PREDICTING THE RANGE OF INBRED LINES

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1. THEORY

ALTHOUGH the prediction of the expected response to selection from estimates of environmental and genetical parameters obtained from the base population has attracted considerable theoretical and practical attention, there have been no corresponding developments in predicting the properties of the extreme phenotypes that are expected to emerge since the initial step was taken by Mather (1949). Nevertheless, such predictions would have at least the same practical and theoretical interest. For the simplest case, where the base population is the F_2 of a cross between two pure breeding lines and the genes are independent in their action and in their segregation, *i.e.* no epistasis and no linkage, the theoretical basis of such predictions follows directly from the treatment of continuously varying characters of Mather and Jinks (1971). And, as we shall see, the experimental observations required to make the predictions are relatively undemanding.

Following Mather and Jinks (1971), we can define the means of any pair of pure breeding lines around their joint mean, m , as

$$\bar{P}_1 = m + r_a \Sigma d_i$$

and

$$\bar{P}_2 = m - r_a \Sigma d_i,$$

where r_a is the coefficient of association of genes of like effect, ($r_a = 1$ to 0) d_i is the additive effect of the i th locus and the summation is over the k loci ($i = 1$ to k) at which P_1 and P_2 differ.

The mean of the F_1 obtained on crossing this pair of lines is then

$$\bar{F}_1 = m + \Sigma h_i,$$

where h_i is the dominance effect of the i th locus ($i = 1$ to k) and

$$\Sigma h_i = \bar{F}_1 - \frac{1}{2}(\bar{P}_1 + \bar{P}_2).$$

The means of the highest (P_H) and lowest (P_L) scoring inbred lines that could emerge from this cross following many generations of inbreeding are then

$$\bar{P}_H = m + \Sigma d_i$$

and

$$\bar{P}_L = m - \Sigma d_i, \text{ respectively}$$

The genetical components of variation which can be estimated from observations on the variation within and between families of appropriate segregating generations are

$$D = \Sigma d_i^2$$

$$H = \Sigma h_i^2$$

and

$$F = \Sigma d_i h_i.$$

If h_i/d_i is a constant for all loci, i.e. $h_i = fd_i$ then,

$$\Sigma h_i \sqrt{\frac{D}{H}} = \Sigma f d_i \sqrt{\frac{\Sigma d_i^2}{\Sigma f^2 d_i^2}} = \Sigma d_i$$

from which we can immediately estimate $\bar{P}_H$ and $\bar{P}_L$ as $m \pm \Sigma d_i$.

If $h_i = fd_i$ the ratio $F/\sqrt{D \cdot H}$ equals one providing that all dominant alleles are present in one of the two parents (P_1 or P_2) and all recessive alleles in the other. If we observe a value of one for this ratio it therefore shows that the assumption of a constant dominance ratio over all loci is valid. However, a value of less than 1, or even 0, is compatible with a constant ratio over all loci if the dominant alleles are equally divided between P_1 and P_2 . We can, therefore, estimate the highest and lowest scoring inbred lines by assuming a constant dominance ratio over all loci and we have a method of proving that this assumption holds in some circumstances. This procedure does not require an estimate of k in order to estimate $\bar{P}_H$ and $\bar{P}_L$: it thus avoids this limiting factor in Mather's earlier approach (Mather, 1949).

2. PRACTICE

An experimental design that produces reliable estimates of all the parameters necessary to make these predictions and at the same time provides tests of the underlying assumptions has been described by Kearsey and Jinks (1968) and Jinks and Perkins (1970). In this design the F_2 of a cross between two pure-breeding lines (P_1 and P_2) is back-crossed to these lines and to their F_1 . The resulting families are raised simultaneously with the pure breeding lines, their F_1 , F_2 and backcrosses of the F_1 to P_1 and P_2 (B_1 and B_2 , respectively). An analysis of variance provides tests of significance of the additive, dominance and epistatic components of variation and in the absence of the latter orthogonal estimates of D , H and F . A joint scaling test on the means of the P_1 , P_2 , F_1 , F_2 , B_1 and B_2 families provides a further test for the presence of epistasis and in its absence weighted least squares estimates of m , $r_d \Sigma d_i$ and Σh_i (Mather and Jinks, 1971). A comparison of the variances of F_2 and $F_2 \times F_1$, B_1 and $F_2 \times P_1$ and B_2 and $F_2 \times P_2$ provide independent tests for the presence of linkage and of the linkage phase (Perkins and Jinks, 1970). Thus we have estimates of all relevant parameters and tests of all assumptions.

3. PREDICTION

This design has been carried out once only as a relatively small part of a much larger experiment. The cross was between varieties 1 and 5 of *Nicotiana rustica* (Mather and Vines, 1952). All the necessary families were grown in 1965 and final height was recorded in inches. The complete experiment, of which this was a part, has been described and analysed in a number of papers (Jinks and Perkins, 1969, 1970; Perkins and Jinks, 1970). Neither the scaling test nor the triple-test-cross gave any evidence of epistasis, although analyses of more extensive bodies of data covering many more generations show that epistasis occurs at a low level in some environ-

ments (Jinks and Perkins, 1969). There was, however, evidence of repulsion linkage of relatively small effect but nevertheless significant because of the large number of degrees of freedom available (Perkins and Jinks, 1970, table 8). While, therefore, the initial assumption of independence of the genes is not fully met the failure is likely to have only marginal consequences. The estimates of the relevant parameters are

$$\begin{aligned}\Sigma h_i &= 6.11 \\ \bar{D} &= 30.69 \\ \bar{H} &= 4.08 \\ \bar{F} &= 0.41 .\end{aligned}$$

The estimate of F is not significantly different from zero and the ratio $F/\sqrt{D \cdot H}$ is clearly less than one. Hence we have no proof that h_i/d_i is constant over all loci, but equally we have no evidence to the contrary. We shall proceed therefore on the assumption that the dominance ratio is constant. The prediction is then:

$$\Sigma d_i = 6.11 \sqrt{\frac{30.69}{4.08}} = 16.76.$$

As part of the same experiment, a second triple-test-cross was carried out on the two first back-crosses, B_1 and B_2 . When pooled, the two back-crosses should yield the same estimates of the relevant parameters as the F_2 . Using the estimates from the backcross population we obtain

$$\Sigma d_i = 16.71.$$

Relaxing the condition that the estimates of all parameters come from the same experiment, considerably more data becomes available. Thus we have a mean estimate of Σh_i over 16 independent experiments (Bucio Alanis, Perkins and Jinks, 1969) and estimates of D , H and F based on the mean estimates from seven complete or incomplete triple-test-crosses (Jinks and Perkins, 1970). These estimates are:

$$\begin{aligned}\Sigma h_i &= 5.82 \\ \bar{D} &= 39.98 \\ \bar{H} &= 11.48 \\ \bar{F} &= -2.08\end{aligned}$$

from which we estimate

$$\Sigma d_i = 10.86$$

These three predictions are sufficiently close to one another for us to place some confidence in them. On the other hand, the errors of these predictions whether based on their theoretical errors or observed errors of the estimates of the parameters are between a half and a third of the magnitude of the values of Σd_i .

The practical value of the predictions can, however, be tested directly in the case of the 1×5 cross. Perkins and Jinks (unpublished) produced 82 F_8 families by repeated selfing from an initial random sample of 100 F_2 plants of the 1965 experiment. The means of the two families that were the extremes for final height were found by our colleague R. J. Brumpton to be 61.49 ± 1.64 and 34.53 ± 0.48 inches respectively when grown in 1970.

These give an estimate of Σd_i equal to 13.48 ± 0.86 , which falls within the range of the predicted values. We can, however, make a further prediction based on the estimate of Σh_i observed in the same 1970 experiment. With the average values of D and H over seven experiments this gives a prediction of

$$\Sigma d_i = 6.79 \sqrt{\frac{39.98}{11.48}} = 12.68,$$

which is a good fit with the observed value. Thus the predictions appear to be somewhat better than their sampling errors would suggest.

We can now use corresponding observed values of $r_a \Sigma d_i$, D and predicted values of Σd_i to estimate r_a and k . The three sets of values available give $r_a = 0.31, 0.26$ and 0.21 and $k = 9.15, 2.95$ and 4.50 respectively. The same estimates made from the analysis of final height in F_8 families are $r_a = 0.22$ and $k = 4$ (Eaves and Brumpton, 1972), which are in a sense realised values of the parameters. It is worth noting that the estimates of r_a , k , Σd_i and Σh_i leave no doubt that the heterosis observed in the F_1 of this cross (Bucio Alanis, Perkins and Jinks, 1969) is due to a number of partially dominant increasing alleles dispersed between the two parents. In these circumstances we expect to be able to extract pure-breeding lines from the cross that exceed the better parent and the F_1 and we have not only done so but we have correctly predicted the mean of the best inbred line six generations in advance.

4. FUTURE DEVELOPMENTS

In spite of the fact that two of the assumptions underlying the predictions, namely, no epistasis and no linkage, are not fully met in the 1×5 cross predictions of the phenotypes of the extremes among the inbred lines appear to be reasonable when judged against those obtained. Only further elaboration of the theory and further experimental tests of the predictions can tell us whether or not the practical value of the predictions is as good as the 1×5 cross would suggest.

The means and variances of families derived from the cross 1×5 contain significant contributions attributable to interactions between genotypes and seasons (Bucio Alanis, Perkins and Jinks, 1969; Perkins and Jinks, 1970). Estimates of the parameters and hence of the predictions based upon them will vary with the season. And we expect and indeed observe better agreement between predictions and between predictions and observations when they are based on information from the same experiment than when they come from different experiments. On the other hand, the earlier in a breeding programme that a reliable prediction can be made, the greater is its prospective practical value. Any general treatment must, therefore, allow for the contribution of genotype-environmental interactions to the parameters used in the prediction. In general we would expect their contributions to be more critical for the estimate of Σh_i than for the ratio of D/H . Further developments of the theory must also remove the assumptions of no linkage and no epistasis if the method is to be more generally applicable, although with inbreeding by selfing the opportunities for recombination after the F_2 generation are so restricted that the components of variation estimated from triple-test-crosses on the F_2 are likely to be biased in the

right direction for predicting the range of inbred lines in later generations in the presence of linkage.

5. SUMMARY

1. A method is described for predicting the range of phenotypes expected among the true-breeding lines that can be obtained by inbreeding from the F_2 of a cross between a pair of inbred lines assuming independence of the genes in action and in segregation, and a constant dominance ratio over all loci.

2. A breeding programme is described which provides estimates of all the parameters required to make the predictions and to test all the underlying assumptions except the constancy of the dominance ratio over all loci for which a test is available only in restricted circumstances.

3. This prediction for final height in the cross between varieties 1 and 5 of *Nicotiana rustica* shows a good agreement with the results of inbreeding by selfing a random sample of 100 F_2 individuals of this cross in spite of the failure of some of the assumptions.

4. The necessary elaborations of the method to make it more generally applicable are outlined.

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