Adaptation to Heterogeneous Environments. III*
The Inheritance of Response to Spacing
in Flax and Linseed (*Linum usitatissimum*)

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Abstract

Random F$_3$ families from two crosses of varieties of *Linum usitatissimum* were grown at two spacings and the following determined: (*a*) the characteristics of the families at each spacing; (*b*) the response of these characteristics to spacing, measured as the value at wide spacing divided by the value at close spacing.

There were significant differences between the families for the characters at each spacing and for their responses. The heritability values for response, calculated from between-family variances, were significant and relatively high for all characters measured.

There was no clear effect of spacing on genetic correlation between the characters, but low genetic correlations between the same character in the two spacings showed that high heritabilities in two spacings may be achieved by independent gene action. Genetic correlations between response characters were character and cross-dependent: there was no evidence of general stability of the genotypes.

A separate experiment showed that there was no evidence for the induction of heritable changes by the application of different spacing treatments in the previous generation.

Introduction

It has been frequently argued that the ability of a character to respond to a change of environment is generally an adaptive feature that can be changed by natural selection (for reviews see Haldane 1946; Waddington 1957; Bradshaw 1965). Evidence for genotypic differences in response, usually manifested as significant genotype × environment interaction effects (see Allard and Bradshaw 1964), is too extensive to review here. Nevertheless, there has been considerable controversy regarding the degree to which the response of a character to the environment is determined by additive gene effects and the degree to which response is character- rather than genotype-specific. Evidence that there is frequently an appreciable additive component to the genetic variance in response comes largely from artificial selection experiments in *Drosophila* (Waddington 1959, 1960, 1961; Kindred 1965; Waddington and Robertson 1966; Druger 1967) and from studies of selection for behavioural responses (e.g. McClearn 1970). In contrast to these studies, there is an appreciable body of evidence that the general stability of an organism with regard to a broad spectrum of characters is determined by non-additive effects. This evidence comes

mainly from studies of parents and their F_1 progeny, whether in pair crosses (Shank and Adams 1960; Griffing and Langridge 1963) or in diallel crosses (Gamble 1962). Much of the literature has been reviewed by Levin (1970).

The previous paper of this series (Khan and Bradshaw 1976) showed that different varieties (genotypes) of flax and linseed (Linum usitatissimum L.) differ markedly in their response to spacing, and that these differences can be largely related to the densities at which flax and linseed are grown under cultivation. The magnitude and detailed pattern of responses were clearly dependent on the particular character under consideration. The present paper extends these studies to investigate the inheritance of response to spacing in crosses between flax and linseed varieties.

In addition, since heritable changes induced directly by environmental treatments (Lamarckian effects) have been well authenticated in flax (Durrant 1962), and since the previous paper of this series showed that spacing affected the morphology of flax and linseed plants considerably, it seemed pertinent to investigate whether these effects were heritable.

Heritable changes resulting from fertilizer effects have also been shown recently by Hill (1965) in Nicotiana. Further evidence for such effects comes from reports from Russian workers: for example, in flax, Senko (1963) has claimed that the effects of fertilizer treatment are heritable, and Aniskova (1963) has made a similar claim for the effects of spacing on a wide range of characters.

Table 1. Morphological characters of parental varieties grown at 1 in. and 6 in. spacing

	Spacing (in.)	Variety Redwing	Wiera	Maroc
Height	1	65.4	87.7	56.4
	6	90.9	123.5	70.5
Capsules	1	3.6	3.4	3.0
	6	58.5	39.8	34.5
Branches	1	1.0	1.0	1.0
	6	3.2	3.0	3.2
Dry weight	1	0.7	0.8	0.8
	6	8.3	10.4	8.5

Methods

In this study, F_3 families obtained by continued selfing of each of the following crosses were used:

(a) Redwing × Maroc (linseed × linseed).

(b) Redwing × Wiera (linseed × flax).

The crosses were originally made by Khan (1963) as part of a diallel analysis. Thirty F_3 families came from plants which in the F_2 generation had been grown at 1 in. (2·54 cm) spacing, and 30 from plants which in the F_2 generation had been grown at 6 in. (15·24 cm) spacing. Parental values at the two spacings are shown in Table 1.

The seeds of each F_3 family (and of the parental varieties) were split into two samples: one sample was grown at 1 in. spacing and the other at 6 in. spacing. The plants were arranged in family rows of 10 individuals per row. Spacings refer to distances between plants within rows as well as distances between rows. The position of families within plots, and the position of plots, was randomized. There were two blocks such that each family was replicated in each block.

The plants were grown under field conditions in an experimental garden at Pen-Y-Ffridd Experimental Station, University College of North Wales, Bangor, Wales, in the summer of 1964.

Six plants, selected at random from a total of 10 per family per replicate, were measured for the following characters:

(a) Height (cm).

(b) Total number of capsules.

(c) Number of basal branches: stems at the base, more than 10 cm long and bearing at least one capsule.

(d) Dry weight (grams): all the plant except roots dried at 60°C for 24 hr.

The response to spacing of individual families was estimated for each character as the ratio of the value at 6 in. spacing to its value at 1 in. spacing. This is a relatively direct measure of response, but suffers from the disadvantage that the theoretical distribution of a ratio is non-normal (Cauchy distribution). The data did not appear to depart markedly from normality, yet since there were insufficient replicates for a sensitive test of departure from normality, two other measures of response were used, namely, the logarithm of the above ratio and the difference between the value of the character at 6 in. spacing and its value at 1 in. spacing. These methods of estimating response gave essentially similar results.

The analysis of variance and variance components were as follows (pooling values for families grown at 1 in. and 6 in. spacing in the F_2 generation).:

Source	DF	MS	Expected mean square
Blocks	1	S_b	$\sigma_w^2 + 6\sigma_{bf}^2 + 360\sigma_b^2$
Families	59	S_f	$\sigma_w^2 + 6\sigma_{bf}^2 + 12\sigma_f^2$
Blocks × families	59	S_{bf}	$\sigma_w^2 + 6\sigma_{bf}^2$
Within families	600	S_w	σ_w^2

The variance components can be further partitioned as follows (Mather 1949; Mather and Jinks 1971):

$$\sigma_w^2 = \tfrac{1}{4}D + \tfrac{1}{8}H + E_1, \tag{1}$$

$$\sigma_{bf}^2 = E_2, \tag{2}$$

where D is the additive genetic variance, H the dominance genetic variance, and E_1 the environmental variance between individuals of the same family in the same row;

where E_2 is the environmental variation due to families being grown in different positions; and

$$\sigma_f^2 = \tfrac{1}{4}D + \tfrac{1}{16}H. \tag{3}$$

Since analysis of the response of characters to spacing was performed on family means, there is no within-family component and the mean squares are therefore one-sixth of the above, i.e.

$$S_{bf} = \tfrac{1}{6}\sigma_w^2 + \sigma_{bf}^2$$

$$S_f = \tfrac{1}{6}\sigma_w^2 + \sigma_{bf}^2 + 2\sigma_f^2.$$

Since the genetic contribution to σ_w^2 is small, $\tfrac{1}{6}(\tfrac{1}{4}D + \tfrac{1}{8}H)$,

$$S_{bf} = \tfrac{1}{8}E_1 + E_2.$$

Given the assumption that $E_1 \simeq E_2$ (in fact E_2 is likely to be somewhat larger than E_1), we can estimate

$$E_1 = E_2 = \tfrac{6}{7}S_{bf},$$

i.e.

$$\sigma_e^2 = E_1 + E_2 = \tfrac{12}{7}S_{bf},$$

and, directly from (3)

$$\sigma_g^2 = \tfrac{1}{4}D + \tfrac{1}{16}H = \tfrac{1}{2}(S_f - S_{bf}).$$

Heritability (h^2) has then been estimated as

$$h^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2}.$$

The estimated values of heritability obtained by this method slightly overestimate the true narrow-sense heritability, since the term σ_g^2 contains a component due to dominance effects.

Genetic correlations were calculated from covariance components of analysis of cross products among the characters by the methods of Robertson (1959). Falconer (1960) and Tallis (1959). Significance of genetic correlations was estimated after the method of Tallis (note that his equation contains a subscript error). In view of the large error of genetic correlation estimates, all 60 F_3 families within each cross were pooled for the analysis.

In the experiment to investigate Lamarckian effects, seeds were obtained from six inbred varieties (flax-Wiera, Stormont Gossamer, SV 0228; linseed-Redwing, Maroc, Valuta) which had been grown at 1 in., 8 in., and 32 in. spacing (Khan and Bradshaw 1976). The seeds were sown at 6 in. spacing in a randomized block design with three replicates. The morphological characters of height, total capsules, branches, capsules per branch, and dry weight were again chosen because of their high response to density. A germination test (percentage germination on moist filter paper) of similar design was also performed on the seed used in this experiment.

Results

Heritability of Individual Characters

All the characters except branch number have a significant heritability, at both 1 in. or 6 in. spacing (Table 2). At 1 in. spacing, branching is completely suppressed in both crosses. Otherwise spacing has very little effect on the heritability, and there is no evidence that growing plants at high density (low spacing) suppresses their genetic differences. The spacing of the parental plants in the F_2 generation appears

Table 2. Heritability (h^2) of individual characters in F_3 families

| | Redwing × Weira | | | | Redwing × Maroc | | | |
| | 1 inch | | 6 inch | | 1 inch | | 6 inch | |
F2 spacing: / F3 spacing:	1 inch	6 inch	1 inch	6 inch	1 inch	6 inch	1 inch	6 inch
Height	0·70***	0·51***	0·69***	0·93***	0·42***	0·84***	0·76***	0·79***
Capsules	0·69***	0·44***	0·54***	0·55***	0·34**	0·77***	0·77***	0·78***
Branches	—	0·33**	—	0·51***	—	0·28**	—	0·68***
Dry weight	0·83***	0·42***	0·69***	0·77***	0·39***	0·83***	0·69***	0·80***

** $P < 0.01$.   *** $P < 0.001$.

to have some effect: when the F_2 plants were grown under high density the heritability values in the F_3 progeny were generally lower. This could be accounted for by the fact that some F_2 plants at this high density were very much suppressed and produced insufficient F_3 seed: such families were therefore excluded from the F_3 progeny.

Heritability of Response of Individual Characters

All the response characters show significant differences between the F_3 families and therefore significant heritabilities (Table 3). The heritability values are large:

Table 3. Heritability of response of individual characters in F_3 families

| | Redwing × Weira | | Redwing × Maroc | |
F2 spacing:	1 inch	6 inch	1 inch	6 inch
Height	0·49***	0·45***	0·72***	0·76***
Capsules	0·36**	0·63***	0·60***	0·73***
Branches	0·33**	0·51***	0·28**	0·68***
Dry weight	0·65***	0·60***	0·57***	0·68***

** $P < 0.01$.   *** $P < 0.001$.

genetic variance in response is similar to genetic variation in the morphological characters themselves under uniform spacing (see below). The high values obtained also argue in favor of a strong additive component since, although the values are overestimates of the true narrow-sense heritability, the dominance and interaction components would have to be very large if they were the only components responsible for the differences between families.

The high heritability of response of characters shown by Redwing × Maroc appears surprising at first glance, since this is a cross between two linseed varieties,

but a study of the differences in the response of characters of the parental varieties (see Fig. 1) reveals that Redwing and Maroc do differ considerably. Further comparison between responses of the parents and F$_3$ families (Fig. 1) shows that the response of some individual families exceeds the response of the parents: such 'transgressive segregation' is well known to plant breeders and the phenomenon is a major basis for varietal improvement (Weber and Moorthy 1952; Culbertson 1954; Finker 1966; Smith 1966). It indicates that parents with relatively similar phenotypes have very different genotypes, such that segregation produces a wide range of progeny: indeed the high heritabilities are to a large extent due to the number of families showing transgressive segregation.
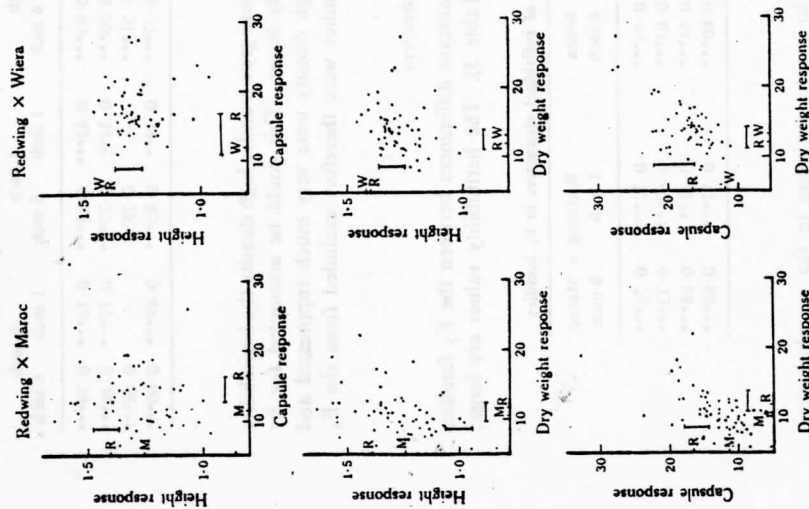
Fig. 1. The correlation between the response of some characters for 60 families per two different crosses.

Genetic Correlations between Characters within each Environment

The genetic correlation between characters within each environment (Table 4) indicates that some characters show high significant correlations, yet others are essentially independent with low non-significant correlations. In the absence of tests of significance between genetic correlations (Tallis 1959), it is not clear if the genetic correlations are significantly influenced by density. However, there is no

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obvious systematic effect of density. Increasing negative correlations between yield components with increasing density have been reported by Adams (1967), but this is not reflected in the characters measured here.

Table 4. Genetic correlations between characters within each environment

HT, height; BR, branch number; CA, capsule number; DW, dry weight

	Redwing × Maroc		Redwing × Weira	
Spacing:	1 inch	6 inch	1 inch	6 inch
HT and BR	—	-0·020	—	-0·003
HT and CA	0·335*	0·200	0·188	-0·048
HT and DW	0·336*	0·450**	0·316*	0·029
BR and CA	—	0·367*	—	0·003
BR and DW	—	0·316*	—	0·260
CA and DW	0·510**	0·812***	0·561***	0·646***

Genetic Correlations between Characters at 1 in. and 6 in. Spacing

Genetic correlations between characters in two environments provide information regarding the degree to which genetic variation in the two environments is determined by identical gene systems, or conversely, the degree to which different gene systems

Table 5. Genetic correlations between characters in two environments

Character abbreviations as in Table 4; suffixes refer to spacings (in.) at which plants were grown

	Redwing × Maroc	Redwing × Weira
HT$_1$ and HT$_6$	-0·246	0·654***
BR$_1$ and BR$_6$	—	—
CA$_1$ and CA$_6$	0·044	0·594***
DW$_1$ and DW$_6$	0·145	0·000

*** $P < 0·001$.

are involved. The results (Table 5) show that in some cases (for example, capsule number in the cross Redwing × Maroc) the character shows a relatively high and similar heritability in both environments yet the genetic correlation is low and not

Table 6. Genetic correlations between response characters

Character abbreviations as in Table 4

	Redwing × Maroc		Redwing × Weira	
	Ratio	Difference	Ratio	Difference
HT and CA	0·449**	0·369*	-0·111	-0·192
HT and DW	0·418**	0·470**	0·187	-0·027
CA and DW	0·661***	0·812***	0·807***	0·650***

** $P < 0·01$ *** $P < 0·001$.

significantly different from zero. Clearly, different gene systems are responsible for genetic variation in the two environments with regard to such characters. Yet in the cross of Redwing × Wiera there are significant genetic correlations for both height

and capsule number in the two environments, which indicates that similar gene systems are in action in the two environments.

Genetic Correlations between Response Characters

Genetic correlations between response characters (Table 6) again indicate that there is no general relationship between responses of the various characters: the level of genetic correlation appears to be both character-dependent and cross-dependent. The response of all characters appears somewhat related in the cross Redwing × Maroc, yet in the cross Redwing × Wiera only capsule number and dry weight are correlated.

Table 7. Variance ratios for individual characters of six varieties previously grown at different spacings' compared at a uniform spacing

Variance due to	DF	Dry wt.	Capsules	Branches	Caps./branch	Height	Germination
Parental spacing	2	0·5	1·1	0·6	2·0	0·1	0·8
Types	1	0·6	24·6***	1·0	29·8***	396·4***	4·8*
Variety within linseed	2	10·9***	19·3***	11·1***	10·8***	2·3	4·6*
Variety within flax	2	17·3***	1·3	3·2	7·5**	11·2***	0·2
Parental spacing × types	2	1·6	1·4	0·7	1·5	0·3	0·2
Parental spacing × var. linseed	4	0·8	0·4	1·5	2·0	0·5	3·1*
Parental spacing × var. flax	4	1·0	1·1	0·8	3·1*	0·7	0·9
Error	34						

$*\ P < 0·05.$ $***\ P < 0·001.$

Lamarckian Effects

The results (Table 7) show that there is no evidence that the previous spacing of the parent has any effect on any character in the subsequent generation. No trends were detectable in the data, and this is evidenced by the low F ratios obtained. Parental spacing × variety interactions were just significant at the 5% level for capsules per branch and for germination when tested against the overall error. However, when the tests were based on the within-type error, rather than the overall error, the interactions did not approach significance. The significance obtained in the overall analysis is therefore the result of a difference in the error variance between the two types for the characters in question.

Discussion

The results presented here show clearly that the response to spacing of individual characters of linseed and flax is highly heritable. Previous work on genotypic differences suggested that this would be the case, and the data presented here show that the magnitude of heritability for response is similar to that for straightforward morphological characters.

Even though this work has demonstrated the existence of additive genetic variance for response, there are both a priori and empirical reasons for believing that non-additive gene systems can be important. It can be argued that genes determining the instability of the phenotype in reaction to the environment may themselves be more prone to interaction with the 'internal environment' of other genes; the work of Gamble (1962) supports this view. In addition, the phenotypic stability of F_1

hybrids is well documented (Levin 1970). The present evidence is inadequate for any general assessment of this hypothesis but provides counter evidence to concepts of phenotypic plasticity (Bradshaw 1965) relying heavily on non-additive genetic variance. Surprisingly, such direct counter evidence has been largely absent.

The presence of transgressive segregation argues not only for independence of action of the gene systems, but also for the independence of transmission (segregation) of different genes determining the same phenotypic expression. It suggests that selection for responses more extreme than the parental ones should be possible; The response of all characters appears somewhat related in the cross Redwing × Maroc, yet in the cross Redwing × Wiera only capsule number and dry weight are correlated.

The conclusion that the response of different characters is frequently controlled by genes which are independent in transmission and/or gene action complicates any concepts involving measures in the 'general stability or instability of a genotype'. Arguments about this feature are seen to be a long way divorced from any realistic considerations: extensive evidence for this was provided in the previous paper in this series (Khan and Bradshaw 1976). The response of a character and the relationship of this response to other characters is dependent on genotype and environment.

The recent demonstration of Lamarckian type effects has made it necessary to reinvestigate this phenomenon by means of modern statistical procedures (Hill 1965), not necessarily just to confirm that these effects can occur, but also to establish situations where there is no evidence for them and so to obtain some estimate of their extent. The present study failed to detect any effect of spacing on subsequent generations, although a wide range of varieties and spacings with drastic effects on the phenotype were used. The results are also not in agreement with those of previous workers on flax. The experimental details of Senko (1963) and Aniskova (1963) in Russia are not available. The contrast with the findings of Durrant (1962) could have arisen because the phenotypic effects of fertilizer treatments are different in certain essential details from the effects of spacing (Khan 1967). Moreover, Durrant (personal communication) found that the effects of fertilizer were inherited only when they were applied at a very early stage (cf. Breese et al. 1965). The effects of spacing are almost certainly not severe in the early stages when the plants are still seedlings. Also Durrant (1962) used different breeding material for his studies. There is clearly need to assess the frequency of Lamarckian effects by further investigations.

The previous paper in this series showed that there were differences in response of flax and linseed varieties to spacing, and analysed these differences in terms of morphology, growth and physiology of the characters of these varieties. The present paper has extended and amplified these results to show that phenotypic plasticity is a clearly inherited feature and a highly specific phenomenon. Many of the evolutionary and practical implications of this have been discussed by other workers (Bradshaw 1965; Lazenby 1965): the present work gives us information which such discussion has up to now only assumed in general terms.

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Manuscript received 19 August 1975

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