Theor. Appl. Genet. 64, 91–96 (1982)

Some Implications of a First-Order Model of Inter-Plant Competition for the Means and Variances of Complex Mixtures

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Summary. Factorial models commonly used in the analysis of overall and component yields of binary mixtures of genotypes are generalised to include mixtures of any number of components (size, m) and the form of an analysis of variance for fitting such a model to tertiary mixtures is outlined. Such a model contains main effects and interactions up to the mth order, and is specific to the size of mixture so that no equivalence necessarily exists between similar parameter sets for different sized mixtures. Monocultures can be regarded as a special case of the general model.

A simple model of intra-and inter-component competition is defined which assumes that plants do not interact in their competitive effects on others, a condition which is equivalent to an absence of second and higher order interactions in statistical analyses of mixtures of any size. Simple scaling tests involving the yields of components or whole mixtures of different sizes can also be used to test the adequacy of the model. This competition model least to a linear relationship between the mean yield of a mixture and the reciprocal of the number of components it contains, and thus allows the prediction of means and other statistical parameters for mixtures of one size from those of others.

Key words: Competition – Component yields – Tertiary mixture – First-order model

1 Introduction

Concern about the deleterious effects of uniformity in crops and particularly their consequent vulnerability to disease epidemics has led to a renewed interest in the culture of mixtures of genotypes or varieties, and experimental work has confirmed that they are effective in reducing the severity of disease attacks in cereal crops (Browning and Frey 1969; Wolfe and Barrett 1981) with consequent benefits for yield. Opinion as to the yield advantage of mixtures in the absence of disease is divided, but most experiments have shown mixtures to give higher average yields than monocultures, particularly when measured over a range of environments, and also to be more stable (Trenbath 1974).

Most work dealing with mixtures has been concerned with binary combinations and the comparison of all possible pairwise combinations among n components in a design analogous to the diallel mating scheme familiar in quantitative genetics (Griffing 1956). Various methods have been suggested for the analysis of such designs (Williams 1960; McGilchrist 1965; Gallais 1970), generally applying a factorial model to estimate the average effects of components in all mixtures and the specific effects of particular combinations. The average effect of a component, defined as the mean value of all mixtures into which it enters, is of obvious utility as a selection criterion in a breeding programme aimed at the production of mixture components. The concept has been extended by Federer (1979) to mixtures of m components which allow general effects and specific effects of combinations of 2, 3 … and up to m components to be defined.

These definitions of general and specific component effects for mixtures are closely paralleled by the general and specific effects of parents appropriate to the theory of synthetic variety development (Hill 1966; Wright 1974; Gallais and Wright 1980). In the cases of both synthetic varieties and mixtures, however, the definitions of general and specific effects relating to groups of a particular size bear no necessary relation to those for groups of a different size; the theory for different values of m is distinct.

The purpose of the present paper is to define a simple model for the description of mixture yields in terms of intra- and inter-component competition effects, to establish its relationship to operational statistical models with a view to developing methods of testing its adequacy, and to pursue its implications for the prediction of mixture mean values and their variances.

0040-5752/82/0064/0091/$ 01.20

2 Statistical Models and Their Analysis

2.1 Basic Models

2.1.1 Mixture Components

The yield of a component of a mixture of two genotypes or varieties can be described by the factorial model

$$x_{i/j} = u + v_i + a_j + (v\,a)_{ij}$$

where $x_{i/j}$ is the half-plot yield of the ith variety in binary mixture with the jth, u is the general mean of all such component yields, v_i is the direct effect of the ith component, a_j the average associate effect of the jth, and $(v\,a)_{ij}$ is the interaction of these two effects. To this model must be added a further term to accommodate errors of measurement. All effects have zero means and covariances, and variances equal to σ_v^2, σ_a^2 and $\sigma_{(va)}^2$ respectively.

Such a model could be used in the analysis of a diallel set of binary mixtures. It is easily and logically extended to cater for larger mixtures, although as the number of mixture constituents is increased, the number of orders of interaction among them also increases, so that for mixtures of size m, there are m_1 interactions. (The abbreviation m_i will be used to denote $(m-i)$ throughout the paper.) A general model for a component of a mixture of arbitrary size m, including interactions up to the second order, is therefore

$$x_{i/j\ldots m} = u + v_i + \sum_{j\neq i} a_j + \sum_{j\neq i} (va)_{ij} + \sum_{j\neq i} \sum_{k>j} (aa)_{jk} + \sum_{j\neq i} \sum_{k>j} (v\,a\,a)_{ijk} \qquad (1)$$

where summation is over the $1 \ldots m$ components in the mixture. The new effects are $(a\,a)_{jk}$ the average interaction of the jth and kth associates, and $(v\,a\,a)_{ijk}$, its specific effect on the ith genotype. It is immediately appararent that, because more terms are being included into the model and used to describe the yield of a smaller area of land (i.e. 1/m of a plot), the parameters in models used to describe different sized mixtures are unrelated and in fact are of different orders of magnitude. This factor will be more fully discussed later. A more complete notation would therefore include m as a subscript to all parameters to emphasise this distinction.

As in the case of binary mixtures, the parameters are independent and by definition have the following summation properties:

$$\sum_i v_i = \sum_j a_j = \sum_{i\neq j} (v\,a)_{ij} = \sum_{j\neq i} (v\,a)_{ij} = \sum_{j\neq k} (a\,a)_{jk} = \sum_{k\neq j} (a\,a)_{jk} = 0\,,$$

$$\sum_{i\neq j,k} (v\,a\,a)_{ijk} = \sum_{j\neq i,k} (v\,a\,a)_{ijk} = \sum_{k\neq i,k} (v\,a\,a)_{ijk} = 0\,,$$

where summation is over all n members of the reference population from which the components are drawn.

2.1.2 Mixture Totals

The conventional model for the analysis of binary mixtures is that familiar from diallel analysis of both mixtures and genetic crosses (Griffing 1956) where g_i is the general effect of the ith variety and d_{ij} the interaction of the ith and jth. The model is easily generalised to arbitrary sizes of mixtures, so that, including only the first two out of the m_1 possible orders of interaction.

$$y_{ij\ldots m} = \mu + \sum_i g_i + \sum_i \sum_{j>i} d_{ij} + \sum_i \sum_{j>i} \sum_{k>j} t_{ijk} \qquad (2)$$

with summation over m components and where t_{ijk} is the interaction of varieties i, j and k. As before, error terms must be added to describe actual observed yields. The model parameters are constrained so that

$$\sum_i g_i = \sum_{i\neq j} d_{ij} = \sum_{j\neq i} d_{ij} = \sum_{i\neq j,k} t_{ijk} = \sum_{j\neq i,k} t_{ijk} = \sum_{k\neq i,j} t_{ijk} = 0$$

with the sequence of subscripts for any d or t term being arbitrary, and summation is over the reference population of size n. The parameters are defined so as to have zero means and covariances, and variances σ_g^2, σ_d^2, and σ_t^2.

The parameters in the models for mixture components and totals are related so that:

$$\begin{aligned} g_i &= v_i + m_1\,a_i \\ d_{ij} &= (v\,a)_{ij} + (v\,a)_{ji} + m_2 (a\,a)_{ij} \\ t_{ijk} &= (v\,a\,a)_{ijk} + (v\,a\,a)_{jik} + (v\,a\,a)_{kij}\,. \end{aligned} \qquad (3)$$

The term $(\mu + g_i)$ is the average of all possible mixtures of size m with one common constituent, defined as the general mixture ability (g.m.a.) of the ith variety or genotye. This differs from the definition given by Federer (1979) but is analogous with the genetic quantities general combining ability (g.c.a.) (Griffing 1956) and general varietal ability (Wright 1974).

2.2 Analyses of Variance

The most comprehensive set of data for the fitting of either of models (1) or (2) and the testing of the significance of the various effects will include all possible mixtures of a given size among a set of n varieties or genotypes. If these are themselves a sample from a larger population about which information is required, then the observed mean squares can be used to derive estimates of the population variances

$$\sigma^2_{g(m)} = E(g_{(m)i})^2, \quad \sigma^2_{v(m)} = E(v_{(m)i})^2, \quad \text{etc.}$$

Although the analysis of mixtures of size m will allow the detection of interactions of up to m components, the presence (or absence) of a kth order interaction (say) in mixtures of size m cannot be taken to necessarily imply the presence of a kth order interaction in mixtures of a different size because no correspondence between parameters defined for different sizes of mixtures has been established.

The form of the analysis to be applied will depend both on the size of mixture grown and on whether the components are separately measured. The growth and analysis of a 'diallel' set of $n n_1/2$ binary combinations is a well established technique, and the analysis of mixture totals according to model (2) can be carried out by the method of Griffing (1956) for diallel sets of crosses, according to McGilchrist (1965), Chalbi (1967) and Gallais (1970).

As in the case of diallel analysis, there is an obvious analogy between the analysis of all $n n_1 n_2/6$ tertiary ($m = 3$) mixtures among n varieties or their $n n_1 n_2/2$ components and the 'triallel' analysis of three-way crosses given by Rawlings and Cockerham (1962a). Application of the full triallel analysis to data from tertiary mixture components gives orthogonal sums of squares due to

(a) $g_i = v_i + 2a_i$
(b) $d_{ij} = (va)_{ij} + (va)_{ji} + (aa)_{ij}$
(c) $t_{ijk} = (vaa)_{ijk} + (vaa)_{jik} + (vaa)_{kij}$
(d) $h_i = v_i - 2a_i$
(e) $(va)_{ij} + (va)_{ji} - 2(aa)_{ij}$
(f) $(va)_{ij} - (va)_{ji}$
(g) heterogeneity among $(vaa)_{ijk}$, $(vaa)_{jik}$, and $(vaa)_{kij}$.

Thus, main effects are tested by items (a) and (d), first order interactions by (b), (e) and (f), and second order interactions by (c) and (g). The problem of correlated yields of components taken from the same plot can be most easily dealt with by the computation and application of separate replicate interactions for each item.

A simple modification of this analysis would allow the analysis of mixture totals to give sums of squares due to items (a), (b) and (c). The $n n_1 n_5/6$ degrees of freedom for item (c) means that at least 6 varieties must be included to allow second order interactions to be detected.

Following the detection of any particular source of variation, its population variance can be estimated from the mean squares following the usual procedure of equating them to their expectation. In principle, analyses for sets of larger mixtures could be devised, and for quaternary mixtures the 'quadriallel' analysis of Rawlings and Cockerham (1962b) could probably be adapted. Some of the principles and constraints involved when analysing sets of mixtures of arbitrary size have been discussed by Federer (1979), although he used a somewhat different model from those examined here.

3 Models of Competition and Their Properties

The analyses and predictions described in the previous section are based on purely statistical models which deal with the performance of any mixture in terms of the statistical effects and interactions of its components without any attempt to translate or interpret these at the level of competition among plants belonging to the same or different components. A simple competition model will now be described which can be related to the foregoing statistical models and which allows the effects and statistics defined for various sizes of mixtures to be integrated into a common framework which can lead to useful general predictions.

3.1 Competition Model

In a binary mixture of equal proportions of components A and B, half of the competitive influences experienced by the plants of one component are expected to derive from A and half from B. Even if this is not true for any individual, it will be true on average for all the plants in an intimate mixture. If these competitive influences are independent from plant to plant, that is, there are no pairwise or higher order interactions of plants with respect to the competitive influence they jointly exert on others, then a model including only these simple effects will provide an adequate description of all competitive phenomena occurring in mixtures involving any number of components.

Thus, if $x_{i/j}$ is the yield of component i in binary association with component j (i.e. a half-plot yield) then

$$x_{i/j} = 1/4\,(c_{i/i} + c_{i/j})$$

where $c_{i/j}$ is the whole plot yield of component i in purely intercomponent competition (i.e. if each i plant could be surrounded totally by j plants). The whole-plot mixture yield is therefore

$$y_{i/j} = x_{i/j} + x_{j/i} = 1/4\,(c_{i/i} + c_{i/j} + c_{j/i} + c_{j/j})\,.$$

This is essentially the model used by Hill (1974) and embodies the same assumptions as that of Schutz et al. (1968). It is easily expanded to mixtures of any size, so that

$$x_{i/j\ldots m} = \sum_{i}^{m} c_{i/j/m^2}, \quad \text{and} \quad y_{i/j\ldots m} = \sum_{i}^{m} \sum_{i}^{m} c_{i/j/m^2}\,. \tag{3}$$

The simplicity of this model immediately leads to some useful properties. Looking at the expectation of a component in terms of first order effects (3), one is an intra-component effect while the remaining m_1 are inter-component. Thus the average yield of all mixtures of a given size from a population is a linear function of the reciprocal of the number of components, the rate of change of yield depending on the difference between the average within and between component effects. This suggests that when the first order model is appropriate, there is a basis for linear prediction of mixtures of one size from the yields of those of other sizes; but the presence of second or higher order effects may introduce errors.

3.2 The Relationship Between the Competition and Statistical Models

The equivalence between the effects defined for the first order competition model and those for either of the statistical models (1) and (2) can be established as follows. If $c_{.}$ is the mean of the intracomponent effects $c_{i/i}$ over the whole of the population, $c_{i/.}$ and $c_{./i}$ the mean direct and associate inter-component effects for the ith genotype, and $c_{./.}$ the grand mean of all inter-component effects, and putting $c_{ij} = c_{i/j} + c_{j/i}$ and $c_i = c_{i/.} + c_{./i}$, then

$$\begin{aligned}
u_{(m)} &= (c_{.} + m_1 c_{./.})/m^2 \\
v_{(m)i} &= ((c_{i/i} - c_{.}) + m_1 (c_{i/.} - c_{./.}))/m^2 \\
a_{(m)i} &= (c_{./i} - c_{./.})/m^2 \\
(va)_{(m)ij} &= (c_{i/j} - c_{i/.} - c_{./j} + c_{./.})/m^2 \\
(aa)_{(m)ij} &= (vaa)\,(m)_{ij} = 0, \quad \text{and} \\
\mu_{(m)} &= (c_{.} + m_1 c_{./.})/m \\
g_{(m)i} &= ((c_{i/i} - c_{.}) + m_1 (c_i - 2c_{i/i}))/m^2 \\
d_{(m)ij} &= (c_{ij} - c_i - c_j + 2c_{./.})/m^2 \\
t_{(m)ijk} &= 0\,. \qquad (4)
\end{aligned}$$

These relations hold for any size of mixture for any population with respect to which the statistical and competition effects are defined. Thus the first-order competition effects contribute only to main effects and first-order statistical interactions in models (1) and (2), so that the analysis of variance of a set of mixtures with three or more components will provide a test for the adequacy of the competition model. It is also clear from (4) that when statistical analysis reveals only main effects (g, v or a) then this means that the inter-component $c_{i/j}$ terms show no deviation from their average $c_{i/.} - c_{./j} + c_{./.}$.

3.3 Scaling Tests

The analysis of variance provides a test for the existence of second and higher orders of competition from relatively large structured arrangements of mixtures of a particular size. An alternative approach is the application of scaling tests to mixtures of different sizes made up from the same components. The simplest such test uses tertiary and smaller combinations so that

$$A = 9x_{i/jk} - 4(x_{i/j} + x_{i/k}) + y_i\,,$$

and when the components cannot be separately measured:

$$B = 9y_{ijk} - 4(y_{ij} + y_{ik} + y_{jk}) + y_i + y_j + y_k\,.$$

Similar tests using larger mixtures could be derived. These tests are distinct from those used by Hill and Shimamoto (1973) and have a different purpose. The significance of the departure of the compound from zero can be tested by comparison with a standard error derived from the variances of the monocultures and mixtures of each type around their means.

A disadvantage of this method is that only one combination of components and hence only one deviation is tested at a time, and that, unlike the analyses of variance, it gives little indication of the overall importance of deviations from the model in a population of mixtures.

3.4 Predictions of Mixture Yields

It has been shown that, in the absence of second-order competition effects, there is a linear relationship between the mean value of a mixture and the reciprocal of the number of components it contains. The larger the mixture, the higher the proportion of inter-component competition occurring. Thus, simple formulae can be developed which allow the prediction of the value of a mixture from measurements made on mixtures of two different sizes (usually smaller) but involving the same components. Essentially, such a prediction formula is the scaling test cast in a different form. The general formula is

$$y_m = (p(m-q)\,\bar{y}_p - q(m-p)\,\bar{y}_q)/m(p-q) \qquad (5)$$

where $m > p > q$, and $\bar{y}_p$ and $\bar{y}_q$ are the means of all possible mixtures of size p and q which can be made from the m components contributing to y_m.

The same principle can be used to predict the performance of a single component of any mixture:

$$x_m = (p^2(m-q)\,\bar{x}_p - q^2(m-p)\,\bar{x}_q)/m^2(p-q)\,.$$

This relationship allows some general predictions about the expected performance of constituents of different types; a weak competitor which, on average, contributes less to binary mixture yields than to its own monoculture will be even weaker in larger mixtures, the reverse trend applying to a strong competitor.

The above formulae can be used to generate a whole hierarchy of predictions when a diallel set of binary mixtures and monocultures is grown. This is most easily done by making direct estimates of the $c_{i/j}$ effects, using the relation

$$c_{i/j} = 4x_{i/j} - y_i$$

where the components are separately measured, or

$$c_{ij} = (c_{i/j} + c_{j/i}) = 4y_{ij} - (y_i + y_j)$$

where they are not. The expected mean of any mixture of any size is then found as the mean of all m^2 c effects contributing to it.

The linear relationship between mean and the reciprocal of mixture size extends to the statistical effects themselves, as is apparent in (5). Thus the average effects with respect to mixtures of one size can be predicted from those of another as

$$g(m)_i = (p^2(m-q)\,\bar{g}(p)_i - q^2(m-p)\,\bar{g}(q)_i)/m^2(p-q).$$

Similar expressions could be developed for higher order effects.

4 Variances

4.1 *The Statistical Models*

The expected variances of the yield totals of mixtures of size m made up by random or systematic association of components from a large population, ignoring contributions from error, can be derived directly from (2) as

$$\sigma_y^2 = m\,\sigma_g^2 + \tfrac{1}{2}\,m m_1\,\sigma_d^2 + 1/6\,m m_1 m_2\,\sigma_t^2 + \ldots$$

and so on up to the mth order. A subscript (m) to these statistics is implied throughout, as it is to the following formulae. Using model (1) and noting the relations (3), the mixture variance can be further expanded, so that, including interactions up to the second order

$$\begin{aligned}\sigma_y^2 = {} & m\,\sigma_v^2 + 2\,m m_1\,\sigma_{v.a} + m m_1^2\,\sigma_a^2 + m m_1\,\sigma_{va}^2\\ & + \tfrac{1}{2}\,m m_1 m_2^2\,\sigma_{aa}^2 + 2\,m m_1 m_2\,\sigma_{aa.va}\\ & + \tfrac{1}{2}\,m m_1 m_2\,\sigma_{vaa}^2 .\end{aligned}$$

This form illustrates the contributions of the covariances of v and a ($\sigma_{v.a}$) and of va and aa ($\sigma_{va.aa}$), due to the correlated distribution of these effects in mixture totals. As expected, aa and va terms only contribute when m exceeds 2.

The overall variance of all mixture components, from (1), is found to be

$$\sigma_x^2 = \sigma_v^2 + m_1\,\sigma_a^2 + m_1\,\sigma_{va}^2 + \tfrac{1}{2}\,m_1 m_2\,\sigma_{aa}^2 + \tfrac{1}{2}\,m_1 m_2\,\sigma_{vaa}^2 ,$$

and this is free from all covariances. The average variance of components within mixtures, that is around their respective mixture means, again to the second order, can now be derived from the above results as

$$\begin{aligned}\sigma_{x'}^2 &= \sigma_x^2 - \sigma_y^2/m^2\\ &= m_{1/m}(\sigma_v^2 + \sigma_a^2 - 2\,\sigma_{v.a} + m_1\,\sigma_{va}^2 + m_2\,\sigma_{aa}^2\\ &\qquad - 2\,m_2\,\sigma_{va.aa} + \tfrac{1}{2}\,m_1 m_2\,\sigma_{vaa}^2) ,\end{aligned}$$

where x′ is the within mixture deviation of a component yield. This variance is affected by the covariances $\sigma_{v.a.}$ and $\sigma_{va.aa}$, but in the opposite direction from the variance of mixture totals. If, as expected, the direct and associate (v and a) effects of a population of genotypes or varieties are negatively correlated, then their covariance will reduce the variance among mixtures and increase that within them.

This formulation of the variances of mixture totals and components can be used to derive the expectations of the mean squares estimable from the analysis of a balanced set of mixtures. However, although of value for descriptive purposes, these results have little predictive values for mixtures of different sizes because the model parameters bear an unknown relationship.

4.2 *Competition Model*

As in the case of mixture and component mean values, the competition model, where applicable, has useful predictive properties across mixtures of different sizes. Writing var $c_{i/i}$, var c_i, var $c_{i/.}$, and var $c_{./i}$ for the population variances of the various effects already defined around their means, cov $c_{i/i}\,c_i$, cov $c_{i/i}\,c_{i/.}$, cov $c_{i/i}\,c_{./i}$, and cov $c_{i/.}\,c_{./i}$ as their covariances, and var $c_{i/j}$ as the residual variance among the $c_{i/j}$ terms, then, using (4)

$$\begin{aligned}\sigma_{g(m)}^2 &= 1/m^4(\text{var}\,c_{i/i} + 2\,m_1\,\text{cov}\,c_{i/i}\,c_i + m_1^2\,\text{var}\,c_i)\\ \sigma_{d(m)}^2 &= 4/m^4(\text{var}\,c_{i/j})\\ \sigma_{v(m)}^2 &= 1/m^4(\text{var}\,c_{i/i} + 2\,m_1\,\text{cov}\,c_{i/i}\,c_{i/.} + \text{var}\,c_{i/.})\\ \sigma_{a(m)}^2 &= 1/m^4(\text{var}\,c_{./i})\\ \sigma_{v(m)a(m)}^2 &= 1/m^4(\text{cov}\,c_{i/i}\,c_{./i} + m_1\,\text{cov}\,c_{i/.}\,c_{./i})\\ \sigma_{va(m)}^2 &= 1/m^4(\text{var}\,c_{i/j}), \text{ other statistics being zero.}\end{aligned}$$

Substituting these relations into the foregoing statistical formulae,

$$\begin{aligned}\sigma_{y(m)}^2 = {} & 1/m^3(\text{var}\,c_{i/i} + 2\,m_1\,\text{cov}\,c_{i/i}\,c_i + m_1^2\,\text{var}\,c_i\\ & + m_1\,\text{var}\,c_{i/j}) ,\end{aligned}$$

$$\begin{aligned}\sigma_{x(m)}^2 = {} & 1/m^4(\text{var}\,c_{i/i} + 2\,m_1\,\text{cov}\,c_{i/i}\,c_{i/.} + m_1^2\,\text{var}\,c_{i/.}\\ & + m_1\,\text{var}\,c_{./i} + m_1\,\text{var}\,c_{i/j}) ,\end{aligned}$$

and

$$\begin{aligned}\sigma_{x'(m)}^2 &= m_1/m^5(\text{var}\,c_{i/i} + 2\,m_1\,\text{cov}\,c_{i/i}\,c_{i/.}\\ &\qquad - 2\,\text{cov}\,c_{i/i}\,c_{./i} - 2\,m_1\,\text{cov}\,c_{i/.}\,c_{./i} + m_1^2\,\text{var}\,c_{i/.}\\ &\qquad + \text{var}\,c_{./i} + m_1\,\text{var}\,c_{i/j})\\ &= m_1/m^5(\text{var}\,(c_{i/i} + m_1\,c_{i/.} - c_{./i}) + m_1\,\text{var}\,c_{i/j}) .\end{aligned}$$

Unlike those derived from the statistical model, these expressions are completely explicit with respect to mixture size (m), as terms like var $c_{i/i}$ are constants. All variances are seen to decrease with increasing m, but at rates dependent on the properties of the competition effects. The contribution of main effects to the variance within mixtures is a function simply of the variance of (v − a) which leads to the condensed form for the competition model given above.

5 Discussion

The statistical effects and interactions in terms of which the means and variances of mixtures of components have been expressed are analogous with those used in the genetic theory of synthetic varieties (Gallais and Wright 1980), and like these are distinct for each size of mixture. The first-order competition model, on the other hand, by separating mixture yields into portions arising under intra- and inter-component competition, fills the same underlying causative role as that occupied in the context of synthetics by a Mendelian model of inheritance which is restricted to non-interacting genes. The scaling test is a familiar genetic device for the detection of epistasis (Mather and Jinks 1972), but is used here in conjunction with analysis of variance to detect second and higher order competitive interactions. When these are shown to be absent, then the means and variances of mixture components can be related to mixture size and the distinct models unified in a common theory.

With first-order competition associated with statistical models showing only main effects or main effects and two component interactions, all means and effects are linearly related to the reciprocal of mixture size (1/m), so that any average advantage of mixtures over monocultures will increase with mixture size. It should be noted that the presence or absence of first-order statistical interactions does not necessarily relate to the presence or absence of mixture advantage. Sampling theory would suggest that the variance among large mixtures should be less than that among smaller mixtures or monocultures, and if the components behaved independently in mixtures, then the variance would be a function of 1/m. Even with first order competition however, the relationship can vary between extremes of 1/m and $1/m^3$, a fact which could explain the five-fold difference in variances among monocultures and binary mixtures of oats reported by Shorter and Frey (1979). Whatever the exact relationship, because the mean of mixtures increases with m while their variance decreases, it is difficult to predict the size of the single best mixture out of all those possible.

Covariances among mixtures of different sizes can be formulated in the same way as the variances given here, and with first-order competition can also be expressed in terms of mixture size. Some predictions of the relative efficiences of different types of component selection formulated in terms of these covariances and variances will be given in a subsequent paper.

Literature

Browning, J.A.; Frey, K.J. (1969): Multiline cultivars as a means of disease control. Annu. Rev. Phytopathol. **7**, 355–382

Chalbi, N. (1967): Biométrie et analyse quantitative de la compétition entre génotypes chez la luzerne. Ann. Amelior. Plant. **17**, 119–158

Federer, W.T. (1979): Statistical designs and response models for mixtures of cultivars. Agron. J. **71**, 701–706

Gallais, A. (1970): Modèle pour l'analyse des relations d'associations binaire. Biom. Praxim. **XI**, 51–80

Gallais, A.; Wright, A.J. (1980): A general approach to the concept of varietal ability for synthetic varieties. Theor. Appl. Genet. **57**, 81–87

Griffing, B. (1956): Concept of general and specific combining ability in relation to diallel crossing systems. Aust. J. Biol. Sci. **9**, 463–471

Hill, J. (1974): Methods of analysing competition with special reference to herbage plants. III. Monoculture v. binary mixtures. J. Agric. Sci. **83**, 57–65

Hill, J.; Shimamoto, Y. (1973): Methods of analysing competition with special reference to herbage plants. I. Establishment. J. Agric. Sci. **81**, 77–89

Hill, R.R. (1966): Designs to estimate effects of clone substitution in alfalfa synthetics. Crop Sci. **6**, 471–473

Mather, K.; Jinks, J.L. (1972): In: Biometrical genetics (2nd ed.). London: Chapman and Hall

McGilchrist, C.A. (1965): Analysis of competition experiments. Biometrics **21**, 974–985

Rawlings, J.O.; Cockerham, C.C. (1962a): Triallel analysis. Crop Sci. **2**, 228–231

Rawlings, J.O.; Cockerham, C.C. (1962b): Analysis of double cross hybrid populations. Biometrics **24**, 963–978

Schutz, W.M.; Brim, C.A.; Usanis, S.A. (1968): Inter-genotypic competition in plant populations. I. Feed-back systems with stable equilibria in populations by autogamous homozygous lines. Crop Sci. **8**, 61–66

Shorter, R.; Frey, K.J. (1979): Relative yields of mixtures and monocultures of oat genotypes. Crop Sci. **19**, 548–553

Trenbath, B.R. (1974): Biomass productivity of mixtures. Adv. Agron. **26**, 177–210

Williams, E.J. (1962): The analysis of competition experiments. Austr. J. Biol. Sci. **15**, 509–525

Wolfe, M.S.; Barrett, J.A. (1981): The agricultural value of variety mixtures. In: Proc. 4th Barley Genetics Symposium

Wright, A.J. (1974): A genetic theory of general varietal ability. Theor. Appl. Genet. **45**, 163–169

Received June 9, 1982
Accepted September 10, 1982
Communicated by R. Riley

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