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

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Abstract

Random F2 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 Allerd 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 res-  
ponses (e.g. McClean 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 F₁ progeny, whether in pair crosses (Shank and Adams 1960; Griffing and Langridge 1963) or in dialled 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 character of parental varieties grown at 1 in. and 6 in. spacing

<table>
<thead>
<tr>
<th>Spacing (in.)</th>
<th>Redwing</th>
<th>Variety</th>
<th>Wiera</th>
<th>Maroc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height</td>
<td>1</td>
<td>65.4</td>
<td>87.7</td>
<td>56.4</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>90.9</td>
<td>123.5</td>
<td>70.5</td>
</tr>
<tr>
<td>Capsules</td>
<td>1</td>
<td>3.6</td>
<td>3.4</td>
<td>3.0</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>58.5</td>
<td>39.8</td>
<td>34.5</td>
</tr>
<tr>
<td>Branches</td>
<td>1</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>3.2</td>
<td>3.0</td>
<td>3.2</td>
</tr>
<tr>
<td>Dry weight</td>
<td>1</td>
<td>0.7</td>
<td>0.8</td>
<td>0.8</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>8.3</td>
<td>10.4</td>
<td>8.5</td>
</tr>
</tbody>
</table>

Methods

In this study, F₂ families obtained by continued selving 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 dialled analysis. Thirty F₂ families came from plants which in the F₁ generation had been grown at 1 in. (2.54 cm) spacing, and 30 from plants which in the F₁ 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 F₂ 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-Fridd 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 (Gauchy 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 F₂ generation):

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>MS</th>
<th>Expected mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blocks</td>
<td>1</td>
<td>(S_b) (\sigma_b^2 + 6 \sigma_L^2 + 360 \sigma_{\epsilon}^2)</td>
<td></td>
</tr>
<tr>
<td>Families</td>
<td>59</td>
<td>(S_f) (\sigma_f^2 + 6 \sigma_L^2 + 12 \sigma_{\epsilon}^2)</td>
<td></td>
</tr>
<tr>
<td>Blocks × families</td>
<td>59</td>
<td>(S_{bf}) (\sigma_{bf}^2 + 6 \sigma_{\epsilon}^2)</td>
<td></td>
</tr>
<tr>
<td>Within families</td>
<td>600</td>
<td>(S_w) (\sigma_w^2)</td>
<td></td>
</tr>
</tbody>
</table>

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

\[
\sigma_w^2 = \frac{1}{4} D + \frac{1}{4} H + E_1, \tag{1}
\]

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;

\[
\sigma_{\epsilon}^2 = E_2, \tag{2}
\]
where $E_2$ is the environmental variation due to families being grown in different positions; and

$$\sigma^2_e = \frac{1}{4} D + \frac{1}{6} H.$$  \hspace{1cm} (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.

$$S_{MF} = \frac{1}{6} \sigma^2_e + \sigma^2_H,$$

$$S_I = \frac{1}{6} \sigma^2_e + \sigma^2_H + 2 \sigma^2_I,$$

Since the genetic contribution to $\sigma^2_e$ is small, $\frac{1}{6}(D + \frac{1}{6} H)$,

$$S_{MF} = \frac{1}{6} E_1 + E_2.$$

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

$$E_1 = E_2 = \frac{1}{6} S_{MF},$$

i.e.

$$\sigma^2_e = E_1 + E_2 = \frac{1}{6} \frac{1}{6} S_{MF},$$

and, directly from (3)

$$\sigma^2_e = \frac{1}{4} D + \frac{1}{6} H = \frac{1}{6}(S_I - S_{MF}).$$

Heritability ($h^2$) has then been estimated as

$$h^2 = \frac{\sigma^2_e}{\sigma^2_e + \sigma^2_H}.$$

The estimated values of heritability obtained by this method slightly overestimate the true narrow-sense heritability, since the term $\sigma^2_H$ 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 subscripts error). In view of the large error of genetic correlation estimates, all 60 F3 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; lintseed-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 F2 generation appears to have some effect: when the F3 plants were grown under high density the heritability values in the F3 progeny were generally lower. This could be accounted for by the fact that some F3 plants at this high density were very much suppressed and produced insufficient F4 seed: such families were therefore excluded from the F3 progeny.

**Heritability of Response of Individual Characters**

All the response characters show significant differences between the F3 families and therefore significant heritabilities (Table 3). The heritability values are large:

<table>
<thead>
<tr>
<th>Character</th>
<th>Redwing × Weira</th>
<th>Redwing × Maroc</th>
</tr>
</thead>
<tbody>
<tr>
<td>F3 spacing:</td>
<td>1 in.</td>
<td>6 in.</td>
</tr>
<tr>
<td>Height</td>
<td>0.49***</td>
<td>0.45***</td>
</tr>
<tr>
<td>Capsules</td>
<td>0.36**</td>
<td>0.61***</td>
</tr>
<tr>
<td>Branches</td>
<td>0.33**</td>
<td>0.51***</td>
</tr>
<tr>
<td>Dry weight</td>
<td>0.65**</td>
<td>0.60***</td>
</tr>
</tbody>
</table>

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

The high heritability of response of characters shown by Redwing × Maroc appears surprising at first glance, since this is a cross between two lintseed 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 F₃ 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 Mortly 1952; Culbertson 1954; Finkler 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.

![scatter plots showing height and capsule responses for Redwing x Maroc and Redwing x Wiera](image)

**Fig. 1.** The correlation between the response of some characters for 60 families per two different crosses.

<table>
<thead>
<tr>
<th>Character</th>
<th>Redwing x Maroc</th>
<th>Redwing x Wiera</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capsule</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry weight</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**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 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**

<table>
<thead>
<tr>
<th>Character</th>
<th>Redwing x Maroc 1 inch</th>
<th>Redwing x Wiera 1 inch</th>
<th>Redwing x Maroc 6 inch</th>
<th>Redwing x Wiera 6 inch</th>
</tr>
</thead>
<tbody>
<tr>
<td>HT and BR</td>
<td>-0.20</td>
<td>0.03</td>
<td>-0.08</td>
<td>-0.04</td>
</tr>
<tr>
<td>HT and CA</td>
<td>0.335***</td>
<td>0.200</td>
<td>0.316**</td>
<td>0.29</td>
</tr>
<tr>
<td>HT and DW</td>
<td>0.336**</td>
<td>0.450**</td>
<td>0.316##</td>
<td>0.09##</td>
</tr>
<tr>
<td>BR and CA</td>
<td>0.367*</td>
<td>0.260</td>
<td>0.316*</td>
<td>0.260</td>
</tr>
<tr>
<td>CA and DW</td>
<td>0.510**</td>
<td>0.812**##</td>
<td>0.561***</td>
<td>0.646###</td>
</tr>
</tbody>
</table>

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

**Table 5. Genetic correlations between characters in two environments**

<table>
<thead>
<tr>
<th>Character</th>
<th>Redwing x Maroc</th>
<th>Redwing x Wiera</th>
</tr>
</thead>
<tbody>
<tr>
<td>HT₁ and HT₆</td>
<td>-0.246</td>
<td>0.654***</td>
</tr>
<tr>
<td>BR₁ and BR₆</td>
<td>-</td>
<td>0.594***</td>
</tr>
<tr>
<td>CA₁ and CA₆</td>
<td>0.044</td>
<td>0.001</td>
</tr>
<tr>
<td>DW₁ and DW₆</td>
<td>0.145</td>
<td>0.001</td>
</tr>
</tbody>
</table>

***P < 0.001.

**Table 6. Genetic correlations between response characters**

<table>
<thead>
<tr>
<th>Character</th>
<th>Redwing x Maroc Ratio</th>
<th>Redwing x Wiera Ratio</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>HT and CA</td>
<td>0.449**</td>
<td>0.369**</td>
<td>-0.08</td>
</tr>
<tr>
<td>HT and DW</td>
<td>0.418**</td>
<td>0.470**</td>
<td>-0.052</td>
</tr>
<tr>
<td>CA and DW</td>
<td>0.661***</td>
<td>0.812**</td>
<td>-0.151</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Variance due to</th>
<th>Dry wt.</th>
<th>Capsules</th>
<th>Branches</th>
<th>Caps./branch</th>
<th>Height</th>
<th>Germination</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parental spacing</td>
<td>2</td>
<td>0.5</td>
<td>1.1</td>
<td>0.6</td>
<td>2.0</td>
<td>0.1</td>
</tr>
<tr>
<td>Types</td>
<td>1</td>
<td>0.6</td>
<td>24.6***</td>
<td>1.0</td>
<td>29.0***</td>
<td>306.6***</td>
</tr>
<tr>
<td>Variety within lineseed</td>
<td>2</td>
<td>10.9***</td>
<td>19.3***</td>
<td>11.1***</td>
<td>10.9***</td>
<td>2.3</td>
</tr>
<tr>
<td>Variety within lineseed</td>
<td>2</td>
<td>17.3***</td>
<td>13.2</td>
<td>3.2</td>
<td>7.5**</td>
<td>11.2***</td>
</tr>
<tr>
<td>Parental spacing × type</td>
<td>2</td>
<td>1.6</td>
<td>1.8</td>
<td>0.7</td>
<td>1.3</td>
<td>0.3</td>
</tr>
<tr>
<td>Parental spacing × lineseed</td>
<td>4</td>
<td>0.6</td>
<td>0.4</td>
<td>1.3</td>
<td>2.0</td>
<td>0.5</td>
</tr>
<tr>
<td>Parental spacing × var.</td>
<td>4</td>
<td>1.0</td>
<td>1.1</td>
<td>0.4</td>
<td>3.1*</td>
<td>0.7</td>
</tr>
</tbody>
</table>

* 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, 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 lineseed 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 F₁ 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 potential variability in response is more than that revealed by parental variation.

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 these features 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 Antipov (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 lineseed 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 not only assumed in general terms.

Acknowledgments

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