A Multiple Regression Analysis of Hybrid Vigour in Single Crosses of *Dactylis glomerata* L.

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Summary. Thirty-six crosses of *Dactylis glomerata* together with their parents were assessed for seasonal yield at twelve successive harvests during a 16 month period. The yields varied with the environment provided by the climatic seasons of the year. For some crosses, the hybrid approximated to its mid-parental value at one environment but exceeded both parents in another, showing hybrid vigour.

The twelve yield values for a hybrid and for each of its parents were analysed as a multiple regression in the form:

\[ y_{ij} = a + b_i P_i + b_j P_j \]

where \( y_{ij} \), \( P_i \) and \( P_j \) are the yields of the hybrid and parents at any one harvest, \( b_i \) and \( b_j \) are regression coefficients pertaining to the respective parents and \( a \) is a constant. It was found that such a regression accounted for a great part of the seasonal yield variation of each cross, including the situation of a hybrid approximating to the mid-parental value or exceeding both parents.

The \( b \) value pertaining to an individual parent varied according to the parent with which it was crossed. In the discussion the values of \( b \) and \( a \) were considered in relation to the incidence of hybrid vigour, and the use of a multiple regression is compared with other analyses of quantitative inheritance.

1. Introduction

In the majority of analyses undertaken in quantitative inheritance the estimated variances, covariances and effects are obtained as the means of several hybrid combinations. This is true of parent-offspring regressions, heritability estimates and diallel tests. It is rarely that a single cross, on its own, provides sufficient data for estimation of a quantitative parameter and there is therefore little information on such parameters. An estimate becomes feasible when two parents and their hybrid are grown in several different environments and their yields in these environments are obtained. This approach has been followed in recent studies of genotype-environment interactions (Bucio Alanis and Hill, 1966; Perkins and Jinks, 1968; Breese, 1969). It is the purpose of this paper to present results obtained on single crosses and analyses of each of them in the form of multiple regressions.

The experimental material was the pasture grass *Dactylis glomerata* L. Yield was the herbage harvested in the different seasons of the year and therefore in different environments. Yield was determined by cutting to near ground level and weighing the herbage that had grown since the previous cut. By repetition of this procedure many assessments of two parents and their hybrid were made in the environments experienced during a year.

Within *Dactylis glomerata* two major groups can be distinguished on a basis of differences in seasonal growth rhythm. One group, composed of populations from northern Europe, is, in its natural habitat, summer growing and winter dormant, whereas the other group, of Mediterranean origin is indigenously summer dormant and winter growing. In southern Australia, with its Mediterranean-type climate, both groups will grow with more or less vigour at all seasons of the year provided the summer drought is alleviated by irrigation (Knight, 1966) thus permitting many assessments of yield.

The results to be presented are for parents from both groups, and hybrids within and between the groups when grown under irrigation.

2. Materials and Methods

Nine parents were crossed in all combinations to give, after bulking of reciprocals, 36 single cross \( F_1 \) families. Details of the nine parents are given by Knight (1966) but the only feature relevant to the present study is that seven (designated 1 to 7) of the nine parents were of Mediterranean origin and are predominantly winter growing, while two (designated 8 and 9) were from northern Europe and are predominantly summer growing. The parents were not inbreds; they were single individuals chosen at random from seven wild ecotypes of the Mediterranean group, or from two bred strains of the northern European group. Parents and hybrids were planted in a sward trial with a randomised block layout having four replicates. *Dactylis glomerata* is cross-pollinated so that to obtain many individuals of the parental genotypes it was necessary to vegetatively propagate the parents. In this way 256 offsets were obtained for each parent, providing 64 offsets for each of the four plots. Each plot was a metre square, the individuals offsets being at a 12.5 × 12.5 cm spacing.

To be comparable, the \( F_1 \) hybrids were also vegetatively propagated into the trial, each family being represented by approximately 80 genotypes. The 80 genotypes were propagated to produce the required 256 offsets. The trial was planted between June 26 and 28, 1961. At each
harvest, made with a mower cutting to 3 cm (1½ in) above ground level, the herbage of all offsets in a plot was harvested together and a yield of dry matter obtained. The yields from 12 harvests are to be considered. NPK fertiliser was applied liberally before planting and thereafter at 3 monthly intervals. During the summer months (November-March inclusive) the trial was watered with a precision irrigator.

3. Multiple regression analysis

For each hybrid and its two parents a multiple regression was fitted to 12 sets of values corresponding to 12 harvests. Each set consisted of a hybrid yield, \( y \), and the yield of its parents \( i \) and \( j \), namely \( x_i \) and \( x_j \). The regression was

\[
y_{ij} = a + b_i x_i + b_j x_j
\]

or using deviations

\[
y_{ij} - \bar{y} = b_i (x_i - \bar{x}_i) + b_j (x_j - \bar{x}_j)
\]

where \( \bar{y}, \bar{x}_i \) and \( \bar{x}_j \) are the mean yields of the hybrid and parents over the whole period of the experiment.

Fitting of a multiple regression to the data of a hybrid and its two parents was found invariably to account for a great deal of the variation, but it was evident that this was sometimes due to the correlated behaviour of the two independent variables \( x_i \) and \( x_j \), for although the parents were not related in the genetic sense some of them had similar growth rhythms. The Mediterranean parents for example all had low yields in summer and high yields in winter. This problem was met (G. N. Wilkinson, private comm.) by including in the regression a sum of squares derived from variation in the mid-parent value. Midparental values were taken as a measure of the temporal effect, reflecting seasonal changes; the multiple regression was then evaluated for significance after this effect was removed.

The normal regression equation \( y_{ij} = a + b_i x_i + b_j x_j \) may be expanded to

\[
y_{ij} = a + (b_i + b_j) \frac{\bar{x}_i + \bar{x}_j}{2} + (b_i - b_j) \frac{\bar{x}_i - \bar{x}_j}{2}
\]

The second term on the right hand side of the equation is then the regression on the mid-parent.

The analysis of regression then takes the form given in Table 1, where \( C_{11}, C_{22} \) and \( C_{12} \) are the elements in the matrix of multipliers.

<table>
<thead>
<tr>
<th>Regression analysis to establish a significant difference between the two ( b ) values</th>
<th>D.F.</th>
<th>S.S.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Regression on mid-parent</td>
<td>1</td>
<td>by subtraction</td>
</tr>
<tr>
<td>Difference between ( b_i ) and ( b_j )</td>
<td>1</td>
<td>( (b_i - b_j)^2 )</td>
</tr>
<tr>
<td>Multiple regression</td>
<td>2</td>
<td>( b_i \Sigma x_i y + b_j \Sigma x_j y )</td>
</tr>
</tbody>
</table>

4. Results

It is intended to consider in detail representative analyses and then the statistics for all 36 \( F_1 \) hybrids. The results for parent 5, parent 8, and their \( F_1 \) hybrid are given in Figure 1. Successive yields have been joined to show the contrast in growth rhythms of parents and their hybrid. Parent 5 is of Mediterranean origin and had low summer yields (January, February) and high winter yields (July), whereas parent 8, of North European origin, had a complementary growth rhythm. The hybrid between them showed the growth rhythm of parent 5 but at a higher level of yield; as a consequence it was intermediate between its parents during the summer but exceeded its parents in yield during the winter. When a multiple regression is fitted to these data, the \( b \) values are 0.96 for parent 5 and 0.30 for parent 8. Both these coefficients are significant when the other is accounted for, and further, the coefficients are significantly different from one another. The constant \( a \), calculated from \( a = \bar{y} - b_i \bar{x}_i - b_j \bar{x}_j \), was only 30 kg/ha, a negligible quantity in the context of the present yields, so that the estimation equation is reduced sensibly to \( y = b_i x_i + b_j x_j \) or specifically \( y = 0.96 x_i + 0.30 x_j \). The calculated yield of the hybrid in any one environment (i.e. at any one harvest) was then a weighted derivative of its two parental yields. This calculated yield was a good estimate both when the observed hybrid yield was at the mid-parental value (e.g. March 29) and when hybrid vigour was manifest (July 17). The standard error of the parental and \( F_1 \) values were calculated on a logarithmic scale. At a harvest, two yields were significantly different at the 5% level if one of the yields was more than 1.3 times larger than the other.

A second cross with a similar result is presented in Figure 2 where the \( b \) values were 2.36 for parent 2 and 0.41 for parent 8, and the constant \( a \) was -80 kg/ha. These \( b \) values were significantly different from each other at the 0.1% level, while the constant \( a \) was again not significantly different from zero.

The two crosses considered so far have been the combinations 5 × 8 and 2 × 8. The third possible combination between these parents, namely 2 × 5, is given in Figure 3. Both parents are of Mediterranean origin and had low yields during the summer (January, February). In this cross the estimates of \( b_i \) and \( b_j \) are 0.52 and 0.64. They are not significantly different from each other, and their sum is not significantly greater than unity. There was no suggestion of hybrid vigour, and it is with values like these of \( b \) and \( a \) that the calculated hybrid yields approximate to the midparental yields. A still closer approach to the midparental values (\( b \) values each of 0.5 and a constant \( a \) value of zero) was obtained for the cross 3 × 4 (Figure 4), which had \( b \) values of 0.50 and 0.57 and an \( a \) value of 10 kg/ha.