

JOINT SELECTION FOR BOTH EXTREMES OF MEAN PERFORMANCE AND OF SENSITIVITY TO A MACROENVIRONMENTAL VARIABLE

II. SINGLE SEED DESCENT

J. L. JINKS, N. E. M. JAYASEKARA* and HILARIE BOUGHEY

Department of Genetics, University of Birmingham, Birmingham B15 2TT

Received 2.iii.77

SUMMARY

A random sample of 59 F_7 lines were produced by single seed descent from a cross between V2 and V12 of *Nicotiana rustica*. They have been compared in eight environments with F_7 lines selected from the same cross for all four combinations of high (H) and low (L) mean performance and high (h) and low (l) environmental sensitivity in a pair of these environments. The characters considered were flowering time and final height and the environments were provided by four sowing dates at each of two planting densities. Both in the pair of environments in which the selections were made and in the other six environments, there were among the random F_7 s many which met the four selection criteria (Hh, Hl, Lh, and Ll) better than the selected F_7 s. While among the selected F_7 s there was no satisfactory Lh selection for flowering time or Hl selection for final height, there were as many lines among the random F_7 s which met these selection criteria as met the other three selection criteria for each character. Inefficiency in the selection procedures traceable to seasonal differences, rather than shortage of the appropriate segregants, was the primary cause of the unsatisfactory selections. Lines with the Lh phenotype for flowering time and Hh for final height, which are the phenotypes produced by the dominant genes, maintained their mean performance and environmental sensitivity over all sets of environments better than any of the other combinations of performance and sensitivity.

These results demonstrate the superiority of single seed descent over conventional family selection and confirm that mean performance and environmental sensitivity are largely under the control of different gene loci.

I. INTRODUCTION

ALTHOUGH mean performance and sensitivity to macroenvironmental variables are often highly correlated there is evidence that in *Nicotiana rustica* these two aspects of the phenotype are at least in part under independent genetical control and can therefore be reassorted (Perkins and Jinks, 1968, 1971, 1973). Brumpton, Boughey and Jinks (1977) have shown that it is possible using relatively simple selection procedures based on family selection to select for all four combinations of high and low mean performance with high and low sensitivity to a macroenvironmental variable in the cross between varieties V2 and V12 of *Nicotiana rustica*. Using the same F_2 from which these selections were initiated, Perkins and Jinks selfed 60 randomly chosen plants to produce 60 pure-breeding lines by single seed descent. In this paper we compare at the F_7 generation the selections made by Brumpton, Boughey and Jinks (1977) with corresponding selections from among the

* Present Address: Dept. of Genetics and Plant Breeding, Rubber Research Institute Matugama, Sri Lanka.

families produced by single seed descent both in the environments used for selection and in related but different environments. The comparisons demonstrate the overwhelming advantages of the selections produced by single seed descent and confirm that mean performance and environmental sensitivity can be brought together in a wide range of combinations.

2. MATERIALS AND METHOD

The material consists of the F_7 generation of the eight selection lines (S) from the $V2 \times V12$ cross for high (H) and low (L) mean performance in combination with high (h) and low (l) environmental sensitivity (SHh, SHl, SLh and SLl) for each of the two characters, final height (FH) and flowering time (FT). The selection procedures and properties of the selections up to and including the F_5 generation were described by Brumpton, Boughey and Jinks (1977). The derivation of the F_7 generation from the F_5 followed the same procedures.

Fifty-nine F_7 families (D) derived by single seed descent from 60 randomly chosen plants of the F_2 of the $V2 \times V12$ cross were available for assessment and selection in 1972. The following experiments were, therefore, conducted in 1972:

(i) All 59 D lines and eight S lines were raised in the two environments used for selecting the S lines, namely, two sowings 28 days apart at the normal planting density. This enabled us to compare the S selections with a random sample of F_7 families, the D lines, in the environment used for selection and to choose from among them two sets of four families which combined high and low mean performance with high and low sensitivity for FH and FT.

(ii) The 59 D lines and eight S lines were raised in six other environments differing for sowing date and planting density to examine the specificity of the selections in environments which were related to, but not the same as, those in which they were selected.

These comparisons were incorporated into a single experimental design by raising the eight S selections and the 59 D lines in eight environments consisting of four successive sowings (1, 2, 3 and 4) made at fortnightly intervals at each of two planting densities, normal (N) and high (H) (see Perkins and Jinks, 1973, for details). Sowings 2 and 4 at the normal density (2N and 4N) correspond to the selection environments in which the S selections themselves were made and are, therefore, the environments for making the comparisons described under (i). The remaining environments are clearly related to, though different from, the selection environments and are therefore, appropriate for making the comparisons described under (ii).

Ten individually randomised siblings of each of the eight S selections and 59 D lines were grown in each of the eight environments along with the same number of siblings of the original parental varieties V2 and V12 and their reciprocal F_1 s. Overall, therefore, 80 plants of each of 71 families were raised.

Following Brumpton, Boughey and Jinks (1977) one-way analyses of variance were performed for each of the 71 families so that the variation in FT and FH could be partitioned into within (σ_{wb}^2) and between (σ_b^2) environmental components for the appropriate set of environments. The estimate of σ_b for any set of environments was used as the measure of environ-

mental sensitivity while the mean of the same set was used as the corresponding mean performance. To facilitate comparisons both measures have again been expressed as deviations from the average performance and sensitivity of control lines. In this experiment these are the 59 randomly chosen inbred D lines.

3. RESULTS AND INTERPRETATION

(i) Comparisons of the S and D lines

The 59 D lines can be divided into four groups on the basis of the selection criteria used for the S selections. In the Hh group are included all the lines with above average mean performance (positive deviation from the control mean performance) and above average environmental sensitivity (positive deviation from the control environmental sensitivity). In the Hl group are included all the lines with above average mean performance and below average environmental sensitivity and so on for the Lh and Ll groups respectively. The distribution of the 59 D lines among these four groups for FT and FH for mean performance and environmental sensitivity in the selection environments (2N and 4N) is given in table 1. For example, for

TABLE 1

The distribution of the 59 D lines among the four phenotypic classes, Hh, Hl, Lh and Ll for flowering time and final height and the number of lines in each of the classes which meet the selection criteria better than the corresponding S selections

Phenotypic class	Number of D lines	Number of D lines better than S selections
<i>Flowering time</i>		
Hh	11	7
Hl	12	12
Lh	20	20
Ll	16	1
<i>Final height</i>		
Hh	21	5
Hl	9	9
Lh	13	13
Ll	16	1

FT, 11 of the lines are classified as Hh because they had mean performances and environmental sensitivities which are higher than those of the controls; and so on for the other three groups. Although there are differences in the number of lines falling into each group these are no greater than would be expected to arise from sampling variation. There is, however, one comparison that does reach a borderline significance; the combined frequency of the two opposing combinations of mean performance and environmental sensitivity (Hl and Lh) is significantly lower than that of the reinforcing combinations (Hh and Ll) for final height ($P = 0.05 - 0.02$) but the numerical difference is small. All four combinations of performance and sensitivity therefore arise with similar frequencies among the segregants from the V2 × V12 cross.

This contrasts markedly with the assymetry of the response among the S selections and this is reflected in the further comparisons listed in table 1, namely, the number of D lines in each group that meet the selection criterion better than the corresponding S selection. Overall for each character half or more of the D lines meet the four selection criteria better than the S selections but there are large differences in this respect between selections. For example, the H1 and Lh selections for FT and FH respectively are worse than all the D lines in the corresponding groups. At the other extreme the L1 selections for FT and FH are better than all but one of the 16 D lines in the corresponding group. However, there is at least one D line, and in most cases considerably more, that is better than every one of the S selections.

To illustrate further the extent of this superiority of the D lines as a source of the four selections and to facilitate further comparisons, we can select from each of the four groups the lines which best meet the selection criteria for FT and FH. As an example of the procedure used in choosing

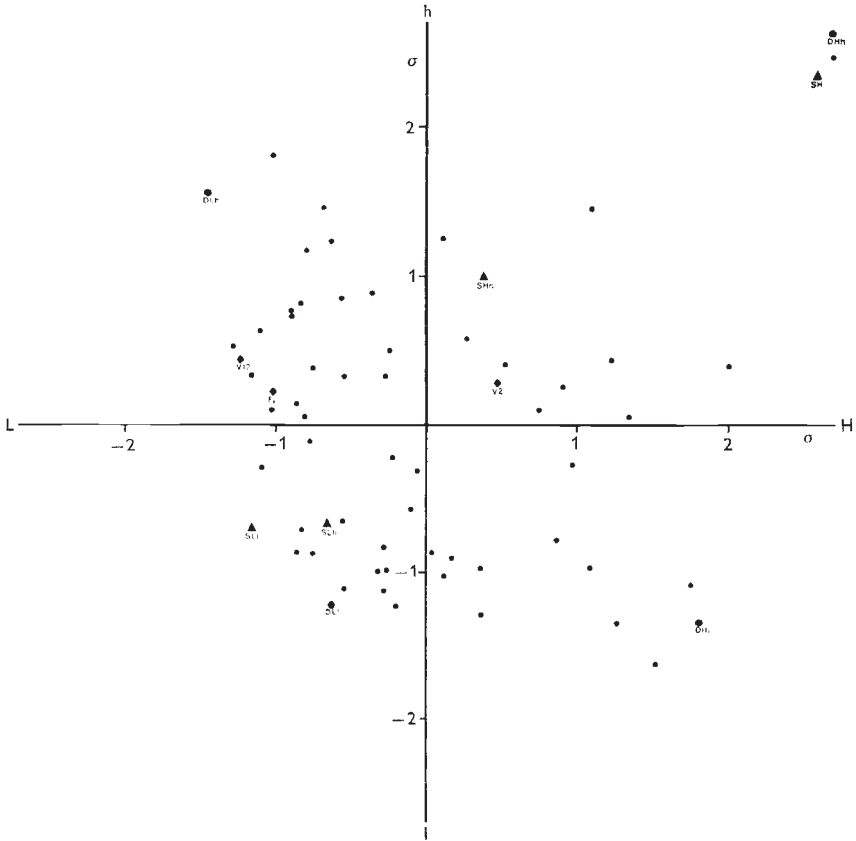


FIG. 1.—The standardised measures of environmental sensitivity for FT in the selection environments (2N + 4N) for each of the 59 D lines and four S lines, parents and average F₁, plotted against the standardised measures of mean performance. All are expressed as deviations from the mean control values. Key: ● = D lines; ▲ = S lines; ◆ = Parents and F₁.

these lines we have plotted in figure 1 the standardised measure of environmental sensitivity in the selection environments against the corresponding standardised measure of mean performance for each of the 59 D lines for FT, all expressed as deviations from the overall means. From these plots and similar plots for FH we can identify the four lines that best meet the selection criteria. These lines for FT are identified in fig. 1 and are listed along with those for FH in table 2. Their mean performances and environmental

TABLE 2

The mean performances and environmental sensitivities of the four D selections and of the corresponding four S selections for flowering time and final height. All are expressed as deviations from the controls

Selection criterion	D selections			S selections	
	No.	Performance	Sensitivity	Performance	Sensitivity
<i>Flowering time</i>					
Hh	D4	24.91	7.84	3.61	2.98
HI	D13	17.06	-4.03	24.01	6.96
Lh	D24	-13.49	4.65	-6.09	-2.05
Ll	D30	-5.89	-3.68	-10.84	-2.09
<i>Final height</i>					
Hh	D55	32.02	15.76	32.57	5.64
HI	D49	13.12	-14.48	18.17	0.92
Lh	D1	-36.13	2.53	-27.18	-8.61
Ll	D10	-50.14	-8.63	-40.58	-9.90

sensitivities (non-standardised) expressed as deviations from the control value are also listed. We have also listed in the table for comparison the corresponding properties of the S selections expressed as deviations from the same controls and their standardised values are shown in fig. 1.

Comparison of these S and D selections illustrates again what is already quite clear from table 1, namely, that with the possible exceptions of the Ll selections for FT and FH and the Hh selection for FH the D lines meet the selection criteria considerably better than the F_7 generations of the S selections. This is most marked for the two S selections, the Lh selection for FT and the HI selection for FH, which were the least satisfactory of the S selections (Brumpton, Boughey and Jinks, 1977). This obviously has a bearing on the cause of the failure of these two S selections which will be discussed in the final section.

(ii) Comparisons in other environments

For no other reason than resource limitations, the S selections were based upon assessments made at two sowing dates at the normal planting density (environments 2N and 4N). Given greater resources we would have made the assessments of mean performance and environmental sensitivity in the standard set of four sowing dates and two densities used in our other investigations (Perkins and Jinks, 1973). Such practical limitations will, however, always apply to a greater or lesser degree in that we can never include in a single selection experiment all or even most of the environmental variables which can affect these two aspects of the phenotype. The problems

this raises are, therefore, general, the most immediate being the extent to which the mean performances and environmental sensitivities of the S and D selections will be maintained in other environments, both related and unrelated. For the D selections, however, we can go further in a way that illustrates one of the advantages of single seed descent over family selection. In the last section we chose D selections in the two environments, 2N and 4N, solely to facilitate comparisons with the corresponding S selections. Our choice of the two environments was in no way determined by practical limitations of the kind that applied during the selection of the S lines. If, therefore, we find among the 59 D lines any that come closer to satisfying the selection criteria in these new environments, or on average over all environments, we can choose them as alternatives to the D lines we chose earlier without the need for further selective breeding.

Our assessments of the S and D lines in all four sowings (1, 2, 3 and 4) and at both densities (N and H) have, therefore, been used to examine the following:

- (a) The extent to which the S and D selections made in environments 2N and 4N maintain their selected phenotypes in environments other than those in which they were selected, and
- (b) whether among the D lines there are some which meet the four selection criteria better than the S and D selections when grown in the new environments.

The conclusions that emerge are so clear-cut that they can be drawn directly from tables 3 and 4 without further analyses. In table 3 are listed the mean performances of the S and D selections in the selection environments (2N and 4N) and in three other combinations of environments, namely, 1N and 3N; 1N, 2N, 3N and 4N; and 1H, 2H, 3H and 4H. Also listed are the three other sets of four selections we can make from among the D lines using the procedures described in Section 3 (i) and fig. 1 which best meet the selection criteria in these three novel combinations of environments. The total number of D lines which meet the selection criteria as well as, or better than, the S and D selections in all four combinations of environments and from which the additional D selections in table 3 are drawn are listed in table 4.

We shall first consider the three related sets of environments at the normal density. For final height (table 3) the reactions of the D and S selections varies with the selection. For example, the Hh selection D55 is chosen as the line which best meets the selection criteria in all three sets. Furthermore, it is the Hh selection among the four S selections that best maintains its selected phenotype over the novel environments at the normal density. In complete contrast the Lh selection made in sowings 1 and 3 (D4) and that made in sowings 2 and 4 (D1) show a complete reversal in their environmental sensitivities when raised in the alternative pair of sowings. And again it is the Lh selection among the four S selections that changes most in its relative sensitivity over these environments. As we shall see later it is significant that the F_1 of the V2 \times V12 cross in general has the Hh phenotype in these environments.

For flowering time as shown in table 3, the situation is completely reversed. It is the Lh selection D24 which is chosen as the line which best meets the selection criteria in all three sets of environments and it is

the Hh selections D57 and D4 which show the complete reversal of their environmental sensitivities between the pair of sowings in which they best meet the selection criteria and the alternative pair of sowings. This pattern, however, does not extend to the S selections for flowering time. All four of these show a complete reversal of their environmental sensitivities between

TABLE 3

The mean performances and environmental sensitivities for flowering time and final height of the D and S selections selected in environments 2N and 4N when raised in this and three other sets of environments (1N and 3N; 1N, 2N, 3N and 4N; 1H, 2H, 3H and 4H) and of the D lines which best meet the selection criteria in these other environments

Selection environment	Selection criteria	Designation	Environmental set								
			2N + 4N		1N + 3N		1N + 2N + 3N + 4N		1H + 2H + 3H + 4H		
			P	S	P	S	P	S	P	S	
<i>Flowering time</i> 2N + 4N	Hh	S	3.61	2.98	0.11	-2.20	1.86	-1.15	0.17	-2.85	
	Hl	S	24.01	6.96	13.24	-7.83	18.62	2.18	22.13	9.39	
	Lh	S	-6.09	-2.05	-3.76	2.05	-4.93	0.68	-5.61	0.91	
	Ll	S	-10.84	-2.10	-9.36	2.86	-10.10	0.91	-11.56	3.45	
	Hh	D4	24.91	7.84	12.09	-1.90	18.50	3.87	18.02	1.47	
	Hl	D13	17.06	-4.03	10.54	-0.61	13.80	-0.81	12.64	0.59	
	Lh	D24	-13.49	4.65	-10.31	7.46	-11.90	4.48	-12.38	3.26	
	Ll	D30	-5.89	-3.68	-5.46	1.05	-5.68	-0.48	-6.83	-0.02	
	1N + 3N	Hh	D57	14.36	-4.85	7.90	1.23	11.13	-0.11	9.52	0.35
		Hl	D5	11.91	-4.03	1.97	-8.88	6.94	-0.72	10.93	3.38
		Lh	D24	-13.49	4.65	-10.31	7.46	-11.90	4.48	-12.38	3.26
		Ll	D10	-12.04	1.58	-10.11	-1.28	-11.08	1.51	-11.83	2.86
1N + 2N + 3N + 4N	Hh	D35	24.96	7.38	9.39	-4.32	17.17	4.65	20.23	7.12	
	Hl	D21	8.16	-2.35	7.29	-5.54	7.72	-5.58	4.62	-2.15	
	Lh	D24	-13.49	4.65	-10.31	7.46	-11.90	4.48	-12.38	3.26	
	Ll	D48	-10.24	-0.86	-7.26	-0.73	-8.75	-0.50	-9.21	0.47	
1H + 2H + 3H + 4H	Hh	D35	24.96	7.38	9.39	-4.32	17.17	4.65	20.23	7.12	
	Hl	D8	12.61	0.18	9.89	-1.81	11.25	-1.88	10.54	-5.93	
	Lh	D24	-13.49	4.65	-10.31	7.46	-11.90	4.48	-12.38	3.26	
	Ll	D16	-7.64	0.15	-5.56	-4.01	-6.60	-0.87	-2.89	-6.63	
<i>Final height</i> 2N + 4N	Hh	S	32.57	5.64	35.28	8.60	33.92	4.12	33.80	1.93	
	Hl	S	18.17	0.92	22.88	1.10	20.52	-0.18	19.57	0.43	
	Lh	S	-27.18	-8.61	-29.17	0.49	-28.18	-6.37	-29.79	-0.46	
	Ll	S	-40.58	-9.90	-34.42	1.14	-37.50	-2.35	-39.13	-5.16	
	Hh	D55	32.02	15.76	38.46	10.52	35.24	9.68	37.80	-2.89	
	Hl	D49	13.12	-14.48	18.58	2.17	15.85	-9.95	17.21	-0.62	
	Lh	D1	-36.13	2.53	-36.22	-6.78	-36.18	-1.12	-33.13	-2.92	
	Ll	D10	-50.13	-8.63	-48.48	0.27	-49.31	-5.90	-42.25	-4.91	
	1N + 3N	Hh	D55	32.02	15.76	38.46	10.51	35.24	9.68	37.80	-2.89
		Hl	D17	52.07	9.32	48.78	-0.62	50.42	3.73	48.00	2.34
		Lh	D4	-34.33	-7.49	-27.57	12.78	-30.95	4.20	-27.40	-7.55
		Ll	D34	-43.08	-2.87	-37.72	-5.52	-40.40	-2.78	-39.58	-4.62
1N + 2N + 3N + 4N	Hh	D55	32.02	15.76	38.46	10.52	35.24	9.68	37.80	-2.89	
	Hl	D49	13.12	-14.48	18.58	2.17	15.85	-9.95	17.21	-0.62	
	Lh	D4	-34.33	-7.49	-27.57	12.78	-30.95	4.20	-27.40	-7.55	
	Ll	D10	-50.13	-8.63	-48.48	0.27	-49.31	-5.90	-42.25	-4.91	
1H + 2H + 3H + 4H	Hh	D17	52.07	9.32	48.78	-0.62	50.42	3.73	48.00	2.34	
	Hl	D55	32.02	15.76	38.46	10.52	35.24	9.68	37.80	-2.89	
	Lh	D5	-18.03	1.31	-23.38	5.13	-20.71	1.76	-22.36	5.30	
	Ll	D9	-12.33	-9.03	-13.52	2.56	-12.93	-3.03	-10.79	-8.89	

P = Performance. S = Sensitivity.

the two pairs of environments. Nevertheless it is the Hh selection which overall meets its selection criteria least satisfactorily if we consider both mean performance and environmental sensitivity. To complete the pattern the F₁ consistently has the Lh phenotype for flowering in these environments. It would appear therefore, that for both characters the selection which maintains its phenotype over the environments has the same combination of mean performance and environmental sensitivity as the F₁. It is presumably the

TABLE 4

The distribution of the 59 D lines among the four phenotypic classes, Hh, Hl, Lh and Ll for flowering time and final height in each of the four environmental sets and the number of D lines in each class and environmental set that meet the selection criteria better than the S and D selections, selected in the 2N+4N environmental set

Environmental set	Phenotypic class	No. of D lines	No. of D lines better than	
			S selections	D selections
<i>Flowering time</i>				
2N+4N	Hh	11	7	0
	Hl	12	12	0
	Lh	20	20	0
	Ll	16	1	0
1N+3N	Hh	6	6	6
	Hl	19	0	9
	Lh	28	17	0
	Ll	6	6	6
1N+2N+3N+4N	Hh	5	5	1
	Hl	20	20	5
	Lh	23	18	0
	Ll	11	11	5
1H+2H+3H+4H	Hh	10	10	1
	Hl	16	16	16
	Lh	23	17	0
	Ll	10	10	1
<i>Final height</i>				
2N+4N	Hh	21	5	0
	Hl	9	9	0
	Lh	13	13	0
	Ll	16	1	0
1N+3N	Hh	17	2	17
	Hl	14	14	11
	Lh	13	13	13
	Ll	15	15	15
1N+2N+3N+4N	Hh	19	4	0
	Hl	11	5	0
	Lh	11	11	11
	Ll	18	4	0
1H+2H+3H+4H	Hh	20	4	20
	Hl	9	9	5
	Lh	12	12	12
	Ll	18	3	2

phenotype produced by the dominant alleles. However, this phenotype is Hh for final height and Lh for flowering time, the Hh phenotype being highly environmentally specific for flowering time and Lh being the same for final height.

If we now extend our comparisons to include the four sowings at the higher density we find further differences between final height and flowering time. For final height the relative environmental sensitivities of the D lines

are reversed between the normal and high density environments. Most remarkable of these reversals are shown by lines D55 and D17 (table 3). D55 was chosen as the Hh selection in all of the normal density environments but at the higher density it is the line which best meets the Hl selection criteria, while D17 which is the Hl selection in sowings 1 and 3 at the normal density emerges as the line which best meets the Hh selection criteria at the higher density. Contrasting with this there is little or no evidence of such a reaction to planting density for flowering time. For example, D24 which was chosen as the Lh selection in all the normal density environments is again chosen as the Lh selection at the higher density. Furthermore, the Hh selections which showed the highest specificity in response to changes in sowing date at the normal density show no such response to change in density; the same line D35 is chosen as the Hh selection over all four sowings at both the normal and the higher density.

This pattern is, if anything, reversed among the S selections. For final height, the S selections appear to maintain their selected phenotypes at the higher density somewhat better than the corresponding D selections. And it is for flowering time that the relative environmental sensitivities are completely reversed at the higher density.

Many of these same points could be made again with reference to table 4 in which are listed the number of D lines which meet the selection criteria better than the S and D selections made in environments 2N and 4N both in these and in each of the other sets of environments. These lists also make another point, namely, the wealth of fixed variation among the D lines which can meet any selection criteria we choose to impose in these environments better than the S selection.

The discussion of the results has centred on the environmental sensitivities because it is the constancy or variability of the sensitivities that has most clearly distinguished the different lines and their reactions to different environments. Reference to table 3 shows that there are changes in mean performance among the S and D lines over the various sets of environments but these changes are quantitative rather than qualitative. For final height there is no case where there is a change in ranking among the four selections made in one set of environments when grown in another set and for flowering time there are only two instances of this occurring. Changes in mean performance do not, therefore contribute significantly to the broad qualitative comparisons we are making in this paper.

4. CONCLUSIONS

From the practical viewpoint the most important conclusion to emerge from these studies is the superiority of the D lines produced by single seed descent as a source of Hh, Hl, Lh and Ll phenotypes over the S lines which were deliberately selected to produce these phenotypes. If we also take into account the relative ease and economy with which the D lines were produced their superiority over the S lines is even more impressive.

No S selection was obtained which had a Lh phenotype for FT or a Hl phenotype for FH. Reference to tables 1, 2, 3 and 4 shows that there is no shortage of D lines with these phenotypes in the environments used for selection and there is no difficulty in choosing from among the D lines selections which have large deviations from the controls in the directions

appropriate for Lh selections for FT and Hl selections for FH. We can be quite certain therefore, that the F_2 from which both the D lines and the S selections were derived contained the genetical potential to produce all four combinations of performance and sensitivity for both characters. Our failure to obtain certain combinations among the S selections must, therefore, be due to shortcomings in the selection procedures.

The greatest single contributor to the shortcomings of these procedures is undoubtedly the confounding effect of seasonal differences on the determination of environmental sensitivity. We noted this effect particularly on final height between the F_3 generation of the S selections grown in 1969 and the F_4 and F_5 selections grown in 1970 and 1971 (Brumpton, Boughey and Jinks, 1977). It can also be inferred from the assessments of the F_7 generations of the S and D lines summarised in table 3. Thus the environmental differences that occur between the two pairs of sowings, 1N and 3N, and 2N and 4N, are of a kind, if not of the magnitude that occur between seasons. Indeed, they were chosen on the basis of earlier studies for this reason (Perkins and Jinks, 1971). Thus we can infer the likely consequences of seasonal differences during the selection process from the comparisons of the S and D lines in these two pairs of environments (table 3). For final height two of the S selections (Lh and Ll) and three of the corresponding D selections (Hl, Lh and Ll) reverse their environmental sensitivities relative to the controls between these two pairs of environments. For flowering time all four S selections and two of the corresponding D selections (Hh and Ll) reverse their environmental sensitivities relative to the controls between these two pairs of environments. If because of seasonal differences changes of this kind and magnitude occurred relative to the contemporary controls between the successive generations of the S selection programme they would more than explain the disappointing responses for environmental sensitivity.

From the theoretical point of view the most important point to emerge from these studies is that the selections with the combination of mean performance and environmental sensitivity characteristic of the F_1 , namely Lh for FT and Hh for FH, maintain both aspects of their phenotypes over all the sets of environments better than the other three combinations of performance and sensitivity. Dominance is clearly for a high level of responsiveness (h) to changes in the date of sowing that is maintained over the full range of sowing dates combined with early flowering (L) or tallness (H). These are presumably the most advantageous combinations of performance and sensitivity.

In contrast, the responsiveness of the high selection (h) to changes in date of sowing in combination with late flowering (H) or shortness (L) varied from high to low over the full range of sowing dates. While, therefore, the D lines confirm that mean performance and environmental sensitivity can be relatively freely combined in all combinations there may well be an incompatibility between certain combinations of performance and sensitivity outside of the very narrow set of environments in which they were selected. Indeed, our only clear exception to this is for the combination where both performance and sensitivity are displaying the dominant phenotype.

In a corresponding series of investigations of mean performance and temperature sensitivity for growth rate in *Schizophyllum commune* (Jinks and Connolly, 1973, 1975; Connolly and Jinks, 1975), a high general responsive-

ness to changes of temperature over the full range used was also determined by dominant genes but a specifically high or low response confined to a relatively narrow range of temperatures was determined by recessive genes. Both in *Nicotiana* and *Schizophyllum* therefore, the dominant phenotype maintains its level of responsiveness consistently over a range of environments while the recessive phenotype does not. But in neither species is heterozygosity a prerequisite for this consistency. All the *Schizophyllum* lines were highly inbred (Connolly and Jinks, 1975) while in *Nicotiana* relatively inbred D lines shared this property with the F₁.

With the selections that are now available from these investigations we have been able to examine the genotypic and phenotypic components of general as opposed to specified responsiveness over a wider range of environments. These will be the subjects of further papers.

5. REFERENCES

- BRUMPTON, R. J., BOUGHEY, HILARIE, AND JINKS, J. L. 1977. Joint selection for both extremes of mean performance and environmental sensitivity to a macroenvironmental variable. I. Family selection. *Heredity*, 38, 219-226.
- CONNOLLY, V., AND JINKS, J. L. 1975. The genetical architecture of general and specific environmental sensitivity. *Heredity*, 35, 249-250.
- JINKS, J. L., AND CONNOLLY, V. 1973. Selection for specific and general response to environmental differences. *Heredity*, 30, 33-40.
- JINKS, J. L., AND CONNOLLY, V. 1975. Determination of the environmental sensitivity of selection lines by the selection environments. *Heredity*, 34, 401-406.
- PERKINS, JEAN, M., AND JINKS, J. L. 1968. Environmental and genotype-environmental components of variability. III. Multiple lines and crosses. *Heredity*, 23, 339-356.
- PERKINS, JEAN M., AND JINKS, J. L. 1971. Specificity of the interaction of genotypes with contrasting environments. *Heredity*, 26, 463-474.
- PERKINS, JEAN M., AND JINKS, J. L. 1973. The assessment and specificity of environmental and genotype-environmental components of variability. *Heredity*, 30, 111-126.