THE ENVIRONMENTAL INDUCTION OF HERITABLE CHANGES IN *NICOTIANA RUSTICA*. EFFECTS OF GENOTYPE-ENVIRONMENT INTERACTIONS

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Received June 10, 1968

SUSCEPTIBILITY to environmental conditions leading ultimately to permanent heritable changes has been uncovered amongst inbred material of two higher plant species, namely *Linum usitatissimum* (DURRANT 1962; DURRANT and TYSON 1964) and *Nicotiana rustica* (HILL 1965, 1967). Although such changes have persisted without much apparent diminution through several sexual generations, nevertheless analysis of the Nicotiana data reveals that this transmutated material retains some sensitivity to the external environment. When interactions between genotype and environment occur, as they commonly do in biological experimentation, they invariably pose problems especially for biometricians and breeders concerned for the most part with estimation and prediction respectively. Apart from the work of YATES and COCHRAN (1938) however, no serious attempts have been made until recently to resolve these problems. This balance has been redressed to some extent by the work of FINLAY and WILKINSON (1963), EBERHART and RUSSELL (1966), BUCIO ALANIS (1966) and BUCIO ALANIS and HILL (1966), all of whom have devised methods for coping with genotype-environment interactions which, though similar in their means, necessarily differ in their ends. Essentially each method involves regressing the phenotypic performance of an individual genotype, variety or line, against an index calculated as the mean of all genotypes, varieties or lines grown in a particular environment.

In the present article some of these techniques have been applied to experiments involving lines derived by treating an inbred variety of *N. rustica* with different fertilizers, not merely because of the genotype-environment interactions known to occur in these data, but also in the hope that they may shed some further light upon the phenomenon of environmentally induced changes or transmutation.

EXPERIMENTAL METHODS

Initially seed from three inbred varieties of *N. rustica* (V.1, V.16 and V.30—see MATHER and VINES 1952) were grown in soil taken from a set of eight limed plots representing all possible combinations of presence (+) or absence (—) of nitrogeneous (N), phosphatic (P) and potassic (K) fertilizers. From the treatment (or C_0) generation self seed (= families) was harvested from three randomly chosen plants within each of the eight treatment lines. The 24 families

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TABLE 1

Details of experimental size for each location

Generation and environment (E) Number	Year	Environment	Number of plants/family/block
C_0 (E_0)	1962–3	BIRMINGHAM—Grown in a glasshouse during winter.	Families derived from individual plants at this stage.
C_1 (E_1)	1963	BIRMINGHAM (old experimental site).	20
C_2 (E_2)	1964	BIRMINGHAM (new experimental site).	5
C_2 (E_3)	1964	BIRMINGHAM (old experimental site).	5
C_3 (E_4)	1965	BIRMINGHAM (new experimental site).	10
C_4 (E_5)	1966	ABERYSTWYTH	25
C_4 (E_6)	1966	BIRMINGHAM (new experimental site).	25
C_5 (E_7)	1967	ABERYSTWYTH	15
C_5 (E_8)	1967	BIRMINGHAM (new experimental site).	15

thereby generated for each variety were subsequently grown under similar nutrient conditions to determine whether any permanent changes had been induced in this material. All test generations (C_1 – – – C_5) were produced by selfing, whilst each experiment was laid out in a randomized block design with two replicates. Details of the experimental size together with the environments involved are furnished in Table 1. Throughout these experiments two characters were recorded, namely flowering time in days from the date upon which the first plant in a particular environment flowered and final height in inches.

RESULTS

Analysis of the C_1 experiment disclosed that for only one of the three originally treated varieties – V. 16 – was there any reason to believe that environmentally induced changes had taken place. Accordingly our attention will be focussed on this one variety. Previous evidence presented by HILL (1967) suggested that the phenotypic alterations induced in this variety had been transmitted through three generations of selfing without recourse to further differential treatments. From the results and analyses given in Tables 2 and 3 it is perfectly clear that these alterations are maintained after five generations of selfing. At the same time it is equally apparent that the families within the treatment lines were not affected to the same extent by the fertilizer treatments. One can only surmise as to the possible causes for this heterogeneity because the precise reasons for the occurrence of transmutation itself are as yet unknown. Residual heterozygosity within the variety could conceivably account for family differences although this seems

TABLE 2

Mean flowering time (days) and final height (inches) of the eight treatment lines over environments

	Flowering time								Final height								
Line	E_1	E_2	E_3	E_4	E_5	E_6	E_8	Mean	E_1	E_2	E_3	E_4	E_5	E_6	E_7	E_8	Mean
N+P-K-	12.14	4.67	5.17	9.25	8.02	10.37	6.84	9.07	43.74	37.70	39.60	42.40	46.37	45.92	42.29	33.84	42.63
N-P+K-	14.42	6.30	5.97	7.82	6.77	10.23	5.73	8.94	41.90	33.07	36.67	37.43	46.27	41.20	43.68	30.90	40.53
N-P-K+	10.18	3.53	3.73	7.38	5.56	7.43	6.18	6.97	44.39	39.37	41.97	44.88	47.15	49.04	47.36	37.06	45.13
N+P+K-	16.74	6.00	5.80	10.52	9.77	12.47	6.74	11.02	45.88	37.87	41.00	44.33	49.49	48.21	44.84	35.19	45.01
N+P-K+	9.89	3.93	3.83	7.22	7.29	8.62	4.77	7.41	48.66	45.33	46.97	47.03	53.69	51.79	52.56	40.08	49.42
N-P+K+	10.68	3.03	2.67	6.32	8.14	9.49	5.06	7.83	42.35	36.53	38.07	39.15	47.13	40.97	41.54	32.34	41.02
N+P+K+	10.48	4.40	4.00	7.53	7.44	9.49	5.64	7.89	46.96	40.30	43.03	43.47	50.34	46.35	49.36	36.02	45.71
N-P-K-	17.77	5.73	6.07	9.22	8.94	10.23	7.77	10.52	49.73	44.07	45.13	47.88	48.96	49.59	48.37	38.93	47.44
Environment mean	12.79	4.70	4.66	8.16	7.74	9.80	6.10	8.71	45.45	39.28	41.56	43.32	48.68	46.62	46.23	35.53	44.60

TABLE 3

Degrees of freedom and mean squares for the analysis of line means over seasons

Item	Flowering time		Final height	
	df	M.S.	df	M.S.
i. Environments	6	541.24***	7	888.89***
ii. Lines	7	79.56**	7	488.04**
iii. Lines × environments	42	7.42**	49	10.91**
iv. Families within lines	16	16.09***	16	82.35***
v. Families within lines × environments	96	3.39***	112	6.13***
vi. Reps within environments accumulated over environments	7	6.93	8	22.87
vii. Reps within environments × lines	49	0.90	56	1.10
viii. Reps within environments × families within lines	112	0.94	128	1.19

Throughout all tables *—P = 0.05–0.01; **—P = 0.01–0.001; ***—P = < 0.001.
Item i has been tested against item iii
Item ii has been tested against item iv
Item iii has been tested against item v
Item iv has been tested against item v
Item v has been tested against item viii

unlikely, bearing in mind the degree of inbreeding which it has undergone. It appears more plausible to suppose that this heterogeneity simply reflects the micro-environmental gradients which existed in the glasshouse during the C_0 experiment. Whichever of these two reasons is the most feasible, the fact remains that there is a pronounced effect of fertilizers over and above this heterogeneity.

Inevitably, however, changes in the relative order or absolute magnitude of these induced effects have been observed during the course of these experiments, and it is these environmental interactions which are of prime concern in the present investigation.

Analysis of genotype-environment interactions: Apart from the marked differences already described, Table 3 confirms that lines and families are interacting with the environment. To permit a more detailed examination of the nature and extent of these interactions, the relevant items in Table 3 have been partitioned so as to yield appropriate orthogonal and between family mean squares (Table 4). Linear effects have also been computed for the main treatment comparisons by means of simultaneous equations. Surprisingly, the environmental interactions as well as the main effects of the treatment lines can be traced mainly to a single—albeit different—nutrient for each character. Thus potassium, besides promoting flowering, produces a response which, in relation to the non-potassic group, varies from one environment to another. Phosphorus and to a much lesser extent nitrogen exert similar effects upon final height.

Descending to the individual family level, practically all families within lines interact with environments for flowering time, although overall only within three of the lines are significant family effects recorded. Evidently the differences in any one environment lack consistency when viewed over the whole experiment. Final

TABLE 4

Linear effects of the fertilizers together with the breakdown of sums of squares of items ii, iii, iv and v of Table 3.

(Tests of significance were carried out as in Table 3)

Item	Flowering time			Final height		
	Linear effect†	df	M.S.	Linear effect†	df	M.S.
ii. Lines:						
Effect of N	0.14 ± 0.41	1	6.23	1.08 ± 0.57*	1	393.13*
P	0.21 ± 0.41	1	13.55	—1.54 ± 0.57**	1	1070.67**
K	—1.18 ± 0.41**	1	479.43***	0.71 ± 0.57	1	226.14
NP	0.39 ± 0.41	1	32.31	1.21 ± 0.57*	1	620.37*
NK	—0.02 ± 0.41	1	0.16	1.16 ± 0.57*	1	565.22*
PK	0.12 ± 0.41	1	0.14	—0.41 ± 0.57	1	30.48
NPK	—0.49 ± 0.41	1	25.07	—1.11 ± 0.57*	1	510.37*
iii. Lines × environments:						
Effect of N × environments		6	5.91		7	2.26
Effect of P × environments		6	6.44		7	28.59**
Effect of K × environments		6	17.46**		7	8.93
Effect of NP × environments		6	7.96*		7	7.31
Effect of NK × environments		6	4.81		7	12.39
Effect of PK × environments		6	1.65		7	11.18
Effect of NPK × environments		6	7.68*		7	6.22
iv. Families within lines:						
Between N families		2	42.19***		2	78.61***
Between P families		2	44.33***		2	158.96***
Between K families		2	5.68		2	35.22**
Between NP families		2	1.55		2	33.16**
Between NK families		2	8.03		2	50.11***
Between PK families		2	7.85		2	116.30***
Between NPK families		2	14.11**		2	104.79***
Between NIL families		2	5.01		2	81.65***
v. Families within lines × environments:						
Between N families × environments		12	3.57***		14	5.22***
Between P families × environments		12	6.20***		14	6.56***
Between K families × environments		12	3.06***		14	6.32***
Between NP families × environments		12	2.63**		14	1.87
Between NK families × environments		12	2.66**		14	5.58***
Between PK families × environments		12	3.57***		14	10.46***
Between NPK families × environments		12	1.13		14	7.03***
Between NIL families × environments		12	4.34***		14	5.99***

† These effects are obtained by simultaneous equation from the overall line means given in Table 2. Thus the effect of N is calculated as $\frac{1}{8}$ [(N+P−K− + N+P+K− + N+P−K+ + N+P+K+) — (N−P+K− + N−P−K+ + N−P+K+ + N−P−K−)]. The variance of this expression is given by $V_N = 1/64\ (V_{\overline{N+P-K-}} + V_{\overline{N+P+K-}} + \cdots + V_{\overline{N-P-K-}})$, and the standard error $= \sqrt{V_N}$. Environmental means are used in computing the variances.

height, on the other hand, presents a different picture, because here the relative differences between families are consistent over environments, thereby generating highly significant effects overall. Despite this consistency however, these differences must vary in absolute magnitude from one environment to the next, otherwise interactions at this level could never have been detected in the first instance.

Given a situation in which genotype-environment interactions figure prominently, the problem of predicting performance then becomes uppermost.

Predicting phenotypic performance: Both weighted and unweighted regression analyses were performed on these data, but because the effects of weighting were marginal, only the results of the latter will be given here. Since each genotype, variety or line is regressed in turn against the environmental mean, it follows that the overall regression coefficient must necessarily equal unity. Consequently this item in the analysis is of no particular interest, though it should approximate to the "Environments" item of Table 3. The main interest centres on the heterogeneity in slope of the individual regression lines around the overall regression. Not only is it apparent from Table 5 that such heterogeneity does exist between the treatment lines in their response to the environment, but for both characters this heterogeneity conforms to the pattern foreshadowed by the previous analyses of variance. Hence for flowering time the main distinction lies between the potassic and non-potassic groups, whereas for final height it lies between the phosphatic and non-phosphatic groups. By calculating the regression coefficients for each treatment line (Table 6) it becomes obvious how these distinctions arise. Considering flowering time first, in general those four lines which received potassium

TABLE 5

Breakdown of the lines × environments and between families within lines × environments mean squares given in Table 3

Item	Flowering time		Final height	
	df	M.S.	df	M.S.
Overall regression	1	2464.02	1	6368.10
Lines × environments:				
Heterogeneity of regressions:				
i. K *vs.* non-K group	1	58.25**	.	....
i. P *vs.* non-P group	.	....	1	46.48*
ii. Within groups	6	9.47	6	6.05
iii. Residual	35	5.40**	42	10.76
Between families within lines × environments:				
iv. Heterogeneity of regressions	16	7.01**	16	7.51
v. Residual	80	2.42***	96	5.90***
vi. Experimental error	112	0.94	128	1.19

Item i has been tested against item iii.
Item ii has been tested against item iii
Item iii has been tested against item v
Item iv has been tested against item v
Item v has been tested against item vi

TABLE 6

Regression coefficients and standard errors for the regressions of treatment line means against overall environmental means

Line	Flowering time	Final height
N+P- K-	0.917 ± 0.078	0.950 ± 0.091
N- P+K-	1.015 ± 0.162	1.184 ± 0.114
N- P- K+	0.758 ± 0.105	0.908 ± 0.122
N+P+K-	1.358 ± 0.057	1.119 ± 0.093
N+P- K+	0.792 ± 0.079	0.994 ± 0.100
N- P+K+	1.011 ± 0.146	0.965 ± 0.117
N+P+K+	0.824 ± 0.077	1.073 ± 0.095
N- P- K-	1.324 ± 0.178	0.805 ± 0.114

initially all have slopes of less than one, whereas the remaining non-potassic lines usually possess slopes greater than unity. Since potassium favours early flowering, this implies that the mean difference between the two groups increases as the environment tends towards later flowering. Visual evidence supports the view that this is a labile character whose expression depends critically upon external conditions at the onset of flowering. Thus in warm weather flowering is compressed into a short period of time, and vice versa if cool conditions prevail.

Turning to final height, whilst phosphorus depresses this character overall, those lines which received this nutrient are nonetheless capable of responding to favourable environments at a rate faster than that of the non-phosphatic group (see Figure 1). One would conclude therefore, firstly, that the phosphatic lines appear to be adapted specifically to favourable conditions and secondly, that over the range of environments covered by these experiments the differences between the two groups are maximized under unfavourable growing conditions. Obviously at the lower end of the scale this particular relationship must undergo a radical alteration. Since extrapolation is fraught with danger, what happens then is necessarily a matter for conjecture. Even so, at least three alternative hypotheses spring to mind. First, the relationship between performance and environment may break down altogether, or , second, a different relationship could then apply. Finally, perhaps the most satisfactory relationship between these two variables over the complete range of environments is curvilinear, though within the range normally experienced it is, to all intents and purposes, linear.

At the family level it can be seen from Table 5 that, whilst the magnitude of the heterogeneity of regressions is similar for both characters, it only proves to be significant for flowering time. This is due primarily to the higher residual mean square for final height.

Information on one further aspect of these regression techniques is also provided by Table 5. The fact that the residual items measuring the pooled deviations of each treatment line or family around its own regression, accumulated over lines or families, are significant implies that the linear models adopted here are not wholly satisfactory. But even so, they are probably adequate for the purposes

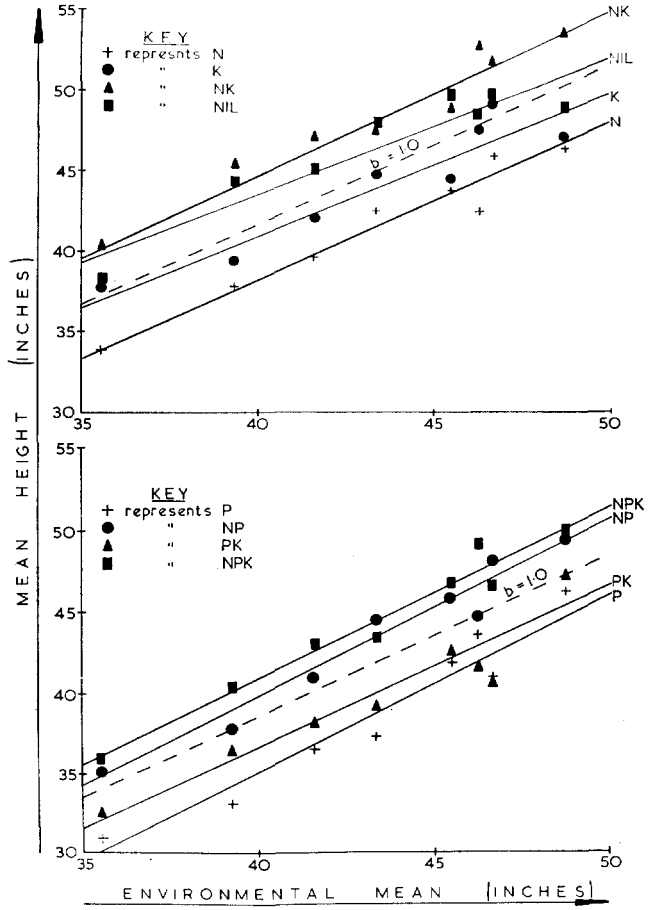

FIGURE 1.—Relationship between individual phenotypic performance and the overall environmental mean of the phosphatic (lower) and non-phosphatic groups (upper) for final height.

of prediction. Moreover, it must be remembered that these experiments have been conducted over a limited number of environments, and this in turn will adversely affect the precision of these techniques.

Stability: Basic to these methods of analysing genotype-environment interactions is the concept of stability. Depending upon the discipline of the experimenter and the objectives of the experiment, it is possible to arrive at different definitions of what constitutes a stable genotype. On the one hand FINLAY and WILKINSON (1963) chose to define it at the phenotypic level, regarding a stable genotype as being one whose absolute performance is virtually independent of the environment. Of necessity, such a genotype will be buffered against environmental fluctuations. On the other hand, the definition proposed by EBERHART and RUSSELL (1966) is perhaps more comprehensive, since it embraces two variables. In their opinion a genotype is stable only if it has a regression coefficient approaching unity allied to a low residual mean square. From an inspection of

Tables 5 and 6 it is evident that none of the individual lines can be classified as stable because they do not comply with the requirements of either definition.

Pursuing this concept further, by plotting the regression coefficient of a genotype against its mean yield over all environments, FINLAY and WILKINSON obtained a triangular scatter of points which, they maintain, enables those varieties adapted to specific environments to be detected. Whilst the selection work of ST-PIERRE, KLINCK and GAUTHIER (1967) on barley under different environments supplies additional evidence for such triangulation, there is no compelling reason for supposing this to be the only expected relationship between these two variables. Thus PERKINS and JINKS (1968) found a strong, positive correlation between the regression coefficient and performance in *N. rustica*. Corresponding scatter diagrams, produced on a family basis for both characters in the present experiment, illustrate these two types of relationship (Figure 2). Whereas flowering time exhibits a positive correlation ($r = 0.62^{**}$),

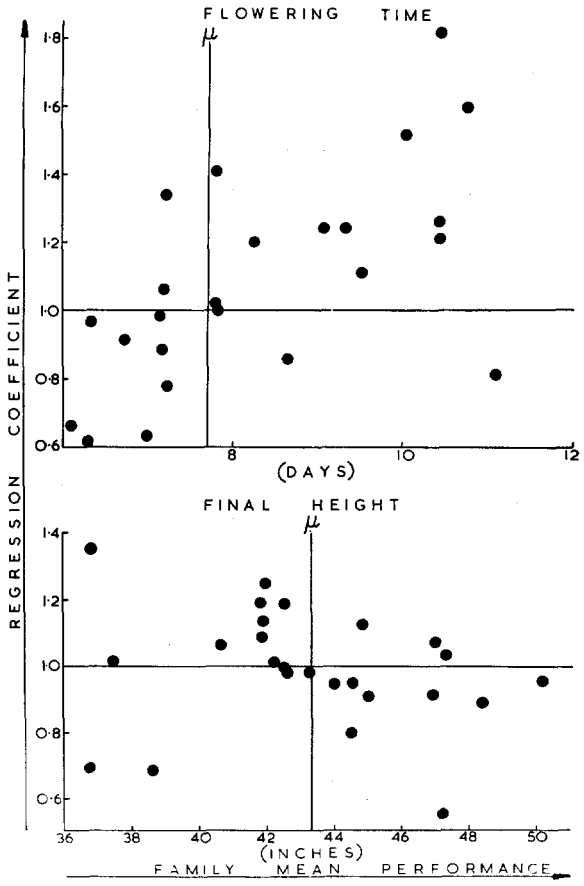

FIGURE 2.—Relationship between family regression coefficient and its overall mean for both characters.

final height tends towards a triangulation of points with no discernible evidence for a linear relationship ($r = -0.19$). Such relationships are not easy to interpret, because environments as well as genotypes must be taken into consideration. But irrespective of the relationship between these variables, it should still be possible to gain some insight into the specific properties of the genotypes concerned.

Innate difficulties of the type just described are largely absent from the definition put forward by EBERHART and RUSSELL, which would thus appear to be simpler and more realistic. Even so, the inclusion of the regression coefficient in their definition is misleading because it contains an implied association between slopes of less than one and poor mean performance. Stability *sensu stricto* would probably be more suitably defined, therefore, solely as the residual deviations of a genotype about its own regression line. Adaptability to specific environments would then be measured jointly by the slope and overall mean performance. However, the pros and cons of these definitions have been elaborated from a biometrical standpoint by PERKINS and JINKS (1968) and from the viewpoint of practical breeding by BREESE (1969).

Genotype-environment interactions and selection: During the C_1 generation selection for early and late flowering ability was practised amongst certain families (for fuller details see HILL 1967). Subsequently these families underwent further cycles of directional selection, its effectiveness being gauged by comparing the performance of the selected families with that of their unselected counterparts. Several interesting features emerge from the analysis of these results given in Table 7. Evidently selection for earliness has proved successful, though its ef-

TABLE 7

Analysis of the effects of selection over seasons

Note that the three late selections were derived from the same family

	Selection Item	Early flowering df	 M.S.	Late flowering df	 M.S.
i.	Between family groups	3	5.80	2	5.39*
ii.	Selected *vs.* Unselected	1	21.60**	1	18.41
iii.	Selected *vs.* Unselected × family groups	3	9.17**	. .	. . .
iv.	Environments	5	109.15***	5	100.11***
v.	Family groups × environments	15	2.61***	10	0.99
vi.	Selected *vs.* Unselected × environments	5	0.49	5	5.69***
vii.	Selected *vs.* Unselected × family groups × environments	15	1.60	. .	. . .
viii.	Replicates within environments	6	2.29	6	2.25
ix.	Pooled error	42	0.39	18	0.59

Item i has been tested against item v
Item ii has been tested against item vi
Item iii has been tested against item vii
Item iv has been tested against item v
Item v has been tested against item ix
Item vi has been tested against item ix

fect is manifestly inconsistent over family groups (each family group comprises a selected family plus its unselected counterpart). On the other hand, the overall response to selection for lateness has been masked to some extent by its interaction with the environment. These conclusions are corroborated by the graphs presented in Figures 3 and 4, in which the performance of each member of a

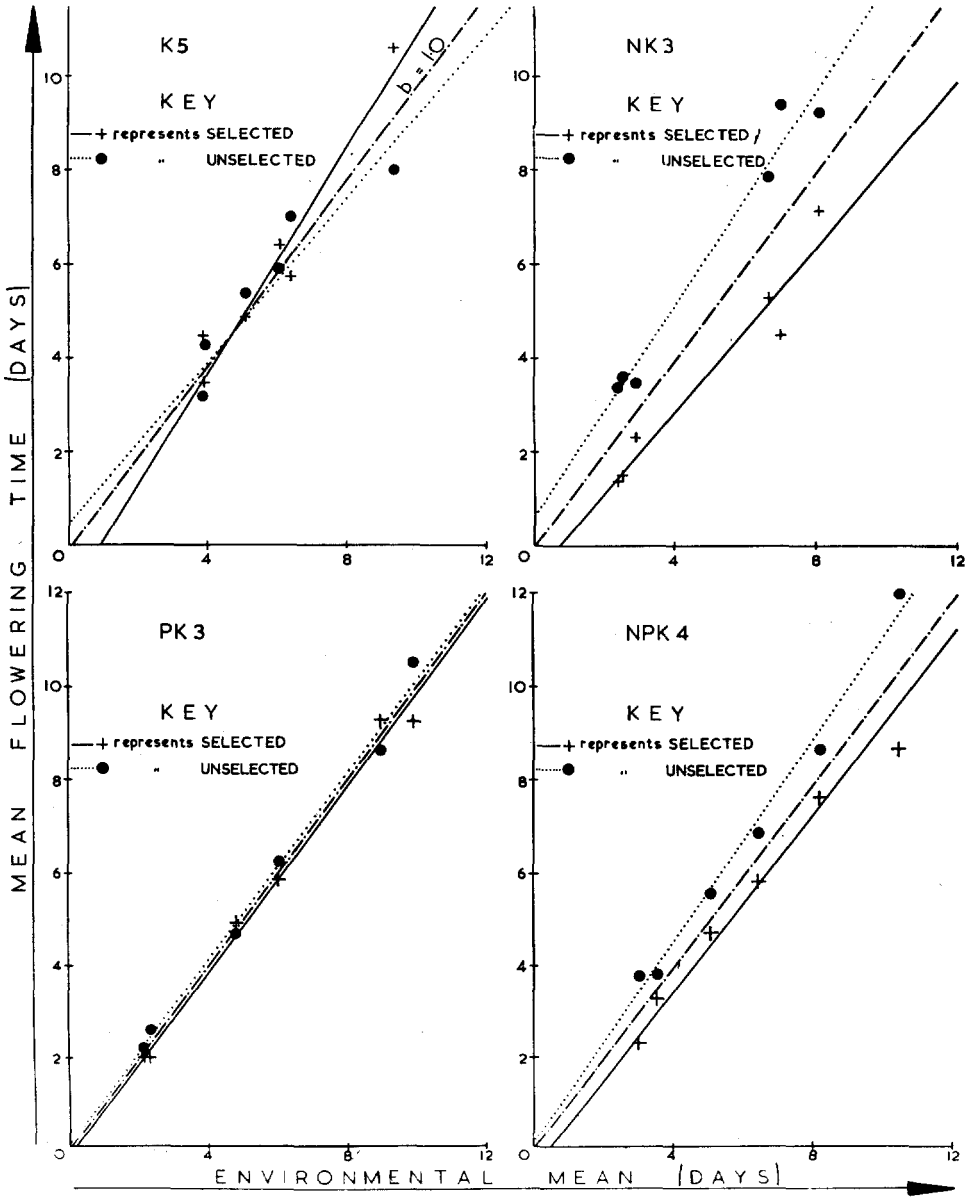

FIGURE 3.—Effects of selection on the environmental response of the four early flowering families.

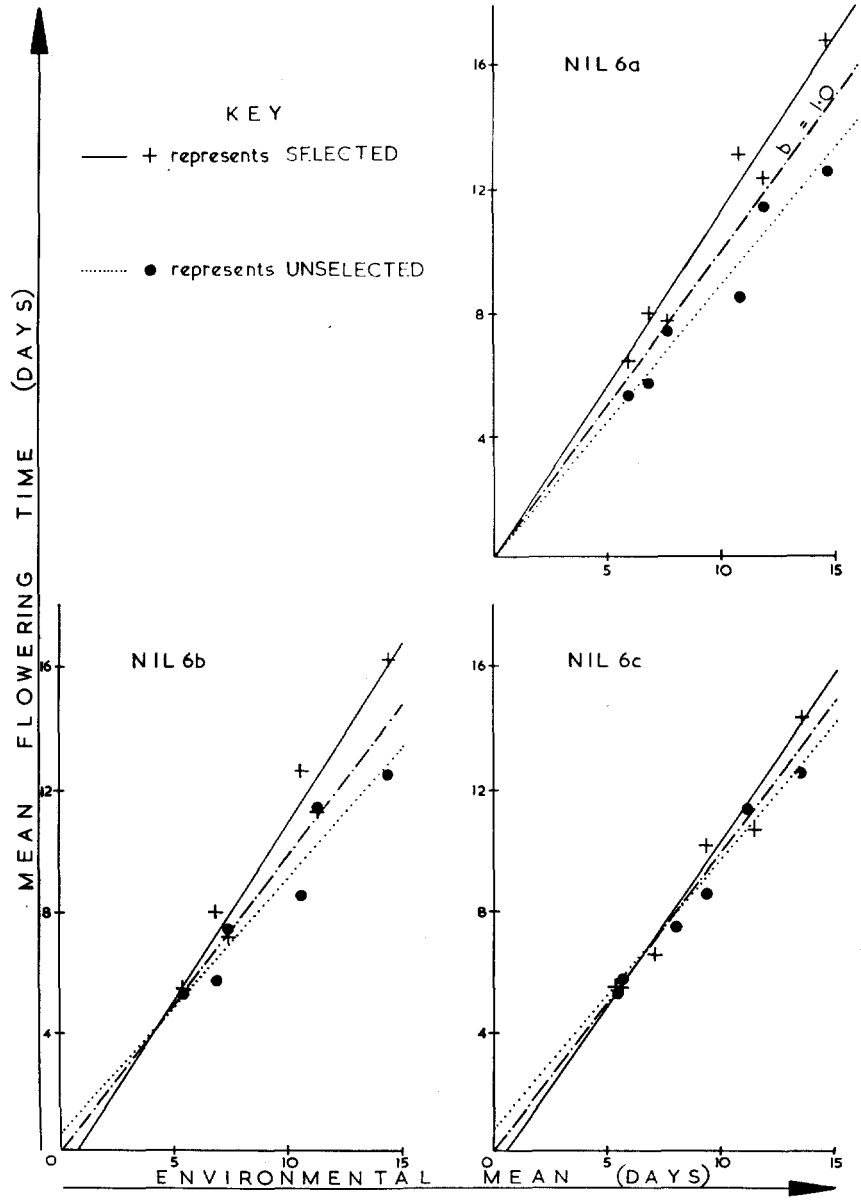

FIGURE 4.—Effects of selection on the environmental response of the three late flowering families.

family group is plotted against the group mean. Amongst the early families the anomalous behaviour of N-P-K+5 accounts not only for the differential effects of selection upon the family groups, but also for the apparent independence of these responses from the environment. As regards the late selections, their re-

sponse increases steadily as the environment tends towards later flowering, hence emphasizing its dependence upon the environment within these families.

In passing it is perhaps worth mentioning that each family group was treated as a pair of inbred lines and subjected to the component analysis devised by BUCIO ALANIS (1966) and BUCIO ALANIS and HILL (1966). Certain trends were suggested by this approach, but the data were insufficient to permit any definite conclusions to be drawn.

DISCUSSION

The fact that environmentally induced changes (= transmutation) have occurred within this variety and further, that these changes are themselves sensitive to environmental fluctuations cannot be seriously disputed on the basis of the evidence given here. However, having said this, questions then arise as to whether the analytical techniques employed have shed any further light either on the possible causes of, or the underlying alterations which have taken place during transmutation. Certainly residual heterozygosity *per se* would fail to account for differences of the magnitude observed between these treatment lines. Essentially induction appears to have altered the inbred variety not so much qualitatively, as one might expect if for example major gene mutations had occurred, but rather at the quantitative level, in the way the various treatment lines and families have responded to the environmental conditions. Because response rates have been principally affected, it is tempting to postulate that such modifications stem from changes which have already taken place at the biochemical level, especially since for both characters the greatest differences occur under unfavourable conditions. It could well be that the rates of certain metabolic reactions have been permanently influenced by the original fertilizer treatments. Indeed, it is not unreasonable to postulate that biochemical changes of this type could themselves have been set in motion by extrachromosomal agencies which, acting in response to the various fertilizer treatments, generate differential changes on the chromosomes. In this manner a plausible chain of events can be built up, beginning with the original external treatments and culminating in permanent heritable changes. Needless to say, this hypothesis can only be speculative for the time being, but even so, the spectrum of variation engendered both in Nicotiana and in flax is in many aspects similar to the range observed within characters known to be governed by many genes whose individual effects are small.

Looking at these techniques in the broader context of practical breeding, it becomes obvious that they could be of immense value because the breeder should be able to define his selection criteria more rigidly. He can now measure the environmental range, which he expects to encounter, in terms of the character for which selection is being practised, and then use this to establish simple linear expressions for specifying differences in the relative performance of his material.

One of the major obstacles to the interpretation of experimental data has resulted from the problems created by the presence of genotype-environment interactions. Thus SPRAGUE (1966) in recognising these problems saw little prospect

at that time of overcoming them because of the near-impossibility of even partially eradicating such interactions under field conditions. Whilst this is certainly true, the possibility of using a different approach in seeking a solution to these problems is ignored. Providing a suitable scale can be devised which will reduce genotype-environment interactions to manageable proportions, one wonders whether it is necessary or desirable even to attempt their elimination. These methods have demonstrated that by reversing the traditional roles of phenotype and environment, using the former to classify the latter, it may then be possible to construct a scale which will enable genotype-environment interactions to be expressed as a simple function of the environment.

Thirty years have elapsed since YATES and COCHRAN established the guidelines for tackling the problems posed by genotype-environment interactions, yet even now many of the wider implications have probably not been grasped fully. Nevertheless such procedures will be of importance because they should lessen considerably the dangers inherent in estimation and prediction from biological material. Before the full benefits can be reaped, however, further experimentation will be required to determine the extent to which regressional techniques can be applied. Doubtless circumstances will arise in which these methods will be of little use, but even here the causes for such a failure could be interesting, especially where they can be linked to morphological, physiological or other known attributes of the material concerned. Amassing this information will prove no easy task, since it could well demand a reappraisal in experimental design, some information on replicate errors within environments being sacrificed so that varietal performance may be assessed under a wider range of external conditions. Armed with this knowledge, however, the biological worker will have at his disposal a technique enabling him to circumvent many of the problems which have appeared intractable hitherto.

We are indebted to PROFESSORS J. L. JINKS and K. MATHER, F. R. S. for their advice and encouragement, to DRS. E. L. BREESE and L. BUCIO ALANIS for many helpful discussions. We are also grateful to MRS. A. ELLINGTON, MR. R. LLEWELYN and MR. H. RICHARDS for their technical and photographic assistance. This work was financed by the Agricultural Research Council of Great Britain.

SUMMARY

Analytical techniques, originated by YATES and COCHRAN and developed extensively by other groups of workers, for handling the problems associated with genotype-environment interactions, have been applied in conjunction with conventional methods of analysis to a set of lines from an inbred variety of *Nicotiana rustica*. This inbred variety was subjected initially to all possible combinations of presence or absence of N, P and K fertilizers, thereby producing eight treatment lines which were selfed for five successive generations, plants within any one generation being treated alike. The treatment lines differ in both their mean flowering time and final height, and while these environmentally induced changes (= transmutation) have persisted for five generations without resort to further differential treatments, nevertheless analysis reveals that this material

retains a certain susceptibility to environmental fluctuations. For both characters the significance of the main and environmental interaction effects stems largely from a single nutrient, namely potassium for flowering time and phosphorus for final height. Applying regressional techniques to the results sheds fresh light onto this situation. The potassic lines, which flower first, generally respond to environmental changes at a rate slower than the non-potassic lines. For final height, the phosphatic group of lines is capable of a more rapid response to favourable growing conditions over the range of environments encountered. Some of the applications and implications of these techniques are discussed.

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