

PREDICTING THE PROPERTIES OF SECOND CYCLE HYBRIDS PRODUCED BY INTERCROSSING RANDOM SAMPLES OF RECOMBINANT INBRED LINES

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SUMMARY

Distributive properties of the second cycle hybrids that are produced by intercrossing the recombinant inbreds extractable from the F_2 of a cross between two pure breeding lines can be predicted from the early generations of the original cross. Hence the frequency of such hybrids that will outperform the extreme recombinant inbreds or the original F_1 can be predicted. Basic generations and triple test cross families provide the most reliable estimates of the predictors and therefore should be used whenever possible although, in the presence of linkage, randomly mated F_2 's may give improved predictions. Simpler experiments consisting of the parental varieties and their F_1 and F_2 generations, however, provide all the information that is likely to be necessary for most practical purposes.

The predictive power of the new approach is demonstrated on material extracted from the cross of varieties 1 and 5 of *Nicotiana rustica*. The predictors were estimated from the means and variances of V_1 , V_5 , F_1 and F_2 raised in six environments between 1973 and 1983. The predicted frequencies of second cycle F_1 's which outperform the extreme recombinant inbred lines derived from this cross are compared with those observed among 190 second cycle hybrids in a diallel between 20 recombinant inbreds derived from the same cross.

1. INTRODUCTION

The breeding value of a cross in respect of its production of superior recombinant inbred lines by pedigree inbreeding, single seed descent and dihaploidy can be readily and reliably predicted (Jinks and Pooni, 1976, 1980; Pooni and Jinks, 1978, 1981) using the basic generations and triple test cross families (Mather and Jinks, 1982; Kearsey and Jinks, 1968; Pooni and Jinks, 1979). The best of these recombinant inbreds may themselves be the appropriate end product of the breeding programme. However, second cycle F_1 hybrids obtained by intercrossing the recombinant inbreds may be superior end products and this may indicate the potential for further improvement of the inbreds by a second cycle of crossing and inbreeding. In this paper we shall, therefore, predict the properties of the second cycle hybrids produced by intercrossing the recombinant inbred lines derivable from the F_2 of a cross. We shall make these predictions using genetical information that has usually already been obtained for other purposes and illustrate the theory by analysing data recorded on the basic generations of the cross between varieties 1 and 5 of *Nicotiana rustica*. We shall use the predictions to assess the breeding value of a cross for producing second cycle F_1 hybrids which are superior to the best of the first cycle recombinant inbred lines.

2. GENOTYPES OF INTEREST

Diallel mating of all possible recombinant inbred lines which can be extracted from a cross between two pure breeding varieties by the method of pedigree inbreeding, single seed descent and dihaploidy produces a diallel table of $2^K \times 2^K$ genotypes. While the overall dimensions of this table depend upon K , the number of gene loci for which the inbreds differ for a particular trait, the 2^K genotypes entered on its leading diagonal are the recombinant inbreds which were used to produce this diallel. We have described the theory and practice of predicting the properties of these inbreds on numerous occasions (Jinks and Pooni, 1976, 1981; Pooni and Jinks, 1978, 1981; Pooni, Jinks and Cornish, 1977). Similarly, each of the 2^K genotypes on the off diagonal is heterozygous for all of the K -loci and therefore identical with the original F_1 , whose properties are also known. The remaining $2^{(K-1)}(2^K - 2)$ genotypes, which are diametrically duplicated in the upper and lower halves of the table, are the F_1 's whose properties are hitherto unknown. These second cycle hybrids are of special interest because amongst them there may be unique genotypes which are capable of outperforming the best of the recombinant inbred lines or the original F_1 .

3. PREDICTIONS FOR THE SIMPLE CASE

To predict the properties of the second cycle hybrids we need to define their distribution in terms of genetical parameters which can be estimated from the early generations of a breeding programme. The joint distribution of the $2^{K-1}(2^K - 2)$ recombinant hybrids described in section 2 and the 2^K original F_1 's which cannot be separated from the former in practice, has the expected mean

$$m + \frac{2^{K-1}}{2^K - 1} [h]$$

and variance

$$\frac{(2^{K-1} - 1)}{(2^K - 1)} D + \frac{2^{K-1}(2^{K-1} - 1)}{(2^K - 1)^2} H - \frac{2^{K-1}}{(2^K - 1)^2} \sum_{j < k}^K h_j h_k + E$$

when an additive, dominance and additive environmental model is sufficient to explain the total variability (for definitions of the genetic parameters see Mather and Jinks, 1971, 1982). These expectations though dependent on " K " in a complex manner approximate very closely with $m + \frac{1}{2}[h]$ and $\frac{1}{2}D + \frac{1}{4}H + E$, the mean and variance of the F_2 generation of the original cross from which the recombinant inbreds were extracted, especially when K is large ($K \geq 6$). Thus even when K takes a small value (say $K = 3$) the expectations of these statistics differ from $m + \frac{1}{2}[h]$ and $\frac{1}{2}D + \frac{1}{4}H + E$ by only $\frac{1}{14}[h]$ and $-\frac{1}{14}D - \frac{1}{196}H - \frac{4}{49} \sum_{j < k}^K h_j h_k$, respectively. Statistics $m + \frac{1}{2}[h]$ and $\frac{1}{2}D + \frac{1}{4}H + E$ will therefore provide estimates of the expected mean and variance of the recombinant hybrids that are satisfactory for all practical purposes.

Estimates of $m + \frac{1}{2}[h]$ and $\frac{1}{2}D + \frac{1}{4}H + E$ can be readily obtained from a number of breeding programmes. For example, the standard P_1 , P_2 , F_1 , F_2 , B_1 and B_2 families provide the most rapid and efficient estimates of both statistics (Mather and Vines, 1952) and a triple test cross in which the F_2

is backcrossed to P_1 , P_2 and F_1 provides the most reliable estimates of $\frac{1}{2}D$ and $\frac{1}{4}H$ (Kearsey and Jinks, 1968; Pooni and Jinks, 1976). Since these are the commonest designs currently used by geneticists and practical breeders, all the information required to predict the second cycle, recombinant F_1 hybrids will already be widely available. If, however, it is not, a small experiment including the original parental varieties and their F_1 and F_2 generations can be used to estimate the genetic and environmental components required for the predictions. From these estimates of the expected means and variances we can predict some useful properties of the recombinant hybrids. For example, we can obtain probabilities of hybrids which will score $>\bar{P}_1$ or $<\bar{P}_2$, the original parental varieties or outperform their \bar{F}_1 if it shows heterosis. But more important, we can predict the probability of obtaining hybrids which outperform the extreme recombinant inbreds ($>\bar{P}_{\text{largest}}$ and $<\bar{P}_{\text{smallest}}$ referred to as $>\bar{P}_l$ and $<\bar{P}_s$ in the formulae) extracted from the original cross. Following Jinks and Pooni (1976) we obtain these probabilities from the integrated density functions of

$$\int_{\bar{P}_1}^{\infty} f(x) \cdot dx; \int_{-\infty}^{\bar{P}_2} f(x) \cdot dx; \int_{\bar{F}_1}^{\infty} f(x) \cdot dx; \int_{\bar{P}_l}^{\infty} f(x) \cdot dx$$

$$\text{and } \int_{-\infty}^{\bar{P}_s} f(x) \cdot dx$$

respectively; and if the distribution of the recombinant hybrids is approximated with a standard normal distribution with mean "0" and variance "1", then these integrals can be replaced by the one tail normal probability integral corresponding with the abscissa values of

$$\frac{[d] - \frac{1}{2}[h]}{(\frac{1}{2}D + \frac{1}{4}H + E)^{1/2}}; \frac{-[d] - \frac{1}{2}[h]}{(\frac{1}{2}D + \frac{1}{4}H + E)^{1/2}}; \frac{\frac{1}{2}[h]}{(\frac{1}{2}D + \frac{1}{4}H + E)^{1/2}};$$

$$\frac{\sum d - \frac{1}{2}[h]}{(\frac{1}{2}D + \frac{1}{4}H + E)^{1/2}} \text{ and } \frac{-\sum d - \frac{1}{2}[h]}{(\frac{1}{2}D + \frac{1}{4}H + E)^{1/2}}$$

respectively for a situation where the estimates of the individuals parameters are available; or with the abscissa values of

$$\frac{\bar{P}_1 - \bar{F}_2}{(VF_2)^{1/2}}; \frac{\bar{P}_2 - \bar{F}_2}{(VF_2)^{1/2}}; \frac{\bar{F}_1 - \bar{F}_2}{(VF_2)^{1/2}}; \frac{\bar{P}_l - \bar{F}_2}{(VF_2)^{1/2}}; \frac{\bar{P}_s - \bar{F}_2}{(VF_2)^{1/2}}$$

when the mean and variance of the F_2 generation are used as predictors.

These probabilities are valid for the phenotypic distribution of the recombinant hybrids but we can obtain predictions based solely on the repeatable genetic performance of these hybrids by excluding the non-repeatable additive environmental variance, E , from the denominator before taking its square root, that is, by using $(\frac{1}{2}D + \frac{1}{4}H)^{1/2}$ instead of $(\frac{1}{2}D + \frac{1}{4}H + E)^{1/2}$ or $(VF_2 - E)^{1/2}$ in place of $(VF_2)^{1/2}$.

4. COMPLICATIONS

(i) Genotype \times environment interaction

In the presence of genotype \times environment interactions our estimates of the predictors $[d]$, $[h]$, $\frac{1}{2}D$ and $\frac{1}{4}H$ become $[d] + g_a$, $[h] + g_h$, $\frac{1}{2}D + \frac{1}{2}G_D$

and $\frac{1}{4}H + \frac{1}{4}G_H$, respectively where g_d , g_h , G_D and G_H are the environmentally dependent components (Mather and Jinks, 1971, 1982). Estimates of the environmentally dependent components of the mean are readily obtained (Bucio Alanis, Perkins and Jinks, 1969) and estimates of the corresponding components of the variances are provided by the triple test cross (Perkins and Jinks, 1971), and approximations to them by the F_2 variance. These modified predictors, however, will correctly predict the properties of the recombinant F_1 hybrids only if there are no significant genotype \times environment interactions between the environments in which the predictors are estimated and those in which the recombinant hybrids are assessed, that is, the two sets of environments can be regarded as having been drawn from the same population. This can be ascertained by growing the same controls, for example, the original parents and their F_1 , in both sets of environments (see Jinks and Pooni, 1976).

(ii) *Linkage disequilibrium*

Provided that K is large, linkage affects neither the actual nor the predicted mean of the second cycle recombinant hybrids in the absence of non-allelic interaction. It does, however, affect both the actual and predicted variances. Thus if K is large the expected variance of the hybrids for many pairs of linked genes is

$$\frac{1}{2} \sum d_j^2 \begin{pmatrix} +C \\ -R \end{pmatrix} \sum \frac{(1-2p_{jk})}{(1+2p_{jk})} d_j d_k + \frac{1}{4} \sum h_j^2 + \frac{1}{2} \sum \frac{(1-2p_{jk})^2}{(1+2p_{jk})} h_j h_k$$

using the definitions of gene effects of Mather and Jinks (1982).

On the same model the expectation of the predicted variance differ, with the source of the predictors (Mather and Jinks, 1982; Jinks and Pooni, 1981). For example, the genetic variance of the F_2 has the expectation

$$\frac{1}{2} \sum d_j^2 \begin{pmatrix} +C \\ -R \end{pmatrix} \sum (1-2p_{jk}) d_j d_k + \frac{1}{4} \sum h_j^2 + \frac{1}{2} \sum (1-2p_{jk})^2 h_j h_k$$

while the estimate of $\frac{1}{2}D + \frac{1}{4}H$ from the F_2 triple test cross has the expectation

$$\frac{1}{2} \sum d_j^2 \begin{pmatrix} +C \\ -R \end{pmatrix} \sum (1-2p_{jk}) d_j d_k + \frac{1}{4} \sum h_j^2 + \frac{1}{2} \sum (1-2p_{jk}) h_j h_k.$$

Linkage disequilibrium, that is an excess of coupling (C) or repulsion (R) linkages and of reinforcing (h_j and h_k same sign) or opposing (h_j and h_k opposite signs) dominance, rather than linkage per se determines the magnitude of the linkage bias of the actual and predicted variance of the second cycle hybrids. But in all circumstances this bias will be smaller in the actual than in the predicted variance. Our experience in predicting recombinant inbred lines (Jinks and Pooni, 1976, 1982; Pooni and Jinks, 1978; Pooni, Jinks and Cornish, 1977) shows that the differences in the biases are usually so small that they do not lead to significant departures between the actual and predicted variances. Furthermore, these differences can be reduced by using the genetic variance of a randomly mated F_2 as predictor (Jinks and Pooni, 1982).

(iii) *Epistasis*

In the presence of epistasis the expectations of the mean and variance of the second cycle recombinant hybrids become

$$m + \frac{2^{K-1}}{2^K - 1} [h] + \frac{2^{K-2}}{2^K - 1} (l)$$

and

$$\begin{aligned} & \frac{(2^{K-1} - 1)}{(2^K - 1)} D + \frac{2^{K-1}(2^{K-1} - 1)}{(2^K - 1)^2} H - \frac{2^{K-1}}{(2^K - 1)^2} \sum_{j < k}^K h_j h_k + \frac{2^{K-2}}{2^K - 1} (I + 2J) \\ & + \frac{2^{K-2}}{(2^K - 1)} \left(1 - \frac{2^{K-2}}{(2^K - 1)} \right) L + \text{cross products,} \end{aligned}$$

respectively (for definitions of I , J and L , see Jinks, 1983). For many loci these statistics reduce to $m + \frac{1}{2}[h] + \frac{1}{4}[l]$ and $\frac{1}{2}D + \frac{1}{4}H + \frac{1}{4}I + \frac{1}{2}J + \frac{3}{16}L$ + cross products, which are the mean and variance of the F_2 , respectively. Similarly, estimates of m , $\frac{1}{2}[h]$ and $\frac{1}{4}[l]$ obtained from the basic generations by maximum likelihood solutions and of $\frac{1}{2}D$ and $\frac{1}{4}H$ estimated from a triple test cross provide reasonably close approximation to the mean and variance of the second cycle, recombinant hybrids. However, as in the case of recombinant inbreds (Jinks and Pooni, 1976; Jinks, 1983) the major differences associated with the presence of non-allelic interactions are the shifts in the means of the five standard genotypes used in predictions (see section 3). The expectations of these genotypes now become:

$$\begin{aligned} \bar{P}_1 &= m + [d] + [i] \\ \bar{P}_2 &= m - [d] + [i] \\ \bar{F}_1 &= m + [h] + [l] \\ \bar{P}_i &= m + \sum d + \sum i \end{aligned}$$

and

$$\bar{P}_s = m - \sum d + \sum i,$$

respectively.

The consequences of these modifications can be readily seen. For example, if $[i]$, $\sum i$ and $[l]$ take positive values the probabilities of the recombinant hybrids scoring $> \bar{P}_1$, $> \bar{P}_i$ and $> \bar{F}_1$, are reduced and the corresponding probabilities for $< \bar{P}_2$, $< \bar{P}_s$ and $< \bar{F}_1$ increased. The reverse of course is true when these components take negative values. Similarly, the probabilities associated with $> \bar{P}_1$, $> \bar{P}_i$ and $> \bar{F}_1$, are increased when $[h]$ and $[l]$ take opposing signs and reduced when $[l]$ reinforces $[h]$. To accommodate these changes, the definitions of the abscissa values associated with $> \bar{P}_1$, $< \bar{P}_2$, $> \bar{F}_1$, $> \bar{P}_i$ and $< \bar{P}_s$ are modified to become

$$\begin{aligned} & \frac{[d] + [i] - \frac{1}{2}[h] - \frac{1}{4}[l]}{(\frac{1}{2}D' + \frac{1}{4}H')^{1/2}}, \quad \frac{-[d] + [i] - \frac{1}{2}[h] - \frac{1}{4}[l]}{(\frac{1}{2}D' + \frac{1}{4}H')^{1/2}}, \quad \frac{\frac{1}{2}[h] + \frac{3}{4}[l]}{(\frac{1}{2}D' + \frac{1}{4}H')^{1/2}} \\ & \frac{\sum d + \sum i - \frac{1}{2}[h] - \frac{1}{4}[l]}{(\frac{1}{2}D' + \frac{1}{4}H')^{1/2}} \quad \text{and} \quad \frac{-\sum d + \sum i - \frac{1}{2}[h] - \frac{1}{4}[l]}{(\frac{1}{2}D' + \frac{1}{4}H')^{1/2}} \end{aligned}$$

where D' and H' are the estimates of the additive and dominance genetic variances biased by the presence of non-allelic interactions.

(iv) *Non-normality*

Our predictions assume that the genotypic distribution of the recombinant hybrids is approximately normal. This will be true, however, only where all the known sources of non-normality *e.g.*, dominance, epistasis, linkage disequilibrium and genotype \times environmental interactions are either non significant or the non-normalities they produce balance out (Jinks and Pooni, 1976; Pooni, Jinks and Cornish, 1977; Jinks, 1983). In general we therefore expect to find some non-normality in the distribution of hybrids and this may affect the accuracy of the predictions, especially when the probabilities take large values. Previous experience in predicting the properties of recombinant inbred lines suggests that the levels of epistasis, linkage disequilibrium and genotype \times environment interactions encountered in practice are unlikely to cause difficulties. In predicting the properties of recombinant hybrids, however, directional dominance is potentially a more serious source of non-normality but even this is not expected to cause difficulties unless the number of loci involved is small and the dominance ratio is high.

5. EXPERIMENTS AND RESULTS

(i) *Predicted properties*

To make and test the predictions we shall use material derived from the cross between varieties 1 and 5 of *Nicotiana rustica*. This cross, initiated by Mather and Vines in 1952, provides data on the parental varieties and their F_1 and F_2 generations for most of the intervening years. To these sources of data we must add the extreme families present amongst a random sample of 82 inbred lines extracted from the F_2 of this cross by single seed descent (for further information see Perkins and Jinks, 1973; Jinks and Pooni, 1976). As the scores of these inbreds are available together with V_1 , V_5 , F_1 and F_2 for 1973, 1978–81 and 1983 only we shall use the data from these seasons for making predictions. References to the sources of these data and the structure of each experiment is given in table 1.

The number and detail of the characters scored in *Nicotiana rustica* experiments vary with the objectives and their potential usefulness. All are scored however for flowering time and final height. The overall mean

TABLE 1

The sources, structure and dimensions of the data used to estimate the statistics for making predictions

Year	Source	Family size					
		V_5	V_1	F_1	F_2	$P_{largest}$	$P_{smallest}$
1973	Pooni, Jinks and Jayasekara (1978)	140	120	140	240	10	10
1978	Authors	40	40	40	150	10	10
1979	Al-Banna (1983)	25	25	50	820	10	10
1980	Authors	30	30	60	60	10	10
1981	Authors	30	30	60	120	10	10
1983	Authors	20	20	40	25	10	10

performances of V_1 , V_5 , F_1 , F_2 , $P_{largest}$ $P_{smallest}$ families and the mean genetic (V_1F_2) and environmental (E) components of variance averaged over the 6 environments (table 1) are given in table 2. Scores for flowering time represent the number of days taken to flower from an arbitrary date and the final height measurements are presented in cm.

TABLE 2

Averaged estimates of the first and second degree statistics required for making predictions about the mean performance of second cycle hybrids and their predicted properties in respect of flowering time and final height

Source	Flowering time	Final height
(a) Family means		
$P_{largest}$	39.11	151.59
$P_{smallest}$	14.43	87.73
V_5	23.20	126.11
V_1	20.22	112.46
F_1	22.02	138.86
F_2	23.13	129.96
(b) Components of variances		
Genetic (V_1F_2)	19.79	99.34
Environmental (E)	14.97	108.58
(c) Predicted proportions		
$> \bar{P}_1$	0.0002	0.015
$< \bar{P}_5$	0.0253	0.00001
$> \bar{V}_5$	0.494	0.650
$< \bar{V}_1$	0.256	0.040
$> \bar{F}_1$	0.599	0.187
$< \bar{F}_1$	0.401	0.813

Predictions were made from these estimates using the formulae described in section 3 based upon the square root of the genetic variance, as opposed to the phenotypic variance, as denominator. The probabilities thus obtained for the two most important categories $> \bar{P}_1$ and $< \bar{P}_5$ are tabulated in the lower half of table 2 together with the predicted proportions of recombinant hybrids that should score $> \bar{V}_5$, $< \bar{V}_1$, $> \bar{F}_1$ and $< \bar{F}_1$.

(ii) *Observed proportions*

We shall test the reliability of the prediction process by comparing the observed and predicted proportions of second cycle recombinant hybrids that fall within the specified classes. The observed proportions will be taken from a 20×20 diallel produced from a random sample of 20 F_9 recombinant inbred lines each of which was extracted from a separate F_2 plant of the $V_1 \times V_5$ cross by pedigree inbreeding. The diallel crosses and selfs were produced during 1954 and the experiment conducted during 1955 by Dr E. L. Breese. Experimental details and results from this diallel have already been published in one form or another by Jinks, Perkins and Breese (1969), Virk and Jinks (1977) and Pooni, Jinks and Singh (1984).

The scores of the 20 inbred parents and 190 crosses after averaging over reciprocals can be used directly to obtain two sets of observed proportions. For example, for flowering time we can select the earliest and latest flowering

inbred out of the 20 inbred lines and then count the number of hybrids which either flower earlier than the earliest inbred or flower later than the latest flowering inbred. The P_{largest} and P_{smallest} were therefore different from those used to make the predictions, as the latter were not, of course, available in 1955. Normally, of course, they would be the same families. In comparing the predicted and observed proportions we shall, therefore, be introducing an additional source of error.

The observed numbers of hybrids (out of 190) which either score $\geq \bar{P}_1$ or $\leq \bar{P}_s$, or fall within their range are tabulated both for flowering time and final height in table 3, along with the predicted numbers for each of the three categories rounded off as whole numbers.

Since the parental varieties and their F_1 generation were not part of the 20×20 diallel, the remaining comparisons between observed and expected proportions cannot be made. However, observed proportions obtained by extrapolating the scores of V_5 , V_1 and F_1 families, assuming that they show linear responses to an environmental index defined by deviations in the overall means of the F_∞ inbred lines, compared favourably with the predictions given in table 2.

6. CONCLUSIONS

In this paper we have shown how to predict the properties of second cycle F_1 hybrids which can be produced by intercrossing a random sample of inbred lines extracted from the F_2 of a cross by single seed descent or pedigree inbreeding. We have shown (sections 3 and 4) that these predictions can be made by using genetical components that are most readily and reliably estimated in the early stages of a breeding programme. In fact data from the F_2 generation of the original cross is all that is required to predict the expected mean and variance of these hybrids. With this information we can determine the probabilities of obtaining hybrids whose scores fall into any phenotypic class we care to specify. In the early generations of a cross we can now, therefore, simultaneously predict the distribution of the recombinant inbred lines and of the second cycle hybrids that can be derived from them. Hence we can assess the breeding value of a cross whether the intended end products of the breeding programme are superior inbred lines or superior hybrids. We can also predict which would be the better end product in terms of performance and whether a second cycle of extraction of recombinant inbred lines is likely to produce a significant improvement on the first.

At first sight linkage and genotype \times environment interaction may appear to complicate the procedures for making reliable predictions (see section 3) but in general they produce only relatively minor distortions whose presence can be detected. While, therefore, they have some effect on the quantitative accuracy of the predictions no adjustments will usually be required in the prediction procedures to accommodate their effects.

In contrast, non-allelic interactions can produce distortion of a magnitude which must be allowed for in making predictions. But, as we have already shown in predicting the properties of recombinant inbred lines (Jinks and Pooni, 1976; Pooni, Jinks and Cornish, 1977), the major source of these biases arises from the non-allelic interaction components of the means $[i]$ and $[j]$ and these can be estimated and allowed for when making

the predictions. These components are automatically accommodated in the predictors when these are the mean and variance of the F_2 but they must be explicitly allowed for when the predictors are combinations of genetical components estimated from the early generations by weighted least squares.

TABLE 3

Predicted frequencies of the recombinant hybrids falling into the phenotypic classes specified by the scores of the largest and smallest scoring inbred lines and the correspondingly observed frequencies amongst 190 hybrids extracted from a 20 × 20 diallel

Category	Flowering time		Final height	
	Predicted	Observed	Predicted	Observed
$> \bar{P}_l$	0	0	3	1
$< \bar{P}_s$	5	9	0	0
Remainder	185	181	187	189

The main conclusion to emerge from the analyses (section 4) and results (table 3) is that the prediction procedures are reasonably robust. Thus in spite of modest levels of non-allelic interaction, linkage disequilibrium and genotype × environment interaction (Pooni, Jinks and Jayasekara, 1978; Jinks, Perkins and Pooni, 1973; Perkins and Jinks, 1970) and the use of different pairs of extreme recombinant inbred genotypes for making the predictions and for assessing them, the predictions are consistent with the results obtained (table 3). The probabilities used in the predictions, however, are small enough to be determined by the extremes of the expected and observed distributions of the hybrids and are, therefore, less influenced by the distortions in the body and shoulders of the distributions.

The present study also shows that, even where the best recombinant inbred lines are far superior to the original heterotic F_1 , it is still relatively easy to produce second cycle hybrids that perform better than the best inbred provided that they lie in the direction of the dominance, that is, greater final height, earlier flowering (tables 2 and 3). Equally, however, the standard procedures for predicting the distribution of recombinant inbred lines show that we can expect to extend the range of performances by a second cycle of inbreeding. Thus we expect a proportion of $0.0001 > \bar{P}_l$ and $0.017 < \bar{P}_s$ for flowering time and $0.05 > \bar{P}_l$ and $0.017 < \bar{P}_s$ for final height among a random sample of second cycle recombinant inbred lines. These proportions are close to those for superior second cycle hybrids (table 2). It is possible, therefore, that these superior second cycle hybrids are very similar in genotype to the superior second cycle inbreds, that is, they may be homozygous for the same alleles at most loci and heterozygous at only a very few.

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