COMPARATIVE RESULTS OF SELECTION IN THE EARLY AND LATE STAGES OF AN INBREEDING PROGRAMME

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SUMMARY

Selection for final height using three different selection criteria has been applied retrospectively to the records of two inbreeding experiments, using pedigree and single-seed-descent breeding programmes, carried out without selection within crosses of varieties 1 and 5 of *Nicotiana rustica*. In the pedigree programme the results of individual and family selection imposed at the F_3 , F_4 and F_6 generations on the performance of the inbred families from the F_9 generation onwards are compared. In the single-seed-descent programme the results of individual selection in the F_2 are compared with those of delaying selection until the F_7/F_8 generations. The results show that selection is considerably more successful if it is delayed and that family selection is more successful than individual selection in the early generations.

1. INTRODUCTION

BEGINNING in 1946 (Mather and Vines, 1952) and again in 1967 (Perkins and Jinks 1973), two independent random samples of pure-breeding lines of *Nicotiana rustica* have been extracted from an initial cross between varieties 1 and 5 of the Birmingham collection.

The first sample was produced by the method of pedigree breeding, the second by single-seed-descent. The properties of the two samples of pure-breeding lines have been described in numerous publications (for example, Perkins and Jinks, 1968; Eaves and Brumpton, 1972; Perkins and Jinks, 1973; Jinks and Pooni, 1976) and they have been used to initiate a number of further breeding programmes (for example, Jinks *et al.*, 1969; Virk and Jinks, 1977; Pooni *et al.*, 1978; Pooni *et al.*, 1980). They have, however, a value that has not been exploited as yet, namely, they allow us to examine, retrospectively, the consequences of any selection that might have been practised at any stage of the inbreeding programme. In this paper we have, therefore, compared the results of selection practised in the early and late generations.

2. MATERIAL

In the first sample, 20 randomly chosen F_2 plants of the cross of varieties 1 and 5 were self-pollinated to produce 20 F_3 families. Two randomly chosen sibs from each F_3 family of 20 plants were self-pollinated to produce 40 F_4 families and two randomly chosen sibs from each F_4 family were self-pollinated to produce 80 F_5 families. At this point each of the original F_2 plants was represented by four F_5 families. From the F_5 generation onwards the total number of families was kept constant at 80, apart from

random losses, by self-pollinating two sibs from only one of the two families that arose from sibs in the previous generation. A diagrammatic representation of this pedigree taken from Breese (1954) is given by Towey and Jinks (1977).

In the second sample 100 randomly chosen F_2 plants were self-pollinated and two sibs raised from each of the resulting 100 F_3 families. One randomly chosen sib, or occasionally the one surviving sib, of each family was self-pollinated to produce 100 F_4 families. Again two sibs per family were raised and one chosen at random was self-pollinated to produce the 100 F_5 families. By repeating this process 82 pure-breeding lines were obtained each traceable back to a different F_2 plant. Further details of the origin of these lines are given by Perkins and Jinks (1973).

The character we shall use for illustration is final height. This is the largest single component of the total phenotypic variation in material derived from the cross between varieties 1 and 5, it has one of the highest narrow heritabilities and repeatabilities over seasons and a relatively simple genetical control (Bucio Alanis, Perkins and Jinks, 1969; Eaves and Brumpton, 1972; Pooni, Jinks and Jayasekara, 1978).

3. METHOD

(i) *Pedigree data*

Although we have data on the pedigree inbreeding programme from the F_2 to the F_{19} we shall assess the consequences of selection in three early generations, F_3 , F_4 and F_6 , on the performance of the resulting pure-breeding lines. For the latter we shall use the means over the last nine occasions on which the inbred families were assessed.

The advantage of imposing selection retrospectively on a random sample of families is that we can subject them to a wide range of selection procedures and criteria. We shall use six combinations made up as follows:

1. Individual selection in which an individual plant in any generation is selected as parent on the basis of its own performance.
2. Family selection in which a family is selected on the basis of the average performance of all of its members and randomly chosen individuals of the selected families are used as parents.

Individual and Family selection will be used in combination with three selection criteria.

- (a) Selection of the best 25 per cent individuals or families.
- (b) Selection of those individuals or families which are superior to the means of contemporary samples of the better parent (P_1).
- (c) Selection of those individuals or families which are superior to the means of contemporary samples of the heterotic F_1 .

(ii) *Single-seed-descent data*

The emphasis in breeding by single-seed-descent is to go from the F_2 to a relatively inbred state *e.g.*, F_6 or F_7 as rapidly as possible using any environmental treatment that will reduce generation time. There are, therefore, no field assessments under normal growing conditions between

TABLE 1

Percentages of maximum achievable response to selection obtained by six different selection criteria in F_3 , F_4 and F_6 generations

Type of selection	Generation of selection			
		F_3	F_4	F_6
Top 25 per cent	Individual	11.6	40.7	88.9
	Family	74.3	64.5	86.6
> P_1 mean	Individual	26.4	86.4	97.2
	Family	41.2	83.5	100.0
> F_1 mean	Individual	11.7	56.9	47.8
	Family	68.8	56.9	86.5

the F_2 and some later generation such as the F_7 or F_8 . In our experiment, the first field assessment after the F_2 was of 82 inbred families, 71 of which were F_8 's and 11 were F_7 's, the latter having been delayed by one generation because of an above average generation time.

4. RESULTS

(i) *Pedigree data*

The results of imposing the six types of selection at the F_3 , F_4 and F_6 generations on the performance of the pure-breeding families (F_∞ families) derived from the selections are summarised in tables 1 and 2. In table 1 the results are expressed as the percentage of the maximum achievable response to the particular type of selection. This maximum is the deviation of the

TABLE 2

Percentage selected and percentage success in choosing those F_3 , F_4 and F_6 's which produce the best pure-breeding lines using the six different selection criteria

		Generation of selection			
Type of selection			F ₃	F ₄	F ₆
Top 25 per cent	Individual	Selected	25	25	25
		Success	40	60	80
	Family	Selected	25	25	25
		Success	60	80	80
>P ₁ mean	Individual	Selected	30	40	40
		Success	30	50	50
	Family	Selected	75	40	40
		Success	90	50	50
>F ₁ mean	Individual	Selected	25	35	40
		Success	40	60	100
	Family	Selected	40	40	35
		Success	80	80	80

mean of the selected pure-breeding families ($S_{\infty}\bar{F}_{\infty}$) from the mean of all pure-breeding families ($\bar{F}_{\infty}$) when the particular selection criterion is imposed on the population of F_{∞} families themselves. For example, if we select the top 25 per cent of F_3 individuals the mean of the pure-breeding lines derived from them ($S_{3i}\bar{F}_{\infty}$) deviated from $\bar{F}_{\infty}$ by 11.6 per cent of the deviation $S_{\infty}\bar{F}_{\infty} - \bar{F}_{\infty}$ when the top 25 per cent F_{∞} families were selected; that is, $100(S_{3i}\bar{F}_{\infty} - \bar{F}_{\infty})/(S_{\infty}\bar{F}_{\infty} - \bar{F}_{\infty}) = 11.6$. The efficiency of selecting F_3 individuals on this criterion is, therefore, 11.6 per cent of that achieved by delaying selection until pure-breeding families have been obtained.

The same results are presented in table 2 in a way which attempts to show the probability of retaining or discarding those lineages which will produce the best F_{∞} families if selection is based on assessments made at F_3 , F_4 and F_6 . For each of the six selection criteria in each generation we have listed two percentages; the first is the percentage of individuals or families retained in each generation because they meet the selection criterion used; the second is the percentage of lineages retained after selection that will lead to F_{∞} families that would meet the same selection criterion if it were applied to the population of F_{∞} families. For example, when applying the top 25 per cent selection criterion to individuals in the F_3 , the top 25 per cent of F_3 individuals were, of course, retained but only 40 per cent of the lineages that produced the top 25 per cent of F_{∞} families were retained in this selected sample, 60 per cent of the lineages that would have produced the best F_{∞} families were discarded including those that would have ranked 1, 3 and 4.

(ii) *Single-seed-descent*

Statistics summarising the properties of the pure-breeding lines produced by single-seed-descent from F_2 individuals selected on three criteria are given in table 3. For example, where the selection criterion is the

TABLE 3

The percentage selected and percentage success in choosing those F_2 individuals which produce the best pure-breeding lines using the three different selection criteria and the percentage of the maximum achievable response to these selections

	Percentage selected	Percentage success	Percentage response
Top 25 per cent	25	24	19.9
> P_1 mean	55	72	49.0
> F_1 mean	30	33	25.0

top 25 per cent, the highest scoring 25 per cent of F_2 individuals were selected. The pure-breeding families produced from this selected sample by single-seed-descent included only 24 per cent of the highest scoring 25 per cent of pure-breeding families. The F_2 individuals that would have produced the remaining 76 per cent of the highest scoring pure-breeding families were, therefore, discarded because they did not meet the selection criterion imposed on the F_2 . Because of this low rate of success the response to selection, measured as in table 1, was only 19.9 per cent of that which

could have been achieved by delaying selection until the pure-breeding families had been obtained. The summary statistics for the other two selection criteria were similarly obtained (table 3).

(iii) *Correlations between generations*

In table 4 are listed the correlations between the pairs of generations used in the investigation of the pedigree inbreeding programme. Two values

TABLE 4

Correlations between the generations specified. The upper value is between the individual plants chosen as parents and the means of their progenies, the lower value is between the means of the families from which the parents were chosen and the means of their progenies

	F ₄	F ₆	F ₉	F _∞
F ₃	0.65 0.74	0.54 0.57	0.14 0.53	0.18 0.68
F ₄		0.45 0.70	0.45 0.52	0.68 0.65
F ₆			0.70 0.66	0.72 0.69

are given for each pair; the upper value is the correlation between the individual plants chosen as parents and the means of the progeny families derived from them, the lower value is the correlation between the means of the family from which the individual parental plants were chosen and the means of the progeny families derived from them. They correspond to the data used for individual and family selection respectively. The pure-breeding families resulting from the inbreeding programme are represented by two sets of data. Those correlations labelled F_∞ are, as previously, based upon the means of the pure-breeding lines over the last nine occasions on which they were assessed (section 3(i)). Since these means are known with considerably greater accuracy than the corresponding F₃, F₄ and F₆ family means an additional set of correlations based on the means of F₉ families raised on one occasion only are included for comparison.

For the inbred families produced by single-seed-descent, only one correlation can be obtained, namely that between F₂ individuals and the means of the F₈ (or F₇) families derived from them. This has a value of 0.32.

5. CONCLUSIONS

To compare the selection responses produced by different selection strategies we have chosen a character, final plant height in the cross between varieties 1 and 5 of *Nicotiana rustica*, which is particularly favourable because of its high narrow heritability (0.6–0.7), its simple and well established genetical control and its predictable response to environmental variation (including seasonal differences), in order to achieve results which are unambiguous. The results are therefore readily interpreted and convey a number of clear messages.

The first point that emerges from tables 1, 2 and 3 is that by delaying selection until the F₄ or even the F₆ generation a population of inbred lines is

produced which is superior in average performance and in composition to that produced by selection in either the F_2 or F_3 generations.

The second point that emerges from tables 1 and 2 is that on average family selection is superior to individual selection. But this superiority is conditional. It is most pronounced in the F_3 generation or when the selection intensity is high and it is least pronounced in the F_6 generation or when the selection intensity is low.

The points that emerge from table 4 reinforce those already made. The six pairs of correlations between the F_3 , F_4 and F_6 generations on the one hand and the F_9 and F_∞ generations on the other summarise the relationships between the phenotypic variation upon which selection was practised and the realised additive genetic variation responsible for the heritable differences among the inbred lines to which they give rise. The ability of the selection in the F_3 , F_4 and F_6 generations to influence the composition of the population of inbred families is clearly directly related to the magnitude of these correlations. And as already concluded from other comparisons (tables 1, 2 and 3) this ability is lower in the F_3 than in the F_4 or F_6 and lower in individual than in family selection in F_3 but not in the F_6 generation. Two further points are worth noting. The relatively high heritability and repeatability are confirmed by the high parent/offspring mean correlations of the only two successive generations, F_3 and F_4 , raised in different seasons.

The correlations involving F_∞ are consistently greater than those with F_9 , the essential difference being that the F_∞ , which are based on the means of nine independent field trials of the inbred lines will more accurately reflect the heritable by considerably reducing the nonheritable differences among them.

The conclusions of these retrospective selections are supported by actual selections for final height and environmental sensitivity within the cross of varieties 2 and 12 of *N. rustica* (Brumpton *et al.*, 1977; Jinks *et al.*, 1977). A comparison at the F_7 generation of selections obtained by family selection starting in the F_3 and by single-seed-descent with selection delayed until the F_7 showed the latter to be superior. But its superiority was greater for environmental sensitivity than for final height because of its lower heritability and repeatability over seasons.

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