Theor Appl Genet (1985) 71:563–569

Predicting the potential of open-pollinating populations for the production of superior F_1 hybrids

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Accepted August 20, 1985
Communicated by H. F. Linskens

Summary. The distributive properties of a single population or of a population resulting from a cross between two populations are reproduced when inbreds randomly extracted from the population itself or from the two parental populations are randomly paired. Hence, population parameters that are usually obtained during a breeding programme can be used to predict the performance of the F_1 hybrids that can be derived from them at that stage. Multiple allelism, epistasis and deviations from Hardy-Weinberg equilibria should not cause biasis to the predictions. While in theory genotype × environment interaction and linkage disequilibrium may disturb the predictions, in practice they are unlikely to create problems that cannot be accommodated. Genotypic and phenotypic predictions of the proportions of the F_1 hybrid distribution scoring above or below a given standard are made and analysed for three characters, weight of the ears, plant height and height of the ear, in two populations of maize per se and their interpopulational cross. Because no random inbred lines from the experimental populations are presently available we cannot check our predictions. However, genotypic and phenotypic predictions and observations of F_1 hybrids obtained from populations created by computer simulation are provided to illustrate our procedures.

Key words: Genotypic and phenotypic predictions – Open-pollinating populations – F_1 hybrid distribution

1 Introduction

Breeding open-pollinating species often involves the continuous improvement of populations with periodical derivation of inbred lines and their hybrids. To guide the breeder and assess the progress of his work, several mating-selection designs have been proposed in the past for providing estimates of the genetic variance, its components and their relative magnitudes.

Another important aspect of the work involves the prediction of F_1 hybrids, the end product of most programmes. Several methods of predicting F_1 hybrids have been put forward over the years (see Hallauer and Miranda 1981 for a review) but they are not always of practical use because they usually require too restrictive assumptions to be imposed on the genetical control of the character of interest or because they require extensive cross-breeding of material in addition to the normal crossing already needed for the population improvement procedures.

In this paper we extend the concept of making predictions of the properties of second cycle hybrids from single crosses (Toledo et al. 1984a, b) and from crosses involving up to four parental varieties (Pooni and Jinks 1985) to open-pollinated populations. The procedures can be used to predict the F_1 hybrids derivable from single populations using information obtainable from most mating-selection designs in current use. Because the predictions rely on direct and robust statistical analysis they do not depend on assumptions that are difficult to justify or verify in practice.

2 Theory

2.1 Predictions from single populations

Several selection procedures devised for open-pollinating species concern single intra-population improvement. After a

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** J. B. de Miranda Filho is Professor of Genetics at 'Escola Superior de Agricultura Luiz de Queiroz-ESALQ', Caixa Postal 83, 13400-Piracicaba-SP, Brazil certain number of cycles of selection the breeder starts extracting inbred lines which are expected to produce superior F_1 hybrids when intercrossed (Allard 1960).

2.1.1 The simple genetic model

A random set of inbred lines extracted from a large random mating population in equilibrium, when randomly paired, will produce an F_1 hybrid population whose distribution approaches very closely that of the source population when k, the number of loci controlling the character under study, is large (say larger than eight). In consequence, as k becomes large, the mean and variance of the F_1 hybrids, although complex functions of k and of the gene frequencies, approach respectively

$$\left[m + \sum_{i=1}^{k} (u_i - v_i)\, d_i + 2 \sum_{i=1}^{k} u_i v_i h_i\right]$$

and

$$2 \sum_{i=1}^{k} u_i v_i [d_i + (v_i - u_i)\, h_i]^2 + 4 \sum_{i=1}^{k} u_i^2 v_i^2 h_i^2 = \tfrac{1}{2} D_R + \tfrac{1}{4} H_R\,,$$

which also are the mean and variance of the source population (the notation of Mather and Jinks 1982 is used throughout this work).

Given these equalities we can use the estimates of the original population parameters to assess its present potential for producing superior F_1 hybrids. The proportion of the F_1 hybrid distribution expected to score above or below a chosen standad can be expressed as

$$\text{Prop. } F_1 \text{ hybrids} \geqq \text{standard} = \int_{\text{std}}^{\infty} f(x)\, dx$$

which becomes, when we approximate the population distribution with the normal distribution,

$$\text{Prop. } F_1 \text{ hybrids} \geqq \text{standard}$$

$$= \frac{\text{std} - [m + \sum_i (u_i - v_i)\, d_i + 2 \sum_i u_i v_i h_i]}{(\frac{1}{2} D_R + \frac{1}{4} H_R)^{1/2}} = \frac{\text{std.} - \text{pop. mean}}{(\sigma_g^2)^{1/2}}$$

for the genotypic (repeatable) predictions. Phenotypic predictions can be made by adding the appropriate component of environmental variance $E(\sigma_e^2)$ to the components inside the parentheses in the denominator the equation above. The prediction equation then becomes

$$\text{Prop. } F_1 \text{ hybrids} \geqq \text{standard}$$

$$= \frac{\text{std} - [m + \sum_i (u_i - v_i)\, d_i + 2 \sum_i u_i v_i h_i]}{(\frac{1}{2} D_R + \frac{1}{4} H_R + E)^{1/2}} = \frac{\text{std.} - \text{pop. mean}}{(\sigma_g^2 + \sigma_e^2)^{1/2}}\,.$$

2.1.2 Relaxing the simplifying assumptions

(a) Multiple alleles and non-allelic interaction. When we allow for the presence of multiple alleles and digenic non-allelic interaction the distribution of the F_1 hybrid population still approaches that of the source population very closely when k is large. Consequently the mean and genetic variance of the F_1 hybrid population approach, respectively,

$$m + \sum_{i=1}^{k} (u_i - v_i)\, d_i + 2 \sum_{i=1}^{k} u_i v_i h_i$$
$$+ \sum_{ij=1}^{k} [(u_i - v_i)\, (u_j - v_j)]\, [i]$$
$$+ \sum_{ij=1}^{k} [u_i v_i (1 - 2 u_j) + u_j v_j (1 - 2 u_i)]\, [j]$$
$$+ 4 \sum_{ij=1}^{k} u_i v_i u_j v_j\, [l]$$

and

$$\tfrac{1}{2} D_R + \tfrac{1}{4} H_R + \tfrac{1}{4} I_R + \tfrac{1}{8} J_R + \tfrac{1}{16} L_R\,,$$

which are the mean and variance of the source population. Since no partitioning of the genetic variance (σ_g^2) into its components is necessary for prediction purposes, an experimental design providing for an estimate of the population mean and for the separation of the population's total variability into its total genetic and environmental variance will give the necessary estimates of parameters. The equation for genotypic prediction remains

$$\text{Prop. } F_1 \text{ hyb.} \geqq \text{std.} = \frac{\text{std.} - \text{pop. mean}}{(\sigma_g^2)^{1/2}}$$

as indicated earlier for the simple genetic model case.

(b) Genotype by environment interaction. Genotype × environment interaction can bias the predictions. In the presence of g × e interaction the means and variances of the source population and of the F_1 hybrid population become, respectively,

$$m + \sum_i (u_i - v_i)\, (d_i + g\, d_i) + 2 \sum_i u_i v_i\, (h_i + g\, h_i)$$

and

$$\tfrac{1}{2} D_R + \tfrac{1}{4} H_R + \tfrac{1}{2} G D_R + \tfrac{1}{2} G H\,,$$

but the environmental components of the means and variances ($g d_i$, $g h_i$, GD_R and GH_R) will differ between the two populations unless the two relevant environments (those in which the predictions and observations are made) are identical.

When making predictions of inbreds and second cycle hybrids from single crosses Jinks and Pooni (1976) and Pooni et al. (1985) found, however, that the presence of g × e interactions does not materially invalidate the predictions unless the environments concerned are so dissimilar as to cause reversals in the ranking of the genotypes.

(c) Linkage disequilibrium. Linkage disequilibrium can lead to differences between the distribution of the F_1 hybrids and that of the source population. However, if the random inbred lines used to produce the F_1 hybrids are derived by selfing (which restricts recombination) and in large numbers, the departures are not expected to be large. In any case the mean of the F_1 hybrid population will differ from the mean of the source population only if the linked genes also show non-allelic interaction. Although the variance is affected by linkage even under the simple additive and dominance model its square root is taken before being used in the prediction equation. Any bias it may cause will thus have its influence diminished.

Pooni et al. (1977) found that, in practice, linkage disequilibrium does not cause severe biases in the prediction of inbred lines derived from a single cross, while Pooni et al. (1985) found good agreement between the predicted and observed properties of second cycle hybrids from a single cross in the presence of linkage disequilibrium.

(d) Populations not in Hardy-Weinberg (HW) equilibrium. Usually the populations used for making the prediction will not be in HW equilibrium. This is particularly true if the population has been submitted to the most commonly used intra-population selection procedures where for every cycle of evaluation and selection only one single cycle of random mating is allowed.

When the population is not in equilibrium its mean and variance lose their usual relationship with gene frequencies and no simple general formulation exists for them. However, because the genotypes and respective frequencies of the random inbreds depend only on the genotypes of the source population and their relative frequencies when randomly paired they will reproduce in the F_1 hybrid population the same genotypes and relative frequencies as in the source population, so leaving the predictions unaffected. Reference to the discussion on diallels and their respective source populations by Kuehl et al. (1968) will confirm that HW equilibrium in the source populations is not a necessary condition for our predictions.

2.2 Predictions from a cross between two populations

Several methods of selection used in the improvement of cross-pollinating species involve the crossing of two (A and B) populations followed by an analysis of the performance of the resulting hybrid population. For each initial population the parents that produce the best hybrids of the hybrid population are then randomly mated to produce the next cycle of improved A and B populations. After a few cycles inbred lines are derived from both populations and intercrossed to produce F_1 hybrids (Allard 1960).

2.2.1 The simple genetic model

When individuals drawn at random from two different populations are crossed the resulting hybrid population is not in equilibrium (unless for each locus $u_{i\,\text{pop.a}} = u_{i\,\text{pop.b}}$) and its total genetic variance is not simply related to either of the parental populations. This is true even when the parental populations are themselves large randomly mating and in equilibrium. The mean of the cross population was given by Robinson and Cockerham (1961) and Jinks (1955) formulated its variance in terms of two sets of D, H_1, F parameters relating to each population in the cross. Compton et al. (1965) formulated the variance of the cross population in terms of "homologues" of the genetic components of a single population in HW equilibrium. The mean and variance can then be written as

$$m' + \sum_{i=1}^{k} (u_{ia} u_{ib} - v_{ia} v_{ib})\, d_i + \sum_{i=1}^{k} (u_{ia} v_{ib} + v_{ia} u_{ib})\, h_i$$

and

$$\sum_{i=1}^{k} \{u_{ia} v_{ia} [d_i + (v_{ib} - u_{ib})\, h_i]^2 + u_{ib} v_{ib} [d_i + (v_{ia} - u_{ia})\, h_i]^2\}$$

$$4 \sum_{i=1}^{k} u_{ia} v_{ia} u_{ib} v_{ib} h_i^2 = \tfrac{1}{2} D_R^* + \tfrac{1}{4} H_R^* .$$

However, when the two independent sets of inbred lines we can derive from the two populations are randomly paired with each other, they will produce an F_1 hybrid population whose distribution approaches the initial hybrid population very closely when k, is large. Therefore, if k is large, the mean and variance of the F_1 hybrids approach

$$\left[m + \sum_{i=1}^{k} (u_{ia} u_{ib} - v_{ia} v_{ib})\, d_i + \sum_{i=1}^{k} (u_{ia} v_{ib} + v_{ia} u_{ib})\, h_i\right]$$

and

$$\tfrac{1}{2} D_R^* + \tfrac{1}{4} H_R^* ,$$

which are the initial hybrid population mean and variance, respectively.

Thus, as with single populations we can use data from the initial hybrid population, available early in a breeding programme, to assess the potential of the present cross population for producing superior F_1 hybrids. The proportion of F_1 hybrids expected to score above a chosen reference can be written as,

$$\text{Proportion } F_1 \text{ hybrids} \geqq \text{standard} = \int_{\text{std}}^{\infty} f(x)\, dx ,$$

which, when we approximate the initial hybrid distribution with the normal distribution, becomes

$$\text{Prop. } F_1 \geqq \text{std.}$$
$$= \frac{\text{std} - [m + \sum_i (u_{ia} u_{ib} - v_{ia} v_{ib})\, d_i + \sum_i (u_{ia} v_{ib} + v_{ia} u_{ib})\, h_i]}{(\frac{1}{2} D_R^* + \frac{1}{4} H_R^*)^{1/2}}$$

for genotypic predictions. Phenotypic predictions can again be made by adding the appropriate environmental component of variance E (see Sects. 2.1.1 and 3). The lifting of the restrictions imposed on the genetical model follows the same pattern as that for the single population procedure (see Sects. 2.1.2 a–d).

3 Material and methods

Because no random inbred lines have yet been extracted from the experimental populations used in this work, the data available to us from field experiments do not allow the comparison of predicted and observed values. To overcome this limitation we have also analysed data produced by a computer simulation.

3.1 The experimental data

We first consider the data provided by two varieties of maize (*Zea mays* L.): 'ESALQ-PB1', created at Escola Superior de Agricultura Luiz de Queiroz-ESALQ, Brazil and 'BR-105' created at the Centro Nacional de Pesquisa de Milho e Sorgo-EMBRAPA, Brazil. These two populations are being submitted to reciprocal recurrent selection using a half-sib family structure ('ESALQ-PB1' and 'BR-105' are testers of each other). Estimates of the means and genetic and environmental variances were obtained for the two individual populations and for the two reciprocal crosses between them ('ESALQ-PB1' × 'BR-105' and 'BR-105' × 'ESALQ-PB1') in respect of the characters height of the insertion of the first ear (HE), final plant height (FH) and weight of ears per plant (WE).

The means of the two populations and their reciprocal crosses were obtained as the respective mean of the half-sib families. The mean of the cross population was calculated as the average of the means of the two reciprocal crosses (Hallauer and Miranda 1981).

The estimates of the variance of the two individual populations and their reciprocal crosses were obtained as σ_b^2, the component of variance between half-sib families,

σ_w^2, the component of variance within half-sib families, and σ_e^2, the blocks and half-sib family interaction. The phenotypic population variance (σ_{ph}^2) of the single populations, required for the intra-population phenotypic predictions, was obtained directly from these three components as $\sigma_{ph}^2 = \sigma_b^2 + \sigma_w^2 + \sigma_e^2$. The phenotypic variance of each reciprocal crosses was also obtained directly from their estimated components, in the same way, and their average was taken to be the phenotypic variance of the cross population. To obtain an estimate of the genotypic variance (σ_g^2) the environmental component of variance within families (E_w) is needed because $\sigma_g^2 = \sigma_b^2 + \sigma_w^2 - E_w$. E_w can be obtained from the within family variance of the homozygous varieties used as checks in the experiment. As an alternative, because the experiment allowed us to test the significance of the non-additive components of the genetic variance by testing the interaction among type of progenies (intra and inter-populational) x half-sib families, we could make $\sigma_g^2 = 4\,\sigma_b^2$ whenever such interaction was non-significant. As for the phenotypic variance, the genotypic variance of the cross-population was calculated as the average of the genetic variance of the reciprocal crosses (Miranda and Hallauer 1981; Mather and Jinks 1982).

The commercial hybrid variety 'Cargill 511' was used as the standard in the predictions.

3.2 The computer simulation data

The second part of our data is provided by a computer simulation from which a random mating population in equilibrium was created and assessed for its potential to produce F_1 hybrids. The genetic model used in the simulation allowed for additive, dominance and environmental effects. We avoided the complications of multiple alleles, non-allelic interaction, g x e interaction and linkage disequilibrium effects because the main purpose of the simulation was to exemplify the procedures involved in comparing predicted and observed proportions of F_1 hybrids. The simulated source population characteristics are: ten segregating loci, two alleles per locus with the frequency of the increasing allele = 0.25, $\sum d_i = 17.89$ (all d_i equal), $\sum h_i = 8.94$ (all h_i equal), true dominance ratio = 0.50, mean = 52.30, $D_R = 37.5$, $H_R = 4.5$, E = 80.0, single individual narrow sense heritability = 0.20 and Hardy-Weinberg equilibrium.

The mean and the genetic and environmental variances of the population provided the data for the predictions. The observed values were obtained by extracting 100 random inbred lines from the population (by a random walk procedure) and randomly pairing them to produce 50 F_1 hybrids. Each F_1 hybrid had a family size of 25 individuals evaluated in a simulated single individual randomization experiment. The plot based narrow sense heritability was, therefore, the same as that for single individuals, $h_n = 0.20$.

The standards for the comparison were arbitrarily chosen to be the highest and lowest scoring inbred lines used to form the F_1 hybrid population.

4 Results and discussion

Table 1 shows the analyses of variance of the half-sib families for the two populations per se and their inter-populational reciprocal crosses for the characteristics WE, FH and HE.

Table 2 shows the two joint analyses of variance for the intra and inter populational half-sib families. The mean square of the interactions, between type of half-sib families (intra and inter populational) x between

Table 1. Analysis of variance of the weight of ears (WE), final plant height (FH) and height of the insertions of the first ear (HE) of the intra- and inter-half-sib progenies ('ESALQ-PB1' and 'BR-105' are testers of each other)

	Intra-population				Inter-population				
	'ESALQ-PB1'		'BR-105'		'ESALQ-PB1'[a]		'BR-105'[b]		
	df	MS	df	MS	df	MS	df	MS	
(i) WE									
Blocks	1	1,427.8	1	3,276.7	1	1,213.0	1	1,889.2	
Between progenies	92	395.6*	97	407.6^{ns}	92	490.0**	97	353.1^{ns}	$\sigma_w^2/25+\sigma_e^2+2\,\sigma_b^2$
Residual	92	277.5	97	317.1	92	304.7	97	277.8	$\sigma_w^2/25+\sigma_e^2$
Within progenies	4,650	1,982.3	4,704	2,265.1	4,650	2,176.9	4,704	1,984.2	σ_w^2
(ii) FH									
Blocks	1	69.0	1	124.9	1	589.6	1	220.0	
Between progenies	59	194.1**	89	228.9**	59	204.4*	89	203.6**	$\sigma_w^2/5+\sigma_e^2+2\,\sigma_b^2$
Residual	59	82.6	89	99.0	59	71.7	89	81.0	$\sigma_w^2/5+\sigma_e^2$
Within progenies	480	212.5	720	247.7	480	248.3	720	251.3	σ_w^2
(iii) HE									
Blocks	1	43.2	1	73.5	1	75.2	1	451.6	
Between progenies	59	99.7**	89	66.7**	59	109.5**	89	62.8**	$\sigma_w^2/5+\sigma_e^2+2\,\sigma_b^2$
Residual	59	54.0	89	31.7	59	54.2	89	30.0	$\sigma_w^2/5+\sigma_e^2$
Within progenies	480	131.1	720	87.6	480	140.9	720	85.2	σ_w^2

*, **, ns indicate significance at 5% and 1% level and non-significance, respectively

[a] 'ESALQ-PB1' used as female parent

[b] 'BR-105' used as female parent

Table 2. Joint analysis of variance of the weight of the ear (WE), final plant height (FH) and height of the insertion of the first ear (HE) of the half-sib progenies of intra and interpopulational origin ('ESALQ-PB1' and 'BR-105' are testers of each other)

	ESALQ-PB1 [a]		BR-105 [b]	
	df	MS	df	MS
	(i) WE			
Blocks	1	2,636.5	1	5,071.1
Between progenies (B)	92	600.1**	97	514.8*
Residual (a)	92	306.2	97	366.8
Type of progenies (T)	1	6,629.9**	1	5,983.4**
B × T	92	285.5 ns	97	245.9 ns
Residual (b)	93	273.2	98	226.7
	(ii) FH			
Blocks	1	531.0	1	7.2
Between progenies (B)	59	339.3**	89	364.2**
Residual (a)	59	87.0	89	128.1
Type of progenies (T)	1	795.7**	1	5,221.2**
B × T	59	59.2 ns	89	68.3 ns
Residual (b)	60	68.2	90	55.1
	(iii) HE			
Blocks	1	22.0	1	448.9
Between progenies (B)	59	168.2**	89	116.8**
Residual (a)	59	69.9	89	47.7
Type of progenies (T)	1	2,350.0**	1	2,210.2**
B × T	59	41.0 ns	89	12.7 ns
Residual (b)	60	39.7	90	14.7

*, **, ns indicate significance at 5% and 1% level and non-significance, respectively

[a] 'ESALQ-PB1' used as the female parent in the interpopulational cross

[b] 'BR-105' used as the female parent in the interpopulation cross

half-sib families (B × T), were non-significant for all three characters. We, therefore, concluded that the non-additive effects were a relatively unimportant component of the genetic variation for all three characters and estimated σ_g^2 as $4\sigma_b^2$ in each case. The estimates of σ_g^2 plus the estimates of σ_{ph}^2 as $\sigma_g^2 + \sigma_w^2 + \sigma_e^2$ and the population means are shown in Table 3. These estimates were used to produce the genotypic and phenotypic predictions of Table 4.

Although Table 4 includes both genotypic and phenotypic predictions we must emphasize that ultimately the breeder is interested in the repeatable properties of his material and should, therefore, rely on the genotypic predictions. The results indicate that it is fairly easy to derive F_1 hybrids that will outperform the WE of the standard variety either from the ESALQ-PB1 or from the cross-population without further cycles of selection. They also indicate that the cross-population is a better source of high WE F_1 hybrids, than the 'ESALQ-PB1' population itself (no predictions for WE were made from the 'BR-105' population because of the non-significance of the population's variance between half-sib families). This is not surprising since the two populations have been submitted to reciprocal recurrent selection in which they were testers of each other. If two or more cycles of selection and subsequent evaluation of the population parameters are made it is possible to assess the speed of their progress towards the production of high WE scoring F_1 hybrids by simple comparison of the expected proportions in each cycle.

For FH and HE the predictions indicated that the cross population's performance is practically an average of that of the two single populations. However, since the expected proportions are very high (assuming lower FH and HE are desirable characteristics) the

Table 3. Parameter estimates used for the predictions: means and variance components for weight of ears (WE), final height (FH) and height of the insertion of the first ear (HE) for the two populations and their reciprocal interpopulational cross together with means of the standard variety

Population	WE			FH			HE		
	Mean (g/p)	σ_g^2	σ_{ph}^2	Mean (cm)	σ_g^2	σ_{ph}^2	Mean (cm)	σ_g^2	σ_{ph}^2
'ESALQ-PB1'	118.0	236.2	2,239.6	203.9	223.1	308.4	112.8	91.4	181.7
'BR-105'	112.9	–	2,536.9	186.4	259.9	362.1	98.2	70.1	119.3
'ESALQ-PB1' [b] × 'BR-105' (A)	126.4	370.4	2,487.2	200.3	265.5	336.7	106.5	110.5	194.5
'BR-105' [c] × 'ESALQ-PB1' (B)	120.7	150.5 [a]	2,220.3	194.0	245.1	343.3	103.2	65.6	114.5
(A + B) ÷ 2	123.6	260.4	2,353.8	197.1	255.3	340.0	104.9	88.1	154.5
Standard	139.1	–	–	209.1	–	–	115.8	–	–

[a] This value although non-significant was obtained to allow the calculation of σ_p^2 for the average of both interpopulational crosses

[b] 'ESALQ-PB1' used as the female parent

[c] 'BR-105' used as the female parent

Table 4. Predicted genotypic and phenotypic predictions of F_1 hybrids scoring above the standard for weight of the ears (WE) and below the standard for final plant height (FH) and height of the insertion of the first ear (HE), for both populations and their averaged reciprocal interpopulational cross

(i) Genotypic predictions	WE ≧ std	FH ≦ std	HE ≦ std
'ESALQ-PB1'	0.09	0.67	0.62
'BR-105'	–	0.92	0.98
Cross population	0.17	0.77	0.88
(ii) Phenotypic predictions			
'ESALQ-PB1'	0.33	0.62	0.59
'BR-105'	–	0.88	0.95
Cross population	0.37	0.74	0.81

Table 5. Simulation study – population mean, genetic and environmental variances and narrow sense heritability. Standard (std) means

(i) Means	
Population	52.30
High scoring standard (Hstd)	58.40
Low scoring standard (Lstd)	40.85
(ii) Variances and heritability	
D_R	37.5
H_R	4.5
E_1	80.0
$h^2_{(n)}$	0.2

Table 6. Simulation study – predicted and observed phenotypic and genotypic proportions of the F_1 hybrid distribution scoring above or below the high (Hstd) and low (Lstd) standards

(i) Genotypic proportions	Smaller than		Greater than	
	Predicted	Observed	Predicted	Observed
Hstd	0.91	0.92	0.09	0.08
Lstd	0.01	0.00	0.99	1.00
(ii) Phenotypic proportions	Smaller than		Greater than	
	Predicted	Observed	Predicted	Observed
Hstd	0.73	0.74	0.27	0.26
Lstd	0.13	0.11	0.87	0.89

breeder could choose to concentrate his future selection efforts on the advance of the WE character. The joint probability of deriving F_1 hybrids with higher WE and lower FH and HE can be calculated but we shall not do so here.

We have now shown how the proposed methodology can be a powerful tool in the hands of the breeder and that it relies on information already available from the experiments used routinely for selection purposes.

Table 5 shows means, variances and narrow sense heritability of the source population obtained from the computer simulation together with the means of the high and low scoring standards (Hstd and Lstd, respectively). Table 6 shows the expected and observed genotypic and phenotypic proportions of the F_1 hybrid distribution scoring above or below the given standards. It illustrates the kind of data needed for the predictions and gives an indication of the agreement between expected and observed proportions we can expect when there are no complications (for example linkage disequilibrium and/or g × e interaction) in the genetic model. The cases where complications have been added to our model have been discussed in Sects. 2.1.2a–d.

One final point: in making the predictions we assumed that the distributions of the source population and the F_1 hybrids were normal. Strictly speaking, this will be true only when all known sources of non-normality (unequal gene frequency, dominance, non-allelic and g × e interaction and linkage disequilibrium) are absent or the departures from normality that they produce cancel out (Jinks and Pooni 1976; Pooni et al. 1977; Jinks 1983; Toledo et al. 1985). In general, however, we expect some degree of non-normality in the distribution of our populations and F_1 hybrids. Although at present we cannot provide the observed values to check with our predictions made from experimental data, our previous experience suggests that the levels of non-allelic interaction, linkage disequilibrium and g × e interaction encountered in practice cause little distortion of the shape of the distributions and is accommodated by the robustness of the prediction procedures. Directional dominance and unequal gene frequency, however, are potentially more serious sources of non-normality in our populations. Even these however are not expected to cause serious difficulties for the predictions unless the number of segregating loci is small. Confirmation of these expectations, however, must await the availability of appropriate data.

Acknowledgements. The authors are indebted to Professor Sir Kenneth Mather, Professor J. L. Jinks and Dr. H. S. Pooni for helpful discussions throughout the course of the work described in this paper. We are also grateful to Dr. M. J. Kearsey for allowing the use of his computer simulation programmes and to Dr. C. L. de Souza Junior for lending us the maize data from his PhD thesis.

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