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Linear and bilinear models for the analysis of multi-environment trials: I. An inventory of models

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Summary

The multi-environment trial, in which a number of genotypes is evaluated over a range of environmental conditions, is a standard experiment in plant breeding in general, and variety testing in particular. Useful statistical models for the analysis of multi-environment trials, with emphasis on the analysis of genotype by environment interaction, can be found in the classes of linear and bilinear models. Statistical properties of the most important representatives of these model classes are shortly reviewed. Structural differences between the models stem from: (1) the inclusion of random model terms in addition to fixed model terms; (2) the representation of the interaction by additive or multiplicative parameters; (3) the incorporation of concomitant variables on the levels of the environmental factor. For models with bilinear multiplicative structure for the interaction it is described how the interaction can be visualized by biplots. An illustration of the application of the models and biplots is given in a companion paper.

Introduction

A classic experiment in plant breeding is the multi-environment experiment, which in the standard case involves the evaluation of a number of genotypes at a number of locations over a number of years. Inferences to be made from multi-environment trials concern genotypes and environments. For the genotypes, typically, predictions are wanted for performance over years, or over years and locations. For environments discriminatory power prevails. Multi-environment experiments form the core of varietal testing programmes in many countries. These programmes have to assess the agronomic value of new varieties. Eventually, decisions have to be made about admittance of new varieties to the Variety List. A characteristic feature of data collected within Variety List testing programmes is their unbalancedness. The variety sortment changes over the years and not all varieties are tested at all locations within each year. Prediction of performance is better not based on simple mean performance. Two popular methods providing adjusted means are fitting constants (Searle, 1971; Patterson, 1978) and best linear unbiassed prediction (Henderson, 1963; Robinson, 1991; Searle et al., 1992). Both these methods are based on linear models with, usually, only indicator variables as explanatory variables, i.e. classic analysis of variance, or ANOVA, models. Interaction is modelled by a separate, additive parameter for each combination of genotype by environment, coarsely and unparsimoniously. These models are used primarily for arriving at good predictions over a range of environments, thereby in some sense averaging (weighted) over the interaction present. No attempt is made at interpretation of the interaction, thus leaving the causes of interaction for what they are.

As an alternative to linear formulations of interaction, multiplicative formulations can be chosen that do permit interpretation of interaction, as differential genotypic sensitivity to environmental variable(s). Three main classes may be distinguished. The first, and at the moment most popular, class consists of the Additive Main effects and Multiplicative Interaction effects (AMMI) models (Gollob, 1968; Mandel, 1969;

Perkins, 1972; Gauch, 1988), which is a subset of the class of bilinear models (Denis, 1991), also called biadditive models (Denis & Gower, 1992, 1994). For AMMI models no explicitly measured environmental variables are necessary, as they contain implicit, hypothetical environmental variables to which genotypes differ maximally in sensitivity. In contrast, models of the second class, that of factorial regression models (linear models), contain, as a rule, exclusively explicitly measured environmental variables (Denis, 1980, 1988; van Eeuwijk & Elgersma, 1993). For the third class, that of reduced rank factorial regression models (bilinear models), the environmental variables are generalizations of the environmental variables in factorial regression models as well as AMMI models. They are hypothetical and maximize differences in genotypic sensitivity as in AMMI, but under the restriction of having to be linear combinations of measured environmental variables, a feature which links reduced rank factorial regression to factorial regression (Davies & Tso, 1982; van Eeuwijk, 1992).

In comparison with linear models, routine application of bilinear models to unbalanced data may seem more complicated, as special software is required to perform the recommended alternating least squares estimation procedures (Gabriel & Zamir, 1979; Denis, 1991; van Eeuwijk, 1995). However, a simple approximative method may consist in first fitting a mixed model to an incomplete genotype by environment table, subsequently calculating a complete table of best linear unbiassed predictions (BLUPs), and finally applying bilinear model analyses to that complete table.

In the remainder of this paper five classes of models, including linear and bilinear models, will be reviewed. Results of analyses with bilinear models are often presented graphically in the form of biplots (Gabriel, 1971). Their construction and interpretation will also be described. An application of the methods to data from the Dutch Maize Variety Trials is given in a companion paper by van Eeuwijk et al. (1995).

Analysis of variance models with fixed model terms

ANOVA models are used to describe a wide range of phenomena. Phenotypic responses in multi-environment trials are no exception to this rule. In the so-called fixed ANOVA models, observations are written as the sum of a number of fixed model terms and a normally distributed error term. The adjective 'fixed' for a model term is used to indicate that the parameters are deemed constants, expressing the effects of the levels of a factor, or combinations of factor levels, on the response variable. The model is linear in its parameters. For example, a two ANOVA model for the yield, y_{ij}, of genotype i ($i = 1 \ldots 1$) in environment j ($j = 1 \ldots J$) can have the form $\mathcal{E}(Y_{ij}) = \mu + \alpha_i + \beta_j$, with $\mathcal{E}(.)$ the expectation operator, μ the general mean, α_i the genotypic main effect, and β_j the environmental main effect. Identification constraints are chosen as sum-to-zero. This model is straightforward in its application to complete tables, as estimation of parameters is then equivalent to averaging and subtracting. For the incomplete tables from multi-environment trials the simple procedures appropriate for complete tables can no longer be used. Fitting constants is a method developed especially for fitting ANOVA models to unbalanced data (Searle, 1971, p. 138). The method can be understood as regression on dummy (0–1) variables that allocate the parameters of the linear model to the observations (Searle, 1971, pp. 140–145). Therefore, fitting constants can be performed with every software package that includes multiple regression. For unbalanced data the order in which terms are fitted is important (Searle, 1971, pp. 270–279). Later terms in the fitting sequence are corrected for earlier ones. As a rule, effects of lower importance are included first, while main effects are included before their interactions.

Fitting constants is often used to obtain adjusted genotypic means for incomplete genotype by environment tables (Patterson, 1978). To such a table a model is fitted that includes only the genotypic and environmental main effect. From this model adjusted means are calculated, that can deviate considerably from the arithmetic averages. When genotypes were absent in environments with generally high responses, their means are corrected upwards. Means for genotypes absent in unfavourable environments will be corrected downwards.

To an incomplete genotype by environment table no model with interaction, like for example $\mathcal{E}(y_{ij}) = \mu + \alpha_i + \beta_j + \alpha\beta_{ij}$, can be fitted. For the missing cells interaction parameters will be undefined, as will be the main effects for the corresponding levels. For incomplete higher dimensional multi-environment tables, the non-genetic factors are often collapsed into one environmental factor to create a two-dimensional genotype by environment table to which an additive model can be fitted. Because main effects then are defined for all factor levels, adjusted means can be formed without

problems. This is one way of dealing with missing cells.

When data tables are (severely) incomplete, the analysis of variance table is best used as an exploratory tool to get a rough idea of the distribution of the variation over the various sources. Use of F-tests is less straightforward. Due to non-independence of the mean squares, variance ratios are no longer exactly F-distributed, while the hypotheses being tested depend on the structure of the data (Searle, 1971, pp. 316–318).

Analysis of variance models with fixed and random terms

The previous section dealt with ANOVA models in which all model terms except the error were assumed fixed. Assuming not only the error term, but also other model terms to be random, i.e. to come from a (normal) distribution, can have desirable consequences. In multi-environment trials not all genotypes are tested at each location and in each year. For example, two genotypes are tested over a number of years, but the number of locations (trials) at which the genotypes are present differs between years, and the genotypes are not always jointly present in each trial. When a combined estimate of the difference is wanted several options are open. The average difference over the years may be taken, but this cannot be optimal as the difference will be estimated more precisely in years with more trials. Another possibility is to consider only those trials in which both genotypes were present. However, this procedure would clearly not use all information available. Yet another option is to weigh the difference within a year by the number of trials. This procedure will run into problems in the presence of substantial genotype by year interaction. The use of fitting constants on a genotype by environment (location times year) table may provide a reasonable estimate for the difference. However, the optimal procedure should take into account (1) all the possible sources of variation in addition to the error variation, like variation due to years, trials, year by trial interactions, genotype by year interactions, and genotype by trial interactions; (2) recover information on the genotypic difference from year totals, trial totals, etc.; (3) combine the information efficiently by weighing inversely proportional to the estimated variances (Robinson, 1987).

A recommended way to comply with these requirements is by (1) taking appropriate terms random and (2) estimating parameters of fixed and random terms plus the corresponding variance components by the method of residual maximum likelihood, or REML (Patterson & Thompson, 1971; Searle et al., 1992; Genstat, 1993). Models which include fixed and random factors are called mixed models (Searle, 1971). The distributional assumptions entailed by mixed models should be checked. Terms for which less than ten degrees of freedom are available should not be taken random, as they do not allow proper checking of the distributional assumptions.

REML estimation consists of two steps. First, variance components are estimated by maximizing the likelihood of the so-called error contrasts. These REML estimates reduce to the usual analysis of variance estimates in case of balance, and are in contrast to maximum likelihood estimates not biassed downwards. In the second step, the fixed and random effects are estimated, using the variance components from the first step. The estimates for the fixed effects are generalized least squares estimates, which means that the effects can be estimated by a weighted regression in which the weights are equal to the reciprocals of the variances of the contrasts involved. As a consequence, the effects are estimated in such a way that information from different strata is recovered and combined in the most efficient way possible, taking into account unbalancedness.

Estimation of random effects is often called prediction. In contrast to the situation for a fixed factor where parameters are estimated, for a random factor realizations of an unobserved random variable are estimated (predicted). REML estimates of random effects are best linear unbiassed predictions, or BLUPs (Robinson, 1991; Searle et al., 1992). This implies that the estimates will be shrunken in comparison to the generalized least squares estimate that would have been obtained were the random effects chosen fixed. The phenomenon of shrinkage is in plant breeding well known in connection with the notion of heritability. Consider the model for the phenotype y_{ij}, for the j-th observation ($j = 1 \ldots n_i$) on the i-th genotype ($i = 1 \ldots I$); $y_{ij} = g_i + \varepsilon_{ij}$, where g_i and ε_{ij} are random terms with variances σ_g^2 and σ_ϵ^2. The BLUP estimator for the genotypic effect g_i is $\{n_i/(n_i + (\sigma_\epsilon^2/\sigma_g^2))\}y_i$, where y_i is the mean over the observations on genotype i. This BLUP estimator corrects for possible random environmental contributions to the random genetic effects, and thus for selection bias. The amount of shrinkage depends on the ratio of the variances involved, i.e. on

the heritability ($h^2 = \sigma_g^2/(\sigma_g^2 + \sigma_\epsilon^2)$), and the number of observations for a particular genotype, n_i.

Estimated effects for fixed and random factors and their interactions can be linearly combined, i.e. summed, to find the means for the levels of particular factors and their interactions. For unbalanced data the predicted means correspond to hypothetical means that would have been obtained were the data orthogonal and equally replicated.

In cases where it can be defended that factors and factor combinations are taken random, mixed model analysis provides a quick and easy way of dealing with missing cells. Given that the appropriate model term is taken random, for factor levels or combinations of levels without observations, corresponding parameters can be estimated by the expected value for that term (zero), and predicted means calculated without extra problems. For fixed model terms the parameter would have stayed undefined.

AMMI models

Together with the introduction of the acronym AMMI, Gauch (1988) started a popularization of this already known method of describing interaction in terms of singular vectors (Gollob, 1968; Mandel, 1969; Johnson & Graybill, 1972; Perkins, 1972). Essentially, the matrix of residuals from additivity is decomposed by a singular value decomposition (Gabriel, 1978). One way of construing AMMI is that the interaction is described in terms of differential sensitivity to the most discriminating environmental variables that can be constructed. These environmental variables are hypothetical, and obtained from the data themselves, no measured environmental variables enter the model. Because both environmental variables and genotypic sensitivities are estimated from the data table itself, the AMMI model is called a bilinear model: given the column parameters the model is linear in the row parameters, and given the row parameters the model is linear in the column parameters. The AMMI model for a genotype by environment table can be written as

$$\mathcal{E}(y_{ij}) = \mu + \alpha_i + \beta_j + \sum_{m=1}^{M} \lambda_m \gamma_{mi} \delta_{mj} .$$

The additive interaction parameters, $\alpha\beta_{ij}$, of the ANOVA two-way model are replaced by a sum of multiplicative terms, in which the λ_m's represent proportionality constants called singular values, the γ_{mi}'s genotypic sensitivities, or scores, and the δ_{mj}'s environmental values, or scores, on hypothetical environmental variables, or (AMMI) axes (m = 1 . . . M). Identification constraints normally chosen are

$$\sum_{i=1}^{I} \gamma_{mi}^2 = 1, \sum_{j=1}^{J} \delta_{mj}^2 = 1, \sum_{i=1}^{I} \gamma_{mi}\gamma_{m'i} = 0,$$
$$\sum_{j=1}^{J} \delta_{mj}\delta_{m'j} = 0, \ (m \neq m').$$

The first axis represents the hypothetical environmental variable that describes the largest amount of interaction and thus best discriminates between genotypes, the second axis the second largest amount, etc. For interpretational purposes the environmental scores of an axis may be related to the values of measured environmental variables.

Multiplicative modelling of interaction is successful when the additive ANOVA interaction, $\alpha\beta_{ij}$, with (I-1)(J-1) independent parameters, can be replaced by only a few multiplicative terms (M << minimum of I-1 and J-1), thus adequately describing the interaction with considerably fewer parameters. Various methods exist for assessing the number of multiplicative interaction terms (axes) (see Cornelius, 1993; van Eeuwijk, 1995). The most simple one is due to Gollob (1968), and suffices for many practical applications (Gauch, 1992). For each axis a mean square is calculated, that is compared with an error estimate, by means of an F-test. The mean squares are obtained as follows. The sum of squares for axis m is equal to the square of the singular value, λ_m^2. The corresponding number of degrees of freedom is (I-1) + (J-1) - (2m-1). The required mean square is the quotient of these two quantities.

Factorial regression

After fitting main effects to a two-way table of genotypes by environments, one can introduce concomitant variables on the levels of the genotypic and/or environmental factor in an attempt to describe the interaction (Denis, 1980, 1988; Snedecor & Cochran, 1980, Chpt. 16). A factorial regression model for a two-way genotype by environment table with concomitant variables on the environmental factor has the form

$$\mathcal{E}(y_{ij}) = \mu + \alpha_i + \beta_j + \sum_{h=1}^{H} \xi_{hi} x_{hj} .$$

This factorial regression model is very similar to the AMMI model, except that in the interaction part mea-

sured environmental variables, x_h (h = 1 . . . H; $H \leq J-1$) are included instead of estimated hypothetical variables. For that reason the factorial regression model is a linear model, it is linear in its parameters, and the familiar estimation and testing procedures for regression can be used. Interaction in the factorial regression model can be interpreted as differential genotypic sensitivity, expressed in ξ_{1i} till ξ_{Hi}, with respect to the environmental variables x_1 till x_H.

The regression on the mean or row regression model (Yates & Cochran, 1938; Mandel, 1961; Finlay & Wilkinson, 1963) might be interpreted as a special type of factorial regression model with only one, non-measurable, concomitant variable on the environmental factor, namely the environmental main effect. Alternatively, the regression on the mean model may be taken to be an AMMI model with one bilinear interaction term and the environmental scores proportional to the environmental main effect.

Reduced rank factorial regression

Reduced rank factorial regression generalizes both (full rank) factorial regression and AMMI. Just as for AMMI, hypothetical environmental variables, or axes, are constructed, but now under the restriction of having to be linear combinations of measured environmental variables. The reduced rank factorial regression model is again a bilinear model. The model formulation is

$$\mathcal{E}(y_{ij}) = \mu + \alpha_i + \beta_j + \sum_{m=1}^{M} \lambda_m \gamma_{mi} \left[\sum_{h=1}^{H} \rho_{mh} x_{hj} \right].$$

The AMMI axes, δ_{mj}, are replaced by linear combinations of, in general, measured environmental variables, the reduced rank factorial regression axes, $\left[\sum_{h=1}^{H} \rho_{mh} x_{hj} \right]$. The ρ_{mh}'s stand for the coefficients of the environmental variables x_1 till x_H in the m-th reduced rank factorial regression axis. Interaction is described by differential genotypic sensitivity, γ_{mi}, towards the constructed variables represented by the axes. The parameters for the interaction part are now derived from a singular value decomposition of the matrix of fitted values of the interaction residuals on the set of measured environmental variables (Davies & Tso, 1982). Identification constraints for genotypic and environmental scores are usually equal to those for AMMI.

The number of axes necessary for an adequate description of the interaction can be determined similar to that for the AMMI model. Degrees of freedom are attributed as I + H - 2m for axis m. Mean squares can then be calculated, and either a likelihood ratio test as given by van Eeuwijk (1992) may be performed, or an F-test analogous to the one described for AMMI. Given that the full rank factorial regression model was found adequate, reduced rank factorial regression can be called successful when only a few linear combinations of the measured environmental variables explain about the same amount of interaction. The maximum number of axes possible equals the minimum of I-1 and H. Reduced rank factorial regression becomes equivalent to (full rank) factorial regression when this maximum number of axes is incorporated in the model. When the restriction imposed on the reduced rank factorial regression axes of having to be a linear combination of environmental variables is dropped, reduced rank factorial regression becomes equivalent to AMMI. For an extensive treatment of an application of reduced rank factorial regression to a genotype by environment problem see van Eeuwijk (1992).

Biplot representations

The model formulations for AMMI and reduced rank regression showed that their interaction parts consist of summed orthogonal products. Because of this form the interaction lends itself to graphical display in the form of so-called biplots (Gabriel, 1971). Let us start with AMMI and assume that either two terms suffice for an adequate description of the interaction, or else represent the major features, and let us distribute the singular values, λ_m, over the genotypic scores, $\gamma^*_{mi} = \gamma_{mi} \lambda_m^c$, and the environmental scores, $\delta^*_{mj} = \delta_{mj} \lambda_m^{1-c}$, with $0 \leq c \leq 1$. For AMMI the interaction consists then of the sum two products: $\gamma^*_{1i}\delta^*_{1j} + \gamma^*_{2i}\delta^*_{2j}$. The choice of the scaling constant c depends on the purposes of the analysis. Usually one is more interested in the genotypes and c is chosen equal to one (Kempton, 1984). The features of the biplots, however, are not too critically dependent on c, and c = 0.5 may suit well for most problems.

The genotypic scores, γ^*_{1i} and γ^*_{2i}, are now interpreted as coordinates for a planar depiction of the genotypes, and the environmental scores, δ^*_{1j} and δ^*_{2j}, for a similar depiction of the environments. The scores determine the endpoints of genotypic and environmental vectors, which depart from the origin. Simple geom-

etry reveals that the interaction between a genotype i and an environment j can be obtained from a projection of either vector onto the other. The reason is that the interaction according to an AMMI model with two product terms for interaction, $\gamma_{1i}^{*}\delta_{1j}^{*} + \gamma_{2i}^{*}\delta_{2j}^{*}$, is equal to the inner product between the vectors $(\gamma_{1i}^{*},\gamma_{2i}^{*})$ and $(\delta_{1j}^{*},\delta_{2j}^{*})$, or the projection of either vector onto the other, times the length of the vector on which projection takes place. In case of an obtuse angle between genotypic and environmental vector, an additional minus sign is necessary. It is easy to read from a biplot the relative interactions that genotypes exhibit in a particular environment. One only needs to look at the ranking of the projections of the genotypic vectors on the particular environmental vector. Cosines of the angles between genotypic vectors approximate correlations between genotypes with respect to their interactions. The same holds true for the environments.

For reduced rank factorial regression the story is slightly more complicated. We again assume that two multiplicative terms suffice and distribute the singular values over the scores. Interaction can then be described as

$$\gamma_{1i}^{*}\left(\sum_{h=1}^{H}\rho_{1h}x_{hj}\right)^{*} + \gamma_{2i}^{*}\left(\sum_{h=1}^{H}\rho_{2h}x_{hj}\right)^{*} = \gamma_{1i}^{*}\left(\sum_{h=1}^{H}\rho_{1h}^{*}x_{hj}\right) + \gamma_{2i}^{*}\left(\sum_{h=1}^{H}\rho_{2h}^{*}x_{hj}\right).$$

In the reduced rank regression biplot we plot three types of vectors whose coordinates are determined by: (1) the genotypic sensitivities, $(\gamma_{1i}^{*},\gamma_{2i}^{*})$; (2) the environmental characterisations, $\left(\sum_{h=1}^{H}\rho_{1h}^{*}x_{hj}\,,\,\sum_{h=1}^{H}\rho_{2h}^{*}x_{hj}\right)$; and (3) the coefficients for the environmental variables within the reduced rank factorial regression axes, $(\rho_{1h}^{*},\rho_{2h}^{*})$. As in the AMMI biplot the inner product of the genotypic vector i with the environmental vector j gives the interaction (non-additivity) for genotype i in environment j. In addition, inner products between the genotypic sensitivity vectors, $(\gamma_{1i}^{*},\gamma_{2i}^{*})$, and the coefficient vectors, $(\rho_{1h}^{*},\rho_{2h}^{*})$, approximate the (full rank) factorial regression coefficients, $\xi_{hi} = \rho_{1h}^{*}\gamma_{1i}^{*} + \rho_{2h}^{*}\gamma_{2i}^{*}$. For illustrations of the use of biplots in reduced rank regression models see Ter Braak (1990) and Ter Braak & Looman (1994).

Information on measured environmental variables can also be added to AMMI biplots, although these variables had no influence on the determination of the environmental axes. We can indicate directions of greatest change with respect to a particular environmental variable, by depicting the variable by the coefficients of its regression on the axes. When the scaling constant c is chosen equal to one, this is equivalent to using the correlations of the environmental variable with the axes. The sum of the squared correlations over the axes gives a measure for the quality of the representation. Reduced rank regression biplots can be supplemented with environmental information not used in the determination of the axes in the same way.

Epilogue

In this paper linear and bilinear models for the analysis of genotype by environment interaction have been described in a somewhat theoretical context. The best appreciation of what the models may add to the insights of the practical plant breeder is obtained from their application to real life data. In the sequel to this paper (van Eeuwijk et al., 1995), data on dry matter content from the official Dutch Maize Variety Trials will be analyzed and it will be shown how the joint application of the models can lead to an interpretation of genotype by environment interaction in terms of differential sensitivity to external environmental variables.

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