INDIRECT SELECTION FOR ENVIRONMENTAL SENSITIVITY IN *NICOTIANA RUSTICA*

M. K. S. AL-BANNA AND J. L. JINKS

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

Received 31.v.83

SUMMARY

Indirect selection for high and low sensitivity to macroenvironmental differences for final height (FH) has been practised among F_2 individuals of the cross of varieties 2 and 12 of *Nicotiana rustica* using a selection index (R7) proposed by Boughey and Jinks (1978), which is the proportion of FH achieved by the middle of the growing season. The F_3 progenies of the selections and of unselected controls were assessed in the range of environments in which the selection index was both measured and originally validated (2 sowing dates $\times$ 2 planting densities at the University site), as well as in a similar set of environments at the poorer Avoncroft site. A correlation analysis combined with a significant response to selection confirms that pattern of growth as summarised by R7 is a major determinant of environmental sensitivity of FH to the environmental treatments at the University site and that it has a high repeatability and heritability. The same analysis and the absence of a response to selection at the Avoncroft site show that the usefulness of the selection index is limited to the University site.

1. INTRODUCTION

Differences in environmental sensitivity among highly inbred families of *Nicotiana rustica* are related to differences in their patterns of growth (Perkins and Jinks, 1968; Perkins, 1974; Boughey and Jinks, 1978; Boughey, Jinks, Coombs and Shufflebotham, 1978). In particular, pattern of growth, as summarised by the proportion of the final plant height achieved by the middle of the growing season (R7) and the quadratic component of the growth curve, is highly negatively correlated with estimates of the environmental sensitivity (σ_e) of final height to planting density and sowing date at the University site in random samples of recombinant inbred lines derived from the cross of varieties 2 and 12 (Boughey and Jinks, 1978; Boughey *et al.*, 1978). Boughey and Jinks, therefore, suggested that indirect selection for environmental sensitivity of final height could be practised by selecting for the ratio R7 and that this should avoid the difficulties previously encountered in direct selection (Brumpton, Boughey and Jinks, 1977; Jinks, Jayasekara and Boughey, 1977).

We shall now examine whether the relationship between R7 and environmental sensitivity of final height extends to the segregating generation of a cross, we shall estimate its heritability in these generations and test its value and general validity as a selection index for environmental sensitivity.

2. MATERIALS AND METHOD

98 F_3 families were produced by self-pollinating 98 randomly chosen plants of the F_2 of the cross of varieties 2 and 12 of *N. rustica* raised in a completely randomised experiment at the University site in 1978. The F_2

plants were scored individually for height seven weeks after planting in the field (H7) and final height (FH) which are the components of $R7 = H7/FH$. Using $R7$ as an indirect selection criterion for environmental sensitivity of final height, a low sensitivity selection was initiated by choosing the 4 F_2 plants with the highest $R7$ values and a high sensitivity selection was initiated by choosing the 4 F_2 plants with the lowest $R7$ values.

Ten progeny of each of the 98 F_3 families, which include the 8 families of the high and low selections, along with 10 replicate plants of the parental varieties, 2 and 12, and their reciprocal F_1 's and 40 progeny of each of the reciprocal F_2 's were raised in a completely randomised design in each of 8 environments in 1980. The environments consisted of two planting densities (high and normal) on each of two sowing dates (four weeks apart) at each of two sites, University and Avoncroft. The University site is the one in which the selection index $R7$ was measured and the four environmental treatments at this site were the environments in which the relationship between $R7$ and environmental sensitivity for final height had previously been observed.

The Avoncroft site is a poorer environment than the University. At Avoncroft, varieties 2 and 12 and derivatives of the cross between them grow more slowly and on average are 10 to 15 per cent smaller at the end of the season. Larger genotypes are reduced more than smaller ones and as a result the range of plant heights at the end of the season is 12 to 25 per cent less than on the University site. Similarly the range of environmental sensitivities to the four environmental treatments is correspondingly reduced on the Avoncroft site.

Plant height seven weeks after planting (H7) and at the end of the growing season (FH) were scored on each of the 8800 plants raised in total in the 8 environments.

3. RESULTS

(i) *Measures of environmental sensitivity*

Two measures of environmental sensitivity have been used. The first is the square root of the between environments component of variation (σ_b) (Brumpton *et al.*, 1977). This was estimated for each of the 104 families by carrying out one way analyses of variance for the four environmental treatments at each site. The second is the regression coefficient ($1 + b$) of the linear regression of the phenotypic mean of each family in each of the four environments at each site on their additive environmental values (e_j 's) (Perkins and Jinks, 1968). The linear regression coefficient was estimated for each of the 104 families using the mean of all families in each environment as its environmental value. Where there is no significant non-linear component these coefficients measure the relative sensitivities of the 104 families otherwise they measure the relative linear component of these sensitivities.

(ii) *Selection index and environmental sensitivity*

The correlations between the $R7$ values of the 98 F_2 parents and the estimate of the environmental sensitivities of FH in their F_3 families in the four environmental treatments at the University site are given in table 1.

TABLE 1

The correlation between the selection index (R7) in F₂ parents and environmental sensitivities (σ_b and $1+b$) of their F₃ progenies to environmental treatments at the University and Avoncroft sites

Site	R7/ σ_b	R7/(1+b)
University	-0.25 ($P=0.01$)	-0.29 ($P=0.004$)
Avoncroft	0.003 ($P=0.98$)	0.11 ($P=0.27$)

Whether sensitivity is measured by σ_b or $(1+b)$ the correlation is significant and takes a similar negative value. Both, however, are smaller than the correlation of -0.42 reported by Boughey and Jinks (1978) and Boughey *et al.*, (1978). This, however, is probably no more than a reflection of the greater sampling error of the R7 values in the present experiment where they are based on single F₂ plants compared with the earlier experiment where they were based on the means of eight replicates of highly inbred families.

(iii) Heritability of the selection index

To be effective as a selection index R7 must have a high correlation between parent and progeny mean. This correlation for the 98 F₂ parents and their 98 F₃ families averaged over the four environmental treatments is 0.76 ($P=0.001$) at both the University site and at the Avoncroft site. It compares favourably with the estimate of 0.54 for the narrow heritability of the index (Boughey *et al.*, 1978).

(iv) Selections

The relationship between R7 and environmental sensitivity for FH and the high heritability for R7 reported by Boughey and Jinks and Boughey *et al.*, (*loc.cit.*) appear to apply to the early segregating generations of the cross of varieties 2 and 12. It should, therefore, be possible to select for sensitivity in the F₂ using R7. The mean R7 of the 98 F₂ plants raised at the University site in 1978 and of the eight plants chosen from them to initiate the high and low selections are given in table 2. Alongside are given the estimates of the environmental sensitivities (σ_b and $1+b$) to the four

TABLE 2

The mean R7 values of the F₂ parents of the control and high and low selections and the mean environmental sensitivities (σ_b and $1+b$) of their F₃ progenies to environmental treatments at the University and Avoncroft sites

Material	F ₂ parents (1978) R7	F ₃ progenies (1980)			
		University σ_b	(1+b)	Avoncroft σ_b	(1+b)
Control	0.65	3.91	1.08	3.89	1.03
High selection	0.29	6.40	0.94	-1.84	0.39
Low selection	0.89	1.38	0.14	0.36	0.77

environmental treatments at the University site for the F_3 control and the high and low selections. For σ_b the selections show a marked response in the direction expected both relative to one another and to the control. For the alternative measure of environmental sensitivity ($1+b$) the selections also show a marked response in the expected direction relative to one another but the high selection is marginally lower than the control. This suggests that part of the increase in sensitivity in the high selection is non-linear.

(v) *Environmental specificity*

The F_3 families of the high and low selections and control were also raised in the same combination of environmental treatments at a contrasting site, Avoncroft, in order to examine the generality of the findings. The correlations between F_2 parent and F_3 progeny family mean for R7 had the same high value of 0.76 at Avoncroft as at the University site (section iii). On the other hand, the correlations between R7 of the F_2 parents and the environmental sensitivity estimates of their F_3 progenies at the Avoncroft site were much smaller than at the University site and no longer either negative or significant (see table 1). Not surprisingly, therefore, the high and low selections showed no response when assessed at the Avoncroft site although the mean estimates of environmental sensitivity (σ_b and $1+b$) for the controls did not differ from those at the University site (table 2). It is clear, therefore, that the selection index R7 measured on the University site and whose potential value was first recognised at the University site has been effective only at that site.

(vi) *The efficiency of indirect selection*

Since all 98 of the random sample of F_3 families were assessed in all environments it is possible to investigate how successful the indirect selection has been in obtaining high and low selections for environmental sensitivity. If the indirect selection had been 100 per cent successful, F_2 parents of the four most sensitive and four least sensitive of the 98 F_3 families would have been chosen. The F_3 families of these hypothetical perfect high and low selections can be identified among the 98 raised. The relative success of the actual indirect selections can then be measured as the ratio of the differences in environmental sensitivity between the actual and hypothetical high and low selections. For example, the difference between the environmental sensitivities of the indirect high and low selections at the University site measured as σ_b is 5.02 (see table 2), the difference between the corresponding hypothetical selections at this site is 24.19. Thus the indirect selection achieved 21 per cent of the maximum possible response from the same 98 F_2 parents. For the alternative measure of environmental sensitivity ($1+b$), the corresponding success rate is 20 per cent. Bearing in mind that the correlation between the selection index in F_2 parents and the environmental sensitivity of their F_3 progenies as measured by σ_b and $(1+b)$ is only -0.25 and -0.29, respectively (table 1), a 20 per cent success rate is remarkably good.

4. CONCLUSIONS

The results (table 2) show that environmental sensitivity can be selected indirectly using an index which can be measured on single plants raised in a single environment. The selections made on the basis of the index measured at the University site were successful when assessed at that site but not when assessed at the poorer Avoncroft site. This suggests that the differences in environmental sensitivity which are generated by genotype $\times$ treatment interactions within each site differ between the University and Avoncroft sites because of genotype $\times$ site interactions. It remains to be seen whether selections based on the index measured at another site will be successful at that site and only at that site.

Acknowledgements. We gratefully acknowledge the receipt of a grant from the University of Baghdad, Iraq, during the course of this work. We also thank Dr H. S. Pooni for advice and assistance.

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