JOINT SELECTION FOR BOTH EXTREMES OF MEAN PERFORMANCE AND OF SENSITIVITY TO A MACRO-ENVIRONMENTAL VARIABLE

III. THE DETERMINANTS OF SENSITIVITY

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Received 18.vii.77

SUMMARY

Examination of the growth curves of four selections which combine high and low final height with high and low sensitivity to sowing date and planting density have confirmed earlier indications that heritable differences in the pattern of growth are major determinants of environmental sensitivity for final height in *Nicotiana rustica*. The two high-sensitivity selections on the one hand and the two low-sensitivity selections on the other differed in pattern of growth, as expressed by the ratio of 6-week height either to height at flowering time or to final height. The generality of this finding was confirmed by the correlation between these ratios and environmental sensitivities in 59 inbred lines derived from a single cross. No evidence could be found that the mop head, non-mop head difference in habit of growth has any effect on the environmental sensitivity.

1. INTRODUCTION

EVIDENCE that differences in environmental sensitivity among different genotypes of *Nicotiana rustica* is related to differences in their growth habits was first presented by Perkins and Jinks (1968). They showed that the difference in growth habit between mop head and non-mop head genotypes had a marked effect on the pattern of sensitivity to seasonal differences.

Further evidence from 82 inbred lines derived from the cross of varieties 1 and 5 was presented by Perkins (1974). She found a positive correlation between the interaction of genotypes and sowing dates for final height and the genotypic differences for growth rate.

The joint selections for all four combinations of high and low final height and high and low sensitivity to sowing date in the cross of varieties 2 and 12 (Brumpton, Boughey and Jinks, 1977; Jinks, Jayasekara and Boughey, 1977) provide unique material for examining these relationships. The generality of any relationship that emerges can be examined among the 60 random inbred lines which have also been derived from this cross, as well as in the selection lines, when raised in quite a different kind of environment.

Our primary aim is to establish whether environmental sensitivity, which is a difficult trait to measure and select for directly, can be selected for indirectly through a relationship with the pattern of growth.

2. MATERIAL AND METHOD

All the material is taken from the D lines which are 60 inbred families derived by single seed descent from 60 randomly chosen F_2 plants of the

V2 $\times$ V12 cross. Many of the relevant properties of these lines have been described by Jinks, Jayasekara and Boughey (1977).

From analyses of the final height (FH) of these inbreds (F_7) when grown during 1972 in each of eight environments, consisting of the eight combinations of two planting densities for each of four sowing dates, four lines were chosen. These were:

D21 chosen as the best combination of high mean performance over all eight environments and high sensitivity to the differences between the environments (Hh);

D49 chosen as the best combination of high mean performance and low sensitivity over the eight environments (Hl);

D5 chosen as the best combination of low mean performance and high sensitivity over the eight environments (Lh); and

D10 chosen as the best combination of low mean performance and low sensitivity over the eight environments (Ll).

The F_9 generation of these four selections and of the remaining 55 unselected inbred lines were grown at the normal density and sowing date at the Avoncroft experimental field station in 1975. Each family was represented by 10 individually randomised plants. To determine the pattern of growth the height of each plant was measured at 2 ($H1$), 4 ($H2$), and 6 ($H3$) weeks after planting in the field (6, 8 and 10 weeks after sowing), at flowering time (HF) and at the end of the season (FH) (19 weeks after sowing). Although height at flowering time is measured at a time determined by each plant itself, this was chosen in preference to an additional fixed date, because it defines a critical point on the growth curve.

3. RESULTS AND DISCUSSION

In Fig. 1, mean height (in cm.) is plotted against days from sowing for each of the four D selections. For final height the four selections fall as expected into the two classes, high, D21 (Hh) and D49 (Hl), and low, D5 (Lh) and D10 (Ll). They also fall into two equally distinct classes on the rate at which they attain their final height. Two selections, D49 (Hl) and D10 (Ll) do so much earlier in the season than the other two selections, D21 (Hh) and D5 (Lh). This classification, which coincides with their sensitivity to variation in sowing date and planting density is orthogonal to the first. Our earlier indications (Perkins and Jinks, 1968; Perkins, 1974) that environmental sensitivity to these environmental variables and to seasonal differences is related to the pattern of growth appears, therefore, to be borne out by these selections.

Only one of the four selections D5 (Lh) however, shows any trace of the mop head habit of growth, the other three being unambiguously non-mop headed. There is, therefore, no clear indication that this difference in growth habit is a determinant of the differences in environmental sensitivity.

Further examination of the growth curves (fig. 1) shows that all four lines achieve much the same proportion of their final heights by the time they flower; and because the rate of growth rapidly decelerates immediately flowering commences, the two selections with low sensitivity, D49 (Hl) and D10 (Ll), achieve most of their final height early in the season and also

FIG. 1.—The mean height (cm) plotted against days from sowing for the four D lines selected for their mean performances and environmental sensitivities in 1972 when grown in 1975 (♦ is used for height at flowering time).

flower relatively early. As a result, growth is already decelerating by the time the third height measurement (H3) is taken in the two low sensitivity selections (*l*), but is still accelerating in the two high sensitivity selections (*h*). It is not surprising, therefore, that the two statistics which achieve the clearest separation of the two low sensitivity from the two high sensitivity selections are:

- (i) the ratio of the height attained 6 weeks after planting (H3) to that attained by flowering time (HF); and
- (ii) the proportion of the final height (FH) achieved 6 weeks after planting (H3).

No separation is achieved by the proportion of the final height that is attained by flowering time.

To test the generality of the relationship between the pattern of growth and environmental sensitivity displayed by the four selection lines we can, therefore, examine the relationship between the environmental sensitivities of 59 of the random sample of 60 D inbred lines determined in 1972 (Jinks, Jayasekara and Boughey, 1977) and the two ratios H3/HF and H3/FH estimated from the 1975 experiment (section 2). The estimates of the environmental sensitivities (σ_b) and of these two ratios are listed in table 1.

TABLE 1

Estimates of FH environmental sensitivities in 1972 (σ_b) and the ratios H3/HF and H3/FH in 1975 for the 59 D inbreds

D line no.	Height ratios		Environmental sensitivity FH σ_b
	H3/HF	H3/FH	
1	0.80	0.63	4.63
2	0.75	0.57	5.51
3	0.39	0.30	9.86
4	0.47	0.39	6.50
5	0.61	0.43	10.65
6	0.65	0.50	10.69
7	0.65	0.47	8.98
8	0.52	0.37	9.50
9	0.96	0.60	3.27
10	1.13	0.81	1.16
11	0.58	0.45	8.15
12	0.81	0.60	9.28
13	0.44	0.35	8.21
14	0.84	0.63	8.45
15	0.58	0.39	10.47
16	0.92	0.60	6.53
17	0.44	0.36	10.21
18	0.55	0.46	5.46
19	0.83	0.62	7.44
20	0.89	0.66	7.42
21	0.55	0.40	12.83
22	0.88	0.65	6.62
23	0.35	0.29	10.65
24	1.45	0.71	6.20
25	0.96	0.67	8.02
26	0.54	0.34	12.27
27	0.39	0.32	10.10

TABLE 1—(continued)

D line no.	Height ratios		Environmental sensitivity $FH\sigma_b$
	H3/HF	H3/FH	
28	0.98	0.63	5.60
29	0.83	0.54	7.76
30	0.91	0.59	9.55
31	1.11	0.68	5.77
32	0.72	0.48	8.90
33	0.75	0.51	10.27
34	0.79	0.58	4.55
35	0.38	0.30	6.16
36	0.73	0.56	4.33
37	0.88	0.67	8.76
38	0.65	0.45	8.04
39	0.61	0.48	6.35
40	0.79	0.61	6.28
41	0.80	0.62	6.24
42	1.07	0.74	5.42
43	0.46	0.40	7.29
44	0.88	0.63	3.21
45	0.63	0.49	8.44
46	—	—	—
47	0.57	0.44	7.71
48	1.11	0.60	7.42
49	0.97	0.56	4.25
50	0.83	0.60	11.64
51	0.98	0.63	8.40
52	0.71	0.52	8.85
53	0.50	0.41	8.66
54	0.53	0.40	7.56
55	0.80	0.50	10.50
56	0.87	0.64	5.22
57	0.50	0.38	4.55
58	0.64	0.47	6.75
59	0.56	0.44	7.51
60	0.52	0.40	10.44
Mean	0.75	0.52	7.65

D selection lines

D5 = Lh

D10 = Ll

D21 = Hh

D49 = Hl

The correlations between the estimates of σ_b and the two ratios are given in table 2. For comparison all the other correlations that could be derived between these estimates of σ_b and the measurements made on the 60 D inbred lines (H1, H2, H3, FT, HF, FH) and the third ratio HF/FH are also given. They are listed in order of ascending correlation.

These correlations leave no doubt that the relationships between environmental sensitivity and the pattern of growth displayed by the four selections are general properties of the whole population of inbred lines. Before discussing them in detail, however, we should note that we are correlating measures of sensitivity which have a relatively low repeatability with measures of growth characteristics made two generations apart (F_7 and F_9), in different years (1972 and 1975), at two different sites (Edgbaston and

TABLE 2

Correlations of environmental sensitivity scores (σ_b) for FH in 1972 with characteristics of the growth curves for the 59 D lines in 1975

Characteristic	Correlation with σ_b	Probability
HF/FH	0.07 ± 0.13	> 0.05
H3	-0.21 ± 0.13	> 0.05
H1	-0.27 ± 0.13	$0.05 - 0.01$
H2	-0.28 ± 0.13	$0.05 - 0.01$
FH	0.37 ± 0.12	$0.01 - 0.001$
FT	0.39 ± 0.12	$0.01 - 0.001$
HF	0.39 ± 0.12	$0.01 - 0.001$
H3/HF	-0.44 ± 0.12	< 0.001
H3/FH	-0.52 ± 0.11	< 0.001

Avoncroft) and at different sowing dates and planting densities. The highest correlations we could reasonably expect, therefore, would not be much greater than the highest observed in table 2. Indeed the correlation between the 1972 and 1975 experiments for final height, which has a relatively high repeatability and heritability, is 0.87 ± 0.06 .

If we now examine the correlations in table 2 against this background we can see that:

- (i) Sensitivity is independent of the proportion of the final height which has been attained by flowering time (HF/FH).
- (ii) There is a tendency for sensitivity to be negatively correlated with the amount of growth attained in the first 6 weeks after planting (H1, H2 and H3), but to be positively correlated with the amount of growth attained at flowering time and by the end of the season.
- (iii) The highest correlations are the negative ones between sensitivity and the two ratios H3/HF and H3/FH which were the best indicators of the sensitivity among the four selection lines. Indeed H3/FH must come very close to predicting all the significant differences in sensitivity that would be repeatable between the 1972 and 1975 experiments.

As a further test of the ability of these ratios to predict the sensitivity, the 59 lines have been classified into high and low (*h* and *l*) on the basis of the sign of the deviation of their H3/HF and H3/FH ratios from the mean ratios over all lines. For example, if the ratio H3/HF is greater than the mean ratio the line is classified as low. In table 3 we compare these predictions with the classification based on their observed sensitivities to sowing date and planting density in 1972. For both ratios the predictions are significantly better than random chance ($P = 0.01 - 0.001$ for H3/FH and $P = 0.05 - 0.01$ for H3/HF). Using H3/FH 69.5 per cent of the lines are correctly classified while for H3/HF 66.1 per cent are correctly classified. There seems little doubt, therefore, that the pattern of growth is a major determinant of the environmental sensitivity of final height which is itself the most important determinant of the variation in *Nicotiana rustica*.

One last point remains to be made. Among the D lines with the most strongly developed mop head habit of growth all four phenotypes *Hh*, *Hl*, *Lh* and *Ll* are almost equally represented. This confirms our conclusion that the mop head, non-mop head difference cannot be one of the primary

TABLE 3

Comparison of predicted sensitivities for the 59 D inbreds as deviations from the mean inbreds ratios, H3/HF and H3/FH in 1975, with the actual sensitivities to sowing dates and planting densities for the inbreds classified in 1972

		Expected sensitivity						
		(i) H3/HF			(ii) H3/FH			
		<i>h</i>	<i>l</i>	Total	<i>h</i>	<i>l</i>	Total	
Observed sensitivity	<i>h</i>	20	10	30	<i>h</i>	21	9	30
	<i>l</i>	10	19	29	<i>l</i>	9	20	29
	Total	30	29	59		30	29	59
Contingency				Contingency				
$\chi^2_{(1)} = 6.11$				$\chi^2_{(1)} = 8.96$				
Probability = 0.05–0.01				Probability = 0.01–0.001				

causes of differences in environmental sensitivity, although in our collection of pure-breeding varieties of *Nicotiana rustica* it appears to be associated with other characteristics which are.

4. REFERENCES

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