructed to graphically portray the group-mean patterns of adaptation emphasised by the classification.

Classification requires a proximity measure and grouping strategy. For agglomerative hierarchical clas-

sification a commonly-used combination is the proximity measure squared Euclidean distance (SED) and the grouping strategy incremental sum of squares (ISS) (Ward 1963; Burr 1968, 1970; Wishart 1969). Fox and Rosielle (1982) showed that if the raw data are transformed by subtracting the environment mean (centering) and dividing (scaling) by the square root of the phenotypic variance among line means within the environment, the resultant environment-standardised squared Euclidean distance (esSED) provides a dissimilarity measure which compares environments on the basis of their pairwise phenotypic correlation (r_p). The esSED and r_p between two environments provide complementary information (Gower 1966, 1967), i.e., they are complements or complementary proximity measures. Fox and Rosielle (1982) refered to the centering described above as coding.

Cooper et al. (1993b) used the esSED with the simplified expression for indirect selection from one environment to another (Falconer 1952; Burdon 1977; Pederson and Rathjen 1983) to inter-relate indirect selection theory with classification theory. The advantages of grouping environments based on standardised data, over alternative transformations, were discussed theoretically by DeLacy and Cooper (1990) and DeLacy et al. (1990a) and investigated experimentally by Cooper et al. (1993d). From these discussions it is clear that classification of environments based on an agglomerative hierarchical clustering procedure involving ISS with esSED, partitions the environments into groups which reflect the opportunities for exploiting indirect selection among the environments. Complementary information to that identified by classification can be obtained by ordination of the environments. As with classification, there are a number of alternative methods for studying the relationships among environments. DeLacy and Cooper (1990) showed that ordinations based on data standardised as above for classification, will exploit the same information as that of the classification on esSED and will reflect the phenotypic correlation among environments and, therefore, opportunities for exploiting indirect selection among environments.

Recently, ordination methods have recieved renewed attention for the analysis of data from METs with the development of the symmetric decomposition via singular value decomposition (SVD). This enables a graphical display of the relativity among genotypes and environments in a single graph, the biplot, introduced by Gabriel (1971) and applied to plant breeding data by Kempton (1984). The biplot presents the discrimination among genotypes within each environment, as represented by the ordination, for a synoptic inspection. The spatial relationships among the genotypes and environments on the biplot assists the investigation of differences in genotypic adaptation in METs. An increasing number of workers are applying this procedure in various forms (Kempton 1984; Gauch and Zobel 1988; Zobel et al. 1988; Crossa et al. 1990, 1991; Zobel 1990).

There are theoretical relationships which are not fully appreciated between many of the analytical methods which allow a comprehensive statistical analysis of $G \times E$ interactions in METs. We provide a synthesis of the relationships between analysis of variance, indirect selection and pattern analysis [classification and ordination (Williams 1976)] methodologies where the emphasis is on response to selection as opposed to investigating the physiological and environmental causes of $G \times E$ interaction. The methodology is applied to a wheat data set collected in Queensland, Australia, to demonstrate the practical implications of the relationships between the analytical methods.

Materials and methods

Theoretical development

To assist development of the relationship between $G \times E$ interaction in METs and indirect selection theory applied to the same character measured on the same genotypes in different environments, a linear model for describing the phenotypic performance of genotypes in individual environments is first defined. The linear model for one environment is defined such that it can be directly extended and defined for describing the phenotypic performance of genotypes across multiple environments.

The performance of n_g genotypes tested in one of n_e environments with n_r replications can be described in terms of the linear model

$$y_{ikj} = m_j + g_{ij} + \varepsilon_{ikj}, \quad i = 1,\ldots,n_g, \quad j = 1,\ldots,n_e, \quad k = 1,\ldots,n_r, \qquad (1)$$

where y_{ikj} is the kth observation of genotype i in environment j; m_j is the grand mean in environment j; g_{ij} is the effect of the ith genotype in environment j and is $\text{NID}(0, \sigma^2_{g(j)})$[1]; ε_{ikj} is the error effect associated with the kth observation of genotype i in environment j and is $\text{NID}(0, \sigma^2_{\varepsilon(j)})$.

Where the random model above is assumed, the standard analysis of variance procedures can be applied and variance components estimated for genotypes and error by equating the estimated and expected mean squares and solving for the variance components. These variance component estimates give a partitioning of the phenotypic variance among genotype means (Comstock and Moll 1963; Nyquist 1991) as

$$\sigma^2_{p_j} = \sigma^2_{g_j} + \frac{\sigma^2_{\varepsilon_j}}{n_r}, \qquad (2)$$

where $\sigma^2_{p(j)}$ is the phenotypic variance component among genotype means in environment j.[1] These components of variance can be used to estimate genotype mean heritability for environment j as

$$h^2_j = \frac{\sigma^2_{g_j}}{\sigma^2_{g_j} + \frac{\sigma^2_{\varepsilon_j}}{n_r}}, \qquad (3)$$

and the predicted response to selection in environment j as

$$\Delta G_j = i_j h^2_j \sigma_{p_j}, \qquad (4)$$

[1] Because of typesetting difficulties in writing sub-subscripts in the text, sub-subscripts used in equations will appear in the text contained in brackets following subscripts

where i_j is the standardised selection differential in environment j. Since $G \times E$ interaction is not partitioned from the genotypic variance component, equation (4) should be considered to predict advance for the same environment in which selection was practised.

Where the same genotypes are tested over a series of n_e environments, the data collected from the MET can be compiled in a matrix indexed with genotypes as rows and environments as columns. We refer to this form of presentation of the data as a GE matrix. Extending model (1) to a pooled analysis over all environments, genotype performance in the GE matrix can be described in terms of the linear model

$$y_{ijk} = m + g_i + e_j + (ge)_{ij} + \varepsilon_{ijk}, \tag{5}$$

with the same limits as before and y_{ijk} is the kth observation on genotype i in environment j; m is the grand mean over all observations; g_i is the effect of the ith genotype and is NID(0, σ_g^2); e_j is the effect of the jth environment and is NID(0, σ_e^2); $(ge)_{ij}$ is the interaction effect between the ith genotype and jth environment and is NID(0, σ_{ge}^2); and ε_{ijk} is the error effect associated with the kth observation on genotype i in environment j and is NID(0, σ_ε^2).

Again, where the random model is assumed the standard analysis of variance procedures can be applied and variance components estimated for genotypes, $G \times E$ interaction, and error, by equating the estimated and expected mean squares and solving for the variance components. These varaince component estimates give a partitioning of the phenotypic variance, σ_p^2, among genotype means as,

$$\sigma_p^2 = \sigma_g^2 + \frac{\sigma_{ge}^2}{n_e} + \frac{\sigma_\varepsilon^2}{n_e n_r}. \tag{6}$$

These components of variance can be used to estimate line mean heritability over all environments as

$$h^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{n_e} + \frac{\sigma_\varepsilon^2}{n_e n_r}}, \tag{7}$$

and the average predicted response to selection over all environments as

$$\Delta G = i h^2 \sigma_p. \tag{8}$$

Equation (8) predicts genetic advance averaged over the set of environments in which the genotypes were tested. This estimate of response to selection applies to the target population of environments when the sample of test environments used in the MET is a random sample from the target population of environments (Cooper et al. 1993c). From equations (7) and (8) it is seen that as the magnitude of the $G \times E$ interaction component of variance increases relative to the genotypic component both heritability and response to selection are reduced. Because of this inverse relationship, it is widely argued that an investigation of both the statistical and biological nature of $G \times E$ interaction is commonly required in the consideration of results from METs.

It is instructive to investigate the relationships among the form of discrimination among genotypes embodied in the linear models for one environment [equation (1)] and for many environments [equation (5)].

Cockerham (1963) gave an expression for the $G \times E$ interaction component of variance which partitioned components due to heterogeneity of genotypic variance and the lack of genetic correlation among environments,

$$\sigma_{ge}^2 = \frac{\sum_{j<j',j'} [(\sigma_{g_j} - \sigma_{g_{j'}})^2 + 2\sigma_{g_j}\sigma_{g_{j'}}(1 - r_{g_{jj'}})]}{n_e(n_e - 1)}, \tag{9}$$

where $\sigma_{g(j)}$ and $\sigma_{g(j')}$ are the square roots of genotypic variance components in environments j and j', respectively, as defined in the single environment model (1); and $r_{g(jj')}$ is the genetic correlation between environments j and j'. Shorter and Mungomery (1981) referred to the first term of this expression as the component of the $G \times E$ interaction due to heterogeneity of genotypic variance among environments, since

$$V(\sigma_{g_{\text{env}}}) = \frac{\sum_{j<j',j'} (\sigma_{g_j} - \sigma_{g_{j'}})^2}{n_e(n_e - 1)} = \frac{\sum_j (\sigma_{g_j} - \bar{\sigma}_g)^2}{n_e - 1}, \tag{10}$$

where $\bar{\sigma}_g$ is the mean over j of $\sigma_{g(j)}$. The second from of equation (10), also given by Dickerson (1962), is more intuitive as it is recognisable as the variance of the genotypic standard deviation components from each environment. The second term in equation (9), that due to lack of genetic correlation among environments, can be referred to as

$$L(r_{g_{\text{env}}}) = \frac{\sum_{j<j',j'} [2\sigma_{g_j}\sigma_{g_{j'}}(1 - r_{g_{jj'}})]}{n_e(n_e - 1)}. \tag{11}$$

If all the genetic correlations among environments are one, $L(r_{g(env)})$ will equal zero and there will be no $G \times E$ interaction due to this source. Conversely, to the extent that the correlation among the performance of genotypes in different environments decreases there will be a corresponding increase in $G \times E$ interaction. Therefore, the component of the $G \times E$ interaction which complicates selection is described by (11). The component due to heterogeneity of genotypic variance will not directly affect selection decisions. Thus, any study which investigates the impact of $G \times E$ interaction on response to selection should destinguish between these two components.

Dickerson (1962) gave another expression for the $G \times E$ variance: viz.

$$\sigma_{ge}^2 = V(\sigma_{g_{\text{env}}}) + \overline{\sigma_{g_j}\sigma_{g_{j'}}}(1 - r_g), \tag{12}$$

where $V(\sigma_{g(env)})$ is as before, the bar over $\sigma_{g(j)}\sigma_{g(j')}$ refers to the arithmetic average of all the pairwise geometric means among the genotypic variance components of the environments, and r_g is the pooled genetic correlation among all the environments, namely

$$r_g = \frac{\sum_{j<j',j'} \sigma_{g_{jj'}}}{\sum_{j<j',j'} \sigma_{g_j}\sigma_{g_{j'}}} = \frac{\overline{\sigma_{g_{jj'}}}}{\overline{\sigma_{g_j}\sigma_{g_{j'}}}}, \tag{13}$$

where $\sigma_{g(jj')}$ is the genotypic covariance between environments j and j', the bar over $\sigma_{g(jj')}$ refers to the arithmetic average of all pairwise genetic covariances, and the divisors $n_e(n_e - 1)/2$ cancel. Dickerson (1962) also showed that the pooled genetic correlation among the environments r_g is equal to the intraclass correlation among genotypes corrected for heterogeneity of genotypic variance among environments. This relationship of Dickerson in our notation is

$$r_g = \frac{\overline{\sigma_{g_{jj'}}}}{\overline{\sigma_{g_j}\sigma_{g_{j'}}}} = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_{ge}^2 - V(\sigma_{g_{\text{env}}})} = \frac{\sigma_g^2}{\sigma_g^2 + L(r_{g_{\text{env}}})}. \tag{14}$$

From Dickerson's (1962) expression for the $G \times E$ variance given in equation (12) it can be seen that the part of $G \times E$ variation which is due to the lack of correlation among genotypes across all environments is a function of the pooled genetic correlation among environments or the corrected intraclass genetic correlation, [equation (14)]. It can be shown that the average of all the genetic covariances between pairs of environments is the pooled genetic variance component from the pooled analysis of variance as defined for the model in equation (5). Also, the average of all the pairwise geometric means of the genetic variance components from individual environment analysis [equation (1)] is the sum of the genetic and $G \times E$ variance corrected for heterogeneity as defined in the pooled analysis. For further discussion of these relationships see Itoh and Yamada (1990).

To interrelate the $G \times E$ interaction variance component with pattern analysis methodology we give another expression for the $G \times E$ variance as

$$\sigma^2_{ge} = \frac{\sum_{j<j',j'} (\sigma^2_{g_j} + \sigma^2_{g_{j'}} - 2\sigma_{g_{jj'}})}{n_e(n_e-1)} = \frac{\sum_{j<j',j} \frac{n_g}{n_g-1} D_{g_{jj'}}}{n_e(n_e-1)}, \quad (15)$$

where all the terms are as defined previously and $D_{g(jj')}$ is a measure of the difference in genetic performance of the genotypes in environments j and j'. $D_{g(jj')}$ can also be considered as a measure of a difference between environments j and j' in the way in which they discriminate between the genetic performance of genotypes. DeLacy and Cooper (1990) and DeLacy et al. (1990a) discussed alternative forms of $D_{g(jj')}$ which have been used for pattern analysis of relationships among environments in METs. The form of the $G \times E$ interaction variance component given in equation (15) is half the average over all pairs of environments of the measures of difference in genotype performance among environments. The size of the interaction depends on both the genotypic variances within an environment and on the size of the genetic covariance among the pairs of environments. Genotype-by-environment interaction is reduced when the genetic covariance is positive (positive correlation of genotype performance in each environment), which is the expected condition. The first two forms of the expression for the $G \times E$ interaction variation variance component, equations (9) and (12), emphasise that heterogeneity of genotypic variance among environments inflates $G \times E$ interaction. Where heterogeneity of genotypic variance among environments is large the $G \times E$ variance component will overstate the complication to selection introduced by $G \times E$ interaction. A more useful treatment of $G \times E$ interaction in METs would involve an analysis which focuses on the component of the interaction which reduces the correlation of genotype performance among environments and the impact of this on selection.

From the general relationships between similarity and dissimilarity measures given by Gower (1966, 1967) and developed for the analysis of METs by DeLacy and Cooper (1990) and DeLacy et al. (1990a), $D_{g(jj')}$ is recognisable as the squared Euclidean distance between the genetic performance of the genotypes in environments j and j'. $D_{g(jj')}$ is the complement of the genetic covariance, $\sigma_{g(jj')}$, the similarity measure for the genetic performance of the same genotypes measured in environments j and j'. Equation (15) enables a pattern analysis to be undertaken to gain an understanding of all the pairwise relationships between the genetic performance of the genotypes in all environments. As the $G \times E$ interaction variance is the average of all these relationships, an investigation of specific aspects of the $G \times E$ interaction complex should lead to a greater understanding of the nature of $G \times E$ interactions. An investigation of the patterns of genetic performance which reflect that proportion of $G \times E$ interaction caused by failure of genetic correlation between environments, $L(r_{g(\text{env})})$, can be made by defining

$$\frac{n_g}{n_g-1} esD_{g_{jj'}} = 2(1 - r_{g_{jj'}}) \quad (16)$$

as the SED between genotype performance in environments scaled to have a genetic variance of one. A pattern analysis of relationships among environments based on the complement of $esD_{g(jj')}$, $r_{g(jj')}$, is a direct examination of the failure of genetic correlation among environments. From the relationships in equations (15) and (16), the genotypic correlation matrix for all pairwise comparisons among environments can be investigated to assess the impact of $G \times E$ interaction on selection. Mirzawan et al. (1993) adopted this strategy for the analysis of the relationships among environments in sugarcane METs.

The $G \times E$ interaction component can also be investigated by considering the phenotypic correlations among environments. Falconer (1952, 1989) gave the equation for indirect response to selection in one environment from selection in another as

$$\Delta G_{j/j'} = i_{j'} h_j h_{j'} r_{g_{jj'}} \sigma_{p_j}, \quad (17)$$

where $\Delta G_{j/j'}$ is the indirect response in environment j from selection in environment j', and h_j and $h_{j'}$ are the square roots of the genotype mean heritability in environments j and j', respectively. When it is assumed that there is no environmental covariance (Burdon 1977), the phenotypic correlation among a pair of environments is

$$r_{p_{jj'}} = h_j h_{j'} r_{g_{jj'}}, \quad (18)$$

which allows estimation of the genetic correlation among two environments. A simplified expression for indirect selection was derived by Pederson and Rathjen (1983) by substituting equation (18) into equation (17) to give

$$\Delta G_{j/j'} = i_{j'} r_{p_{jj'}} \sigma_{p_j}. \quad (19)$$

Therefore, while the genetic correlation is directly related to the $G \times E$ interaction, equation (9), the phenotypic correlation is directly related to correlated genetic gain in one environment from selection in another through the relationships given in equations (17), (18) and (19). In addition, these relationships allow the incorporation of indirect selection theory into pattern analyses. Fox and Rosielle (1982) showed that the squared Euclidean distance calculated between two environments on data which has been environment standardised (subtracting environment mean and dividing by environment standard deviation) provides a dissimilarity measure which compares environments on the basis of their pairwise phenotypic correlation

$$\frac{n_g}{n_g-1} esD_{p_{jj'}} = 2(1 - r_{p_{jj'}}), \quad (20)$$

which is an expression for squared for Eluclidean distance of the same form as equation (16). The resultant environment standardised squared Euclidean distance, $esD_{p(jj')}$, between the standardised genotype scores in each environment is the complement of the phenotypic correlation among environments, $r_{p(jj')}$, and enables a pattern analysis to be performed. Cooper et al. (1993b) used the $esD_{p(jj')}$, (equation (20)), the $r_{p(jj')}$ and the simplified expression for indirect selection, [equation (19)] to relate indirect selection theory with pattern analysis theory. The advantages of a pattern analysis of environments based on standardised data, over alternative transformations, were discussed theoretically by DeLacy and Cooper (1990) and DeLacy et al. (1990a), and experimentally demonstrated by Cooper et al. (1993d). The hierarchical classification of environments, based on squared Euclidean distance and incremental sum of squares, using the above standardisation, partitions the environments into groups which reflect the opportunities for exploiting indirect selection among the environments (Cooper et al. 1993b).

The two-way classification arising from an analysis on environment standardised data enables an investigation of the genotypic and $G \times E$ interaction variation which is appropriate for investigating their effect on indirect selection among environments. A response plot based on group means can be constructed to portray the group mean patterns of adaptation related to selection which are emphasised by this analysis. To complete the pattern analysis an ordination based on data standardised as above will exploit the same information as that of the classification on $esD_{p(jj')}$. This ordination will reflect the phenotypic correlation among environments and, therefore, opportunities for exploiting indirect selection among environments. The biplot (Gabriel 1971) from the ordination analyses based on environment standardised data portrays these environmental relationships and genotypic discrimination in a graphical form.

Application

Data set. Fifteen wheat lines were yield tested at 10 environments in 1988 in Queensland, Australia: Emerald sowing date 1 (Emd-1) and sowing date 2 (Emd-2), Kingsthorpe (King), Gatton (Gatt), Biloela (Bil), Fernlees (Fern), Toobeah (Toob), The Gums (Gums), Jimbour (Jim) and Pampas (Pamp). The environments sampled the main regions of the Queensland wheat belt identified by Brennan et al. (1981). The lines included three local cultivars, Hartog, Banks and Kite, and 12 advanced lines from the 11th and 17th International

Bread Wheat Screening Nurseries conducted by CIMMYT. Each experiment involved a randomised complete block design with two replicates. Grain yield was measured using small-plot harvesting equipment and was estimated at 12% moisture.

Analysis of variance. A completely random model was assumed and variance components for lines, line by environment ($L \times E$) interaction, and experimental error, were estimated by equating the mean squares with their expected mean squares and solving for the variance components. Line mean heritability for grain yield in environment j (h_j^2) was estimated using equation (3) and line mean heritability across the ten environments was estimated using equation (7).

Indirect selection. The $L \times E$ interaction variance component was partitioned into components due to heterogeneity of genotypic variance and lack of correlation among environments using equation (9). The pooled genetic correlation among environments and the intraclass correlation from the combined analysis of variance were estimated from equation (14). The full matrix of pairwise genetic correlations among environments was estimated from the appropriate phenotypic correlations using equation (18).

Pattern analysis. Prior to the pattern analyses, the line grain yield data were transformed to standardised data following Fox and Rosielle (1982) by subtracting the environment means and dividing by the square root of the phenotypic variance within each environment. The environments and lines were classified using an agglomerative hierarchical classification procedure on the standardised data with squared Euclidean distance as a dissimilarity measure, equation (20), and incremental sum of squares as a grouping strategy (Ward 1963; Burr 1968, 1970; Wishart 1969). The classifications were truncated following the guidelines of DeLacy (1981). A response plot for the two-way classification (Byth et al. 1976) was constructed.

An ordination of the lines and the environments was conducted on the standarised grain yield data using the singular value decomposition procedure. A biplot (Gabriel 1971) of the first two principal components for the line and environment ordinations was constructed to portray the relationships among the environments and the discrimination among the lines in each environment on the first two principal components.

The low dimentional representations of line discrimination from the two-way classification and the ordination were compared.

Results

The environment mean yields ranged from 2.04 to 5.26 t ha^{-1} and there were significant ($P < 0.05$) differences among the line means in each environment (Table 1). Line mean heritability within the environments ranged from 0.675 to 0.945.

The combined analysis of variance identified significant ($P < 0.05$) variation among lines and $L \times E$ interaction (Table 2). The variance component for $L \times E$ interaction component was 0.8-times that for lines. While the $L \times E$ interaction variance component was less than that for lines, 69% of this interaction was associated with the lack of correlation among environments and 31% with the heterogeneity of genotypic variance among environments. The pooled genetic correlation among the environments was 0.651. Therefore, there was strong evidence that the $L \times E$ interaction would complicate selection among these lines.

There was a large range in the genetic and phenotypic correlations among all pairwise comparisons between environments (Table 3). The genetic correlation ranged from the low value of -0.091 between Biloela (Bil) and Emerald sowing date 2 (Emd-2) to the high value of 1.047, between Fernlees (Fern) and Jimbour (Jim), which was slightly greater than the theoretical limit for a correlation. Twenty-six of the forty-five phenotypic correlations among environments were significant ($P < 0.05$) and the range was from -0.067 to 0.898. The wide range in phenotypic and genetic correlations indicated considerable differences in the pattern of discrimination among the lines for yield over the ten environments.

Since both environment and line classifications were based on environment standardised data, the pa-

Table 1 Line mean grain yield (t ha^{-1}) for 15 wheat lines tested in ten environments in Queenland in 1988 and estimates of genotypic and error variance components, phenotypic variance among line means, and heritability of variance among line means

Line	Environment									
	Emd-1	Emd-2	King	Gatt	Bil	Fern	Toob	Gums	Pamp	Jim
17IB7	3.331	4.051	2.592	5.093	1.742	4.977	3.308	3.031	2.909	3.145
17IB30	4.482	4.319	2.951	5.570	2.358	5.750	3.448	4.032	3.032	3.806
17IB31	3.496	3.893	2.571	4.592	1.773	5.151	2.783	3.139	3.130	3.382
17IB38	3.042	4.399	2.693	4.606	1.942	5.285	2.447	3.471	2.919	3.284
17IB53	3.401	4.244	2.846	5.451	2.075	5.432	2.719	3.292	2.929	3.662
17IB64	3.639	4.088	2.704	4.694	1.899	5.433	3.169	3.497	3.411	3.515
17IB92	3.839	3.751	2.267	4.379	2.142	5.172	2.860	3.473	3.315	3.154
17IB129	3.148	3.429	2.168	3.733	2.663	4.782	2.103	3.256	2.486	2.899
17IB173	4.687	4.007	3.357	4.956	2.098	4.834	3.124	3.792	3.064	3.305
17IB206	4.520	4.061	3.393	6.296	2.505	6.480	3.226	3.640	3.231	4.126
11IB50	3.511	3.558	2.883	4.596	1.592	5.039	2.990	3.438	2.923	3.294
Genaro	4.324	4.481	3.250	6.210	2.167	5.801	3.817	3.491	3.356	4.120
Hartog	3.327	4.049	3.113	4.559	2.050	5.408	2.832	3.535	2.934	3.386
Banks	3.028	4.421	1.853	2.821	1.653	5.020	2.096	3.342	2.406	3.080
Kite	3.089	3.363	2.173	5.409	1.910	4.306	2.719	3.024	2.456	2.985
$\bar{x}$	3.656	4.008	2.721	4.864	2.038	5.258	2.909	3.430	2.967	3.409
$LSD_{5\%}$	0.600	0.575	0.395	1.270	0.443	0.581	0.434	0.469	0.225	0.430
$\sigma^2_{\varepsilon(j)}$	0.078	0.072	0.034	0.351	0.043	0.073	0.041	0.048	0.011	0.040
$\sigma^2_{g(j)}$	0.294	0.089	0.196	0.616	0.071	0.223	0.202	0.049	0.094	0.121
$\sigma^2_{p(j)}$	0.333	0.125	0.213	0.792	0.092	0.259	0.222	0.073	0.100	0.141
h^2_j	0.883	0.711	0.920	0.778	0.769	0.858	0.908	0.675	0.945	0.858

Table 2 Estimates of genetic parameters for the combined analysis of grain yield (t ha^{-1}) of 15 wheat lines tested over ten environments in Queensland in 1988

Statistic	Estimate	% of $G \times E$
Genotypic variance component (σ_g^2)	0.109	127
$G \times E$ interaction variance component (σ_{ge}^2)	0.086	–
Heterogeneity of genotypic variance [$V(\sigma_{g(env)})$]	0.027	31
Lack of genetic correlation [$L(r_{g(env)})$]	0.059	69
Error variance component (σ_e^2)	0.079	92
Line mean heritability (h^2)	0.897	–
Pooled genetic correlation (r_g)	0.651	–

rameters pertaining to the classifications were calculated and expressed on environment standardised data. The environment classification was truncated at the five environment group level where 70.6% of the $L \times E$ interaction sum of squares was partitioned among the environment groups. The partitioning of line and $L \times E$ interaction sums of squares among groups for the line classification was investigated at the five environment group truncation level. A high percentage of the line sum of squares was accounted for by a small number of line groups. At the three line group level 91.0% of the line sum of squares was partitioned among the groups. Therefore, differences among the lines for broad standardised grain yield (std-yield) adaptation across the environments were well represented by three line groups. However, for $L \times E$ interaction there was consistently a smaller percentage of the total component sum of squares accounted for by the groups. At the three line group level 14.0% of the total $L \times E$ interaction sum of squares was partitioned among the groups. To allow a more detailed inspection of the $L \times E$ interaction, the line classification was truncated at the five group level where 40.5% of the $L \times E$ interaction sum of squares was partitioned among the groups.

Truncating the environment classification at the five group level resulted in two groups with a single member, two groups with two members, and one with four members (Fig. 1). The truncation of the line classification at the five group level identified two groups with one member, one group with two members, one group with three members, and a larger group with eight members (Fig. 2). Group 22 comprised three lines derived from the same cross (Veery) suggesting there was a genetic basis to the grouping of the lines.

While only 40.5% of the $L \times E$ interaction sum of squares was represented by the two-way classification, the five groups of lines expressed distinctive patterns of std-yield across the five environment groups (Fig. 3). Line groups 22 and 25 both expressed a stable std-yield response across the environment groups; however, these had different average std-yield. Group 22 had a high average std-yield while group 25 was intermediate. The three remaining groups of lines in general expressed high std-yield in one environment group but either low or intermediate std-yield in the other groups of environments. Group 9 had high std-yield in environment group 13 but was intermediate in the other four. Groups 24 and 14 expressed high std-yield in environment groups 5 and 2, respectively, but were generally of low std-yield in the remaining environment groups. Only line group 22 expressed high std-yield in environment groups 11 and 15, which together accounted for six of the ten environments. Therefore, the broad adaptation of the three lines comparising group 23 conferred specific adaptation to the environment groups 11 and 15 which was not expressed by the other groups of lines.

The proximities of the lines and environments on the first two vectors from the ordinations (Fig. 4) strongly reflected the relationships among both lines and environments which were identified by the classification (Figs. 1 and 2). The five groups of lines were clearly distinguished on the first vector, which largely reflected the average std-yield of the lines across the environments (Fig. 4). The second vector distinguished between line groups 14 and 24, the two low performing groups, and to a lesser extent between groups 9 and 25, the two intermediate performing groups. The first two vectors of the environment ordination distinguished between environment groups 5, 13 and 2 but did not separate environment groups 11 and 15.

Table 3 Genetic (upper triangle) and phenotypic (lower triangle) correlation coefficients among all pairwise comparisons among ten environments for grain yield of 15 wheat lines

	Environment									
	Emd-1	Emd-2	King	Gatt	Bil	Fern	Toob	Gums	Pamp	Jim
Emd-1		0.321	0.813	0.737	0.537	0.652	0.818	0.967	0.701	0.797
Emd-2	0.254		0.411	0.211	−0.091	0.742	0.356	0.591	0.399	0.730
King	0.733*	0.333		0.851	0.318	0.709	0.777	0.750	0.675	0.853
Gatt	0.610*	0.157	0.720*		0.418	0.652	0.943	0.338	0.615	0.927
Bil	0.444	−0.067	0.267	0.323		0.494	0.095	0.574	0.132	0.405
Fern	0.568*	0.580*	0.630*	0.533*	0.401		0.569	0.726	0.699	1.047
Toob	0.732*	0.286	0.710*	0.793*	0.079	0.502		0.505	0.785	0.806
Gums	0.746*	0.410	0.591*	0.245	0.413	0.552*	0.395		0.538	0.693
Pamp	0.640*	0.327	0.629*	0.528*	0.113	0.629*	0.727*	0.429		0.735
Jim	0.693*	0.570*	0.758*	0.757*	0.329	0.898*	0.711*	0.527*	0.662*	

* Significant at the 5% probability level

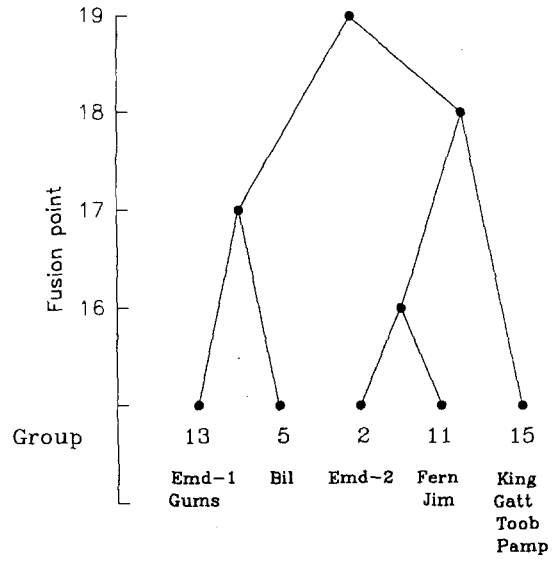

Fig. 1 Dendrogram, truncated at the five group level, for the hierarchical classification by Ward's method on environment standardised grain yield data of ten environments on the data from 15 wheat lines grown in them

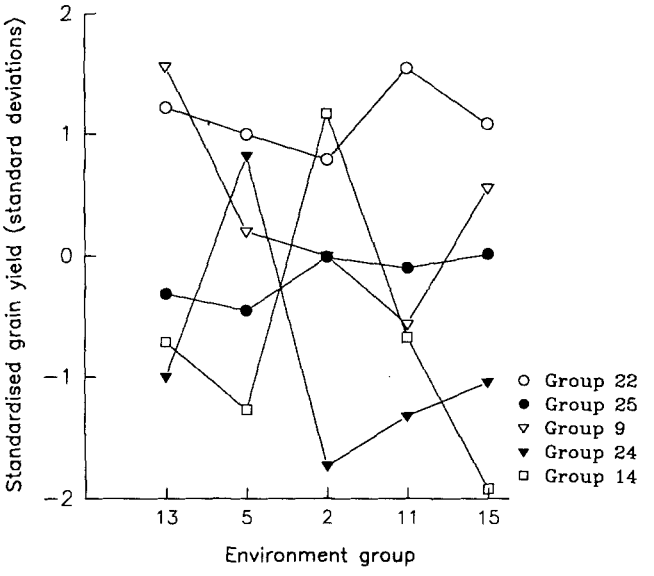

Fig. 3 Response plot of standardised grain yield for five line groups over five environment groups identified by two-way classification of 15 wheat lines evaluated over ten environments

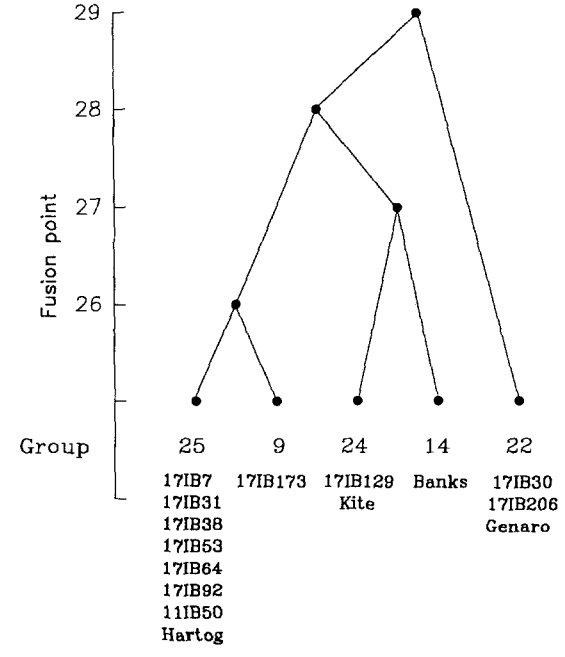

Fig. 2 Dendrogram, truncated at the five group level, for the hierarchical classification by Ward's method on environment standardised grain yield data of 15 wheat lines evaluated in ten environments

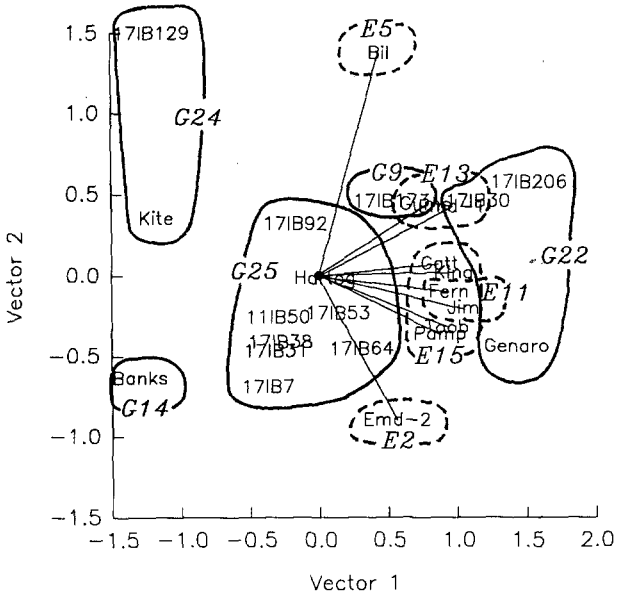

Fig. 4 Biplot for the ordination of environment standardised grain yield of 15 wheat lines evaluated in ten environments. *Solid boundaries* identify the lines included in the five line groups and *dashed boundaries* identify the environments included in the five environment groups produced by two-way classification. Genotype group names preceded by *G* and environment group names preceded by *E*

Projecting the positions of the lines, or the groups of lines, onto the line drawn from the origin to the position of the environment, or groups of environments, gives a prediction of the relative performance of the lines in the environments as represented by the ordination. Therefore, the biplot shows that line group 24, particularly line 17IB129, performed well at environment group 5 and that this line group performed poorly at all other environment groups, particularly environment group 2. This pattern of performance was also observed on the two-way response plot (Fig. 3). Line group 25 was predicted to show average performance in all environment groups because the lines comprising this group were centred around the origin (Fig. 4). Similarly, line group

25 showed intermediate performance on the response plot (Fig. 3). Line group 9 was close to the origin and therefore had generally intermediate std-yield but was predicted to have higher std-yield than line group 25 in environment group 13 and similar or slightly higher std-yield than line group 25 in all other environment groups (Fig. 4). This pattern was also observed on the two-way response plot (Fig. 3). The line group 14, which comprised Banks, was predicted to have intermediate std-yield in environment group 2 and low std-yield in all other environment groups (Fig. 4). The two-way response plot was similar except that group 14 was portrayed as expressing high, rather than intermediate, std-yield in environment group 2 (Fig. 3). The remaining line group 22 was predicted to have intermediate to high std-yield in all environment groups and to be the highest yielding in environment groups 11, 13 and 15 (Fig. 4). Group 22 displayed a high and stable std-yield over the environment groups in the two-way response plot (Fig. 3).

Comparing the results on the response plot for the two-way classification (Fig. 3) and the biplot from the ordination (Fig. 4), it is clear that similar interpretations are obtained for the patterns of line discrimination for std-yield across the environments.

Discussion

The objective of this paper was to show the relationships among the analysis of variance, indirect selection, and pattern analysis methodologies, for the study of genotypic adaptation in plant breeding experiments. The theoretical development was used to present the relationships and the example to show the practical implications of these relationships.

Where the plant breeder is interested in selection among genotypes, $G \times E$ interaction introduces uncertainty into the selection process where it reduces the genotypic correlation among environments for the way in which these environments discriminate among the genotypes. The pooled genetic correlation among all pairwise comparisons between the environments is the corrected intraclass correlation coefficient derived from the combined analysis of variance. Inspecting the relative sizes of the genotype and $G \times E$ interaction components of variance is essentially an implicit attempt to judge the extent to which there will be a lack of correlation among environments. Therefore, direct estimation of the intraclass correlation coefficient is a more explicit way of determining the average degree of lack of genetic correlation among environments.

The genetic correlation between environments is the central component influencing indirect selection between environments. As the pooled genetic correlation decreases, there is a decrease in the opportunity for achieving an indirect response to selection over a wide range of environments from selection in a few environments. Hence, as the pooled genetic correlation decreases, or the ratio of the $G \times E$ interaction on genotypic variance increases, the question of the opportunity to exploit some aspects of the $G \times E$ interaction becomes more relevant. This often leads the plant breeder to an inspection of specific aspects of the $G \times E$ interaction complex. Accordingly, interest is no longer on the pooled genetic correlation among all environments but on the genetic correlations for all or specific sets of pairwise comparisons of environments. Since there is an exponential increase in the number of pairwise comparisons with an increase in the number of environments, inspection of individual comparisons becomes impractical. To overcome this problem, pattern analysis techniques can be used to summarise the relationships among the environments. Where squared Euclidean distance is used as the proximity measure, standardising the data by removing the environment main-effects and dividing by the square root of the phenotypic variance of line means within the environments relates the classification of environments to indirect selection theory. We refer to these data as environment standardised data (es-data). Therefore, for the plant breeder interested in the impact of $G \times E$ interaction on selection, working with pattern analysis methodology based on es-data allows a summarisation of the environmental relationships in a way which is a direct extension of the familiar indirect selection theory and the information derived from inspection of variance components estimated from the pooled analysis of variance.

Inspection of the two-way response plot from the classification, or the biplot from the ordination, provides alternative and complementary ways of inspecting the relationships among genotypes and environments. Where a high proportion of the genotype and $G \times E$ interaction variation is accounted for, the two-way response plot and the biplot will generally give a similar interpretation of the patterns of discrimination among genotypes across the environments. The biplot may be viewed as a sorted and re-orientated presentation of the original data array. Projecting the relative positions of the genotypes onto the environment vectors allows an inspection of the practical consequences of indirect selection among environments. Then, at a defined selection intensity the plant breeder can identify which genotypes will be selected in which environments and the common genotypes selected from each environment. Consequently, the biplot is an extremely powerful graphic for inspecting the results of plant breeding experiments.

Three major components may be defined in the conduct of METs, the process of sampling the environments, the analysis of the results obtained from the MET, and finally the prediction of response to selection for the target population of environments (Fig. 5). Cooper et al. (1993c) used this framework to consider the impact of $G \times E$ interactions on response to selection and the way in which plant breeders have attempted to accommodate the complications presented by $G \times E$ interactions in METs.

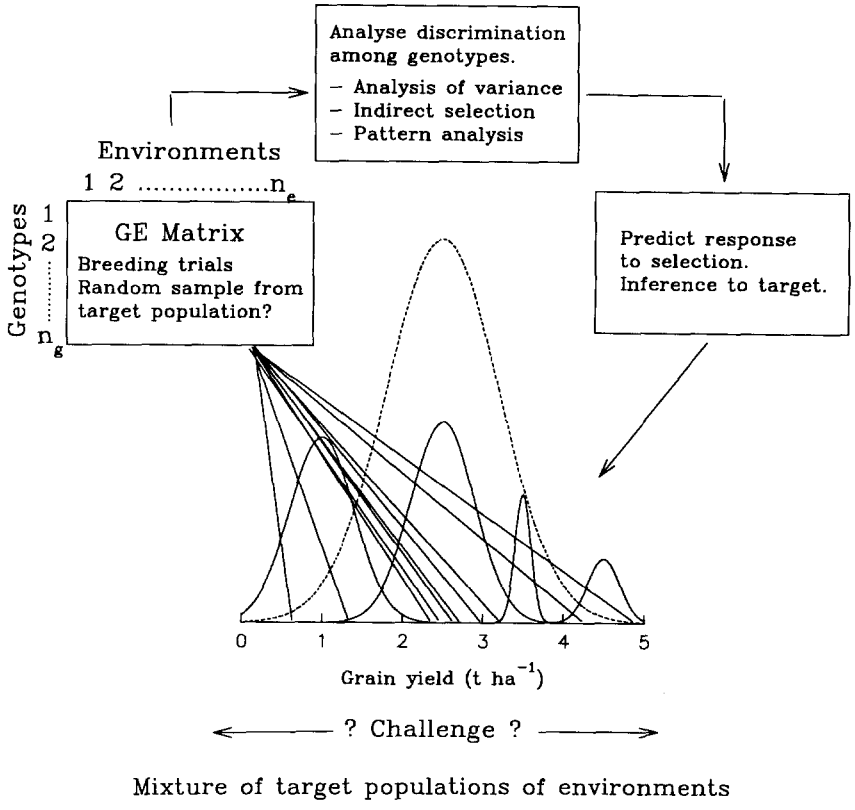

Fig. 5 Schematic representation of the recurrent steps involved in the conduct of multi-environment trials where the objective is to sample test environments from a pre-defined target population of environments

The application of the appropriate analytical methodology is one component of the study of $G \times E$ interactions. To develop a more comprehensive understanding of the nature of the $G \times E$ interactions in a target population of environments, the nature of the environmental challenges encountered must be characterised. This will require paying greater attention to the determination of the environmental factors discrimination among genotypes in METs. Strategies for achieving this for wheat in Queensland have been discussed (Eisemann et al. 1990). Characterising key environmental challenges and their frequency of occurrence in the target population of environments would enable plant breeders to view their targets as a mixture of types of challenges rather than one target population of environments (Fig. 5). Developing such an enhanced understanding of the composition of the target population of environments would lead to the definition of strategies for exploiting specific adaptation associated with $G \times E$ interactions.

Where the plant breeder is attempting to exploit aspects of $G \times E$ interaction, there are two critical questions which must be addressed. The first is, are the aspects of $G \times E$ interaction observed in the multi-environment experiment repeatable? The second is what is the nature of the interaction and how relavant is it to the target population of environments for which the breeding program is responsible (Fig. 5)? Finding answers to these questions will allow definition of what aspects of the patterns of performance of genotypes across environments can be exploited by selection. By separating the repeatable and non-repeatable components of $G \times E$ interaction, more objective decisions can be made on the scope for selecting for specific adaptation.

Clearly these are not easy questions. However, to answer these, more emphasis has to be given to the study of the environmental and physiological bases of the differences in adaptation for quantitative traits observed in plant breeding experiments than has been given in the past. The point we make is that there is now an extensive array of powerful analytical methodology available to the plant breeder and there are clearly-understood relationships among these. Generally the application of these methodologies to the results of plant breeding experiments raises many questions and it is perhaps time that we seriously attempt to answer some of these.

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References

Abou-El-Fittouh HA, Rawlings JO and Miller PA (1969) Classification of environments to control genotype-by-environment interactions with an application to cotton. Crop Sci 9:135–140

Allard RW and Bradshaw AD (1964) Implications of genotype-environmental interactions in applied plant breeding. Crop Sci 4:503–508

Atlin GN and Frey KJ (1989) Breeding crop varieties for low-input agriculture. Am J. Alternative Agri 4:53–58
Atlin GN and Frey KJ (1990) Selecting oat lines for yield in low-productivity environments. Crop Sci 30:556–561
Baker RJ (1969) Genotype-environment interactions in yield of wheat. Can J Plant Sci 49:743–751
Baker RJ (1988a) Analysis of genotype-environmental interactions in crops. ISI atlas of science: animal and plant Science 1:1–4
Baker RJ (1988b) Differential response to environmental stress. In: Weir BS, Eisen EJ, Goodman MM, Namkoong G (eds) Proc 2nd Int Conf Quant Genet. Sinauer Associates, Inc, Sunderland, Massachusetts, pp 492–504
Baker RJ (1988c) Tests for crossover genotype-environmental interactions. Can J Plant Sci 68:405–410
Baker RJ (1990) Crossover genotype-environmental interaction in spring wheat. In: Kang MS (ed) Genotype-by-environment interaction and plant breeding. Louisiana State University, Baton Rouge, Louisiana, pp 42–51
Basford KE, Kroonenberg PM and DeLacy IH (1991) Three-way methods for multiattribute genotype × environment data: an illustrated partial survey. Field Crops Res 27:131–157
Brennan PS and Byth DE (1979) Genotype × environmental interactions for wheat yields and selection for widely-adapted wheat genotypes. Aust J Agric Res 30:221–232
Brennan PS, Byth DE, Drake DW, DeLacy IH and Butler DG (1981) Determination of the location and number of test environments for a wheat cultivar evaluation program. Aust J Agric Res 32:189–201
Bull JK, Cooper M, DeLacy IH, Basford KE and Woodruff DR (1992) Utility of repeated checks for hierarchical classification of data from plant breeding trials. Field Crops Res 30:70–95
Burdon RD (1977) Genetic correlation as a concept for studying genotype-environment interaction in forest tree breeding. Silvae Genet 26:168–175
Burr EJ (1968) Cluster sorting with mixed character types. I. Standardization of character values. Aust Computer J 1:97–99
Burr EJ (1970) Cluster sorting with mixed character types. II. Fusion strategies. Aust Computer J 2:98–103
Byth DE, Eisemann RL and DeLacy IH (1976) Two-way pattern analysis of a large data set to evaluate genotypic adaptation. Heredity 37:215–230
Cockerham CC (1963) Estimation of genetic variances. In: Hanson WD, Robinson HF (eds) Statistical genetics and plant breeding. National Academy of Sciences – National Research Council, Publication 982, Washington, D.C., pp 53–93
Comstock RE and Moll RH (1963) Genotype-environment interactions. In: Hanson WD, Robinson HF (eds) Statistical genetics and plant breeding. National Academy of Sciences – National Research Council, Publication 982, Washington, D.C., pp 164–196
Cooper M, Byth DE, DeLacy IH and Woodruff DR (1993a) Predicting grain yield in Australian environments using data from CIMMYT international wheat performance trials. 1. Potential for exploiting correlated response to selection. Field Crops Res 32:305–322
Cooper M, DeLacy IH, Byth DE and Woodruff DR (1993b) Predicting grain yield in Australian environments using data from CIMMYT international wheat performance trials. 2. The application for classification to identify environmental relationships which exploit correlated response to selection. Field Crops Res 32:323–342
Cooper M, DeLacy IH and Eisemann RL (1993c) Recent advances in the study of genotype × environment interactions and their application to plant breeding. In: Imrie BC, Hacker JB (eds) Focused plant improvement: towards responsible and sustainable agriculture. Proc 10th Aust Plant Breeding Conf, Vol. 1. Organising Committee, Australian Convention and Travel Service, Canberra, pp 116–131
Cooper M, Byth DE and DeLacy IH (1993d) A procedure to assess the relative merit of classification strategies for grouping environments to assist selection in plant breeding regional evaluation trials. Field Crops Res 35:63–74
Crossa J (1990) Statistical analyses of multilocation trials. Adv Agron 44:55–85
Crossa J, Gauch HG and Zobel RW (1990) Additive main effects and multiplicative interaction analysis of two international maize cultivar trials. Crop Sci 30:493–500
Crossa J, Fox PN, Pfeiffer WH, Rajaram S and Gauch HG Jr (1991) AMMI adjustment for statistical analysis of an international wheat yield trial. Theor Appl Genet 81:27–37
DeLacy IH (1981) Cluster analysis for the interpretation of genotype by environment interaction. In: Byth DE, Mungomery VE (eds) Interpretation of plant response and adaptation to agricultural environments. Queensland Branch, Australian Institute of Agricultural Science, Brisbane, pp 277–292
DeLacy IH (1989) Experimental techique and control of micro-environmental variation in agricultural adaptation experiments. In: DeLacy IH (ed) Analysis of Data from Agricultural Adaptation Experiments. Australian Cooperation with the Thai/World Bank National Agricultural Project (ACNARP) Training Course, Bangkok, Thailand, pp 24–35
DeLacy IH and Cooper M (1990) Pattern analysis for the analysis of regional variety trials. In: Kang MS (ed) Genotype-by-environment interaction and plant breeding. Louisiana State University, Baton Rouge, Louisiana, pp 301–334
DeLacy IH, Cooper M and Lawrence P (1990a) Pattern analysis over years of regional variety trials: relationship among sites. In: Kang MS (ed) Genotype-by-environment interaction and plant breeding. Louisiana State University, Baton Rouge, Louisiana, pp 189–213
DeLacy IH, Eisemann RL and Cooper M (1990b) The importance of genotype-by-environment interaction in regional variety trials. In: Kang MS (ed) Genotype-by-environment interaction and plant breeding. Louisiana State University, Baton Rouge, Louisiana, pp 287–300
Dickerson GE (1962) Implications of genetic-environmental interaction in animal breeding. Anim Prod 4:47–63
Eisemann RL, Cooper M and Woodruff DR (1990) Beyond the analytical the analytical methodology – better interpretation of genotype-by-environment interaction. In: Kang MS (ed) Genotype-by-environment interaction and plant breeding. Louisiana State University, Baton Rouge, Louisiana, pp 108–117
Falconer DS (1952) The problem of environment and selection. Am Nat 86:293–298
Falconer DS (1989) Introduction to quantitative genetics, 3rd edn. Longman, London
Finlay KW and Wilkinson GN (1963) The analysis of adaptation in a plant breeding programme. Aust J Agric Res 14:742–754
Fox PN and Rosielle AA (1982) Reducing the influence of environmental main-effects on pattern analysis of plant breeding environments. Euphytica 31:645–656
Freeman GH (1973) Statistical methods for the analysis of genotype-environment interactions. Heredity 31:339–354
Freeman GH (1990) Modern statistical methods for analyzing genotype-by-environment interactions. In: Kang MS (ed) Genotype-by-environment interaction and plant breeding. Louisiana State University, Baton Rouge, Louisiana, pp 118–125
Gabriel KR (1971) The biplot-graphical display of matrices with applications to principal component analysis. Biometrica 58:453–67
Gardner CO (1963) Estimates of genetic parameters in cross-fertilizing plants and their implications in plant breeding. In: Hanson WD, Robinson HF (eds) Statistical genetics and plants breeding. National Academy of Sciences – National Research Council, Publication 982, Washington, D.C., pp 164–196
Gauch HG and Zobel RW (1988) Predictive and postdictive success of statistical analyses of yield trials. Theor Appl Genet 76:1–10
Gower JC (1966) Some distyance properties of latent root and vector methods used in multivariate analysis. Biometrika 53:325–338
Gower JC (1967) Multivariate analysis and multi-dimensional geometry. The Statistician 17:13–28
Haldane JBS (1947) The interaction of nature and nurture. Ann Eugen 13:197–205
Hill J (1975) Genotype-environment interactions – a challenge for plant breeding. J Agric Sci 85:477–493
Horner TW and Frey KJ (1957) Methods for determining natural areas for oat varietal recommendations. Agron J 49:313–315

Itoh Y and Yamada Y (1990) Relationships between genotype × environment interaction and genetic correlation of the same trait measured in different environments. Theor Appl Genet 80:11–16

Ivory DA, Kaewmeechai S, DeLacy IH and Basford KE (1991) Analysis of the environment component of genotype × environment interaction in crop adaptation evaluation. Field Crops Res 28:71–84

Kempton RA (1984) The use of bi-plots in interpreting variety by environment interactions. J Agric Sci 103:123–135

Lawn RJ and Imrie BC (1991) Crop improvement for tropical and subtropical Australia: designing plants for difficult climates. Field Crops Res 26:113–139

Lawn RJ and Imrie BC (1993) Exploiting physiological understanding in crop improvement. In: Imrie BC, Hacker JB (eds) Focused plant improvement: towards responsible and sustainable agriculture. Proc 10th Aust Plant Breeding Conf, vol. 1. Organising Committee, Australian Convention and Travel Service, Canberra, pp 136–146

Lefkovitch LP (1990) Genotype-by-environment interaction, heterogeneous variance, and significance. In: Kang MS (ed) Genotype-by-environment interaction and plant Breeding. Louisiana State University, Baton Rouge, Louisiana, pp 20–27

Mirzawan PDN, Cooper M, and Hogarth DM (1993) The impact of genotype-by-environment interaction for sugar yield on the use of indirect selection in southern Queensland. Aust J Exp Agric 33:629–638

Moll RH and Stuber CW (1974) Quantitative genetics – empirical results relevant to plant breeding. Adv Agron 26:277–313

Nyquist WE (1991) Estimation of heritability and prediction of selection response in plant populations. Crit Rev Plant Sci 10:235–322

Pederson DG, Rathjen AJ (1983) The impact of site selection on breeding progress. In: Driscoll CJ (ed) Proc VIIIth Aust Plant Breeding Conf. The University of Adelaide, pp 32–37

Shaw DV (1989) Genetic parameters and selection efficiency using part-records for production traits in strawberries. Theor Appl Genet 78:560–566

Shorter R, Mungomery RE (1981) Analysis of variance of data from multi-environment trials. In: Byth DE, Mungomery VE (eds) Interpretation of plant response and adaptation to agricultural environments. Queensland Branch, Australian Institute of Agricultural Science, Brisbane, pp 12–26

Shorter R, Lawn RJ and Hammer GL (1991) Improving genetic adaptation in crops–A role for breeders, physiologists and modellers. Exp Agric 27:155–175

Ward JH (1963) Hierarchical grouping to optimise an objective function. J Am Stat Assoc 58:236–244

Westcott B (1986) Some methods of analysing genotype-environment interaction. Heredity 56:243–253

Williams WT (1976) Pattern analysis in agricultural science. Elsevier Scientific Publishing Company, Amsterdam

Wishart D (1969) An algorithm for hierarchical classification. Biometrics 22:165–170

Yamada Y (1962) Genotype-by-environment interaction and genetic correlation of the same trait under different environments. Jpn J Genet 37:498–509

Zobel RW (1990) A powerful statistical model for understanding genotype-by-environment interaction. In: Kang MS (ed) Genotype-by-environment interaction and plant breeding. Louisiana State University, Baton Rouge, Louisiana, pp 126–140

Zobel RW, Wright MJ and Gauch HG (1988) Statistical analysis of a yield trial. Agron J 80:388–393