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**Abstract:** This investigation was conducted at the University of wales in 1991-1994. The work described in this paper concerned with the genetic basis of variation in important characters of linseed (*Linum usitatissimum* L.) A 8x8 full diallel cross including reciprocals was carried out using the cultivars Linda, Lidgate, Cristal, Antares, Barbara, Blue-Chip, Norman and McGregor and eight characters, namely, days to flowering, plant height, number of basal branches per plant, number of seeds per capsule, 1000-seed weight, seed yield per plant, total plant weight and harvest index investigated. The results were subjected to several standard systems of analysis (1, 2, 3, 4) designed to separate additive, dominance and epistatic effects. The extensive genetic variability detected for most characters was due to additive gene action rather than dominant effects. As a consequence none of the parental cultivars were consistently high in general combining ability for all eight traits. So that, due to lack of several complementary gen action, a high variation in the future generations can not be expected.

## Keten (*Linus usitatissimum* L.) Çeşitlerinde Varyasyonun Genetik Esasları

**Özet:** Bu araştırma Wales Üniversitesi'nde 1991-1994 yılları arasında yürütülmüştür. Bu makalede belirtilen çalışmanın konusunu keten (*Linus usitatissimum* L.) bitkisinin önemli karakterlerindeki varyasyonun genetik esasları teşkil etmektedir. Linda, Lidgate, Cristal, Antares, Barbara, Blue-Chip, Norman ve McGregor keten çeşitleri kullanılarak yapılan 8x8 tam diallel melezlemesi sonucunda çiçeklenmede gün sayısı, bitki boyu, bitki başına ilk ana dal sayısı, kapsul başına tane sayısı, 1000-tane ağırlığı, bitki başına tane verimi, toplam bitki ağırlığı ve hasat indeksi olmak üzere sekiz karakter incelenmiştir. Araştırma sonucu; addetif, dominant ve epistatik etkilerin belirlenmesi için birçok analız yöntemi (1, 2, 3, 4) kullanılmıştır. Araştırmada ele alınan karakterlerin çoğundaki genetik varyasyon dominant etkiden çok, büyük ölçüde addetive genlerin fonksiyonudur. Sonuç olarak ebeveynlerden hiçbirisi, ele alınan bütün karakterler için yüksek genel kombinasyon kaabiliyetine sahip değillerdir. Bundan dolayı yüksek genel kombinasyon kabiliyetine sahip olmayan genotiplerin birbirlerini tamamlayan çok sayıda genlere sahip olmadıklarından açılan generasyonlarda yüksek bir varyasyon beklenemez.

## Introduction

It is desirable for breeders to have as much information as possible on the genetic control of the important agronomic and morpho-physiological characteristics of the a crop our knowledge of such systems is fragmentary. The comparatively high performance of current cultivars has been achieved mostly by hybridization but suitable combination of complementary genotypes is often obtained by chance. Linseed is a self-pollinating crop and most of the linseed cultivars have been developed by crossing within the linseed gene pool of *Linum usitatissimum*. However, specialized techniques such as mutation breeding (5), interspecific hybridization (6), embryo rescue or protoplast culture (7, 8, 9) or new breeding techniques, such as haploid breeding via anther culture (10).

The inheritance of the characteristics chosen has a major influence on the strategy employed for cultivar development. Qualitative characters controlled by one or a few major genes are more readily manipulated in a breeding program than quantitative traits controlled by many genes. Nevertheless, the breeder is concerned mainly with quantitative characteristics and analysis of the genetic background relating to such characters should aim at providing knowledge which could be of use in both formulating and performing the breeding program. The goals of linseed breeding programs vary considerably depending on the intended use of the germplasm under development. Nonetheless, there are some traits considered important in most linseed breeding programs (7). Yield receives the greatest attention in cultivar development as it does in other crop species. Genetic improvement of yield and yield components are, nevertheless, the most difficult to achieve due to the complex nature of their inheritance and the numerous environmental factors that influence yield and its

components. Breeding for disease resistance is also a part of most cultivar development programs. The fatty acid composition of an oil determines its quality as well as its value for edible or industrial use. In addition, earliness and lodging resistance are also very important.

**Materials and Methods**

An eight parent complete dialel cross experiment was designed using existing and well-established cultivars representing a range of forms and behaviour. These were as follows; Linda, Lidgate, Cristal, Antares, Barbara, Blue-Chip, Norman and McGregor. All the seeds were from certified seed samples obtained from International Seed Producers (Dalgetty), England. The experiment conducted in three stages.

*(i). Growing parental plants for crossing and producing F2 seeds:* Seeds of the eight parental cultivars were sown in 24 pot multitrays using John Innes Compost No 2 as the growing medium, in a heated Glasshouse in which daylenght was extended by 8 hours using Mercury Vapour Lamps, on 6 November 1991. One multitray containing three seeds per pot of each parental cultivar was used. Six weeks after sowing the plantlets from each micropot were transplanted in to 5 inches diameter pots using the same type of soil compost as before. Crossing commenced at the beginning of January 1992 when flower buds were at the proper stage. Emasculation was done by removing anthers with a fine-tipped forceps. Emasculated flower buds were covered with cellophane bags and pollination was made at mid-day one day after emasculation. The pollinated flower bud was covered with a cellophane bag to avoid uncontrolled pollination and drying up. Crosses were harvested at the beginning of May 1992. In addition to crosses between parents, selfed seed was also produced by the same procedures thereby ensuring that comparisons between parents and F1 plants were not influenced by possible differences in seed quality. For the production of F2 seeds, five seeds per pot of each cross combination and selfed parents were sowed in three five inch pots in a heated Glasshouse at the beginning of June 1992. F2 Seeds of each cross combination and selfed parents were harvested by the end of November 1992.

*(ii). Establishment of plants in the field:* The field experiment design was a randomised complete block with two replications (blocks). Plants of parents, F1's and F2's were randomised individually in each replicate. Each combination of the F1 set (including the parental selfs) consisted of 10 plants. Each combination of the F2 set including the parents (progeny of F1 selfs) consisted of 20 plants. There were 192 rows in each block and each row was. 1.5 m long with 15 cm spacing between plants within the row and also 30 cm spacing between rows.

*(iii). Measurements and records:* Each plant was separately labelled and subsequently hand-harvested on 25 October 1993 when all capsules on the plants were mature as indicated by the lack of green colouring on the capsules. Each row was bagged separately and transferred to heated Glasshouse as rapidly as possible for drying off. The following characters were recorded for each plant. Days to flowering, plant height, number of basal branches per plant, number of seeds per capsule, 1000-seed weight, seed yield per plant, total plant weight and harvest index.

*(iv). Statistical analysis:* The data for each separate character was initially analysed according to a computer programme written by G.M. Evans. This programme involved various steps and analyses as follows;

*(1). Hayman's Analysis (1, 2):* This analysis gives a rapid means of recognising different types of gene action in sets of crosses. Significance of the various components is normally represented in the following way. (a) Component *a* indicates additive genetic effects, (b) Component *bt* indicates overall dominance effects, (c) Component *b1* indicates an overall direction of dominance, (d) Component *b2* indicates asymmetric distribution of dominant genes in the parents, (e) Component *b3* indicates dominance interaction between specific genotypes, (f) Component *c* indicates overall maternal effects, (g) Component *d* indicates residual reciprocal effects.

*(2). Mather and Jinks analysis (3):* Three related forms of analyses using covariance of array values on their corresponding parental values (Wr) together with the variance of the elements along each array (Vr) were used to obtained further information on dominance and non-allelic gene interaction. These are summarised as follow.

*(2a). Wr+Vr Analysis:* The non-additive genetic variance that leads to differences in the magnitude of (Vr+Vr) over arrays may be ascribed solely to be the dominance effects of genes, which are independently distributed among the parental lines.

*(2b). Wr/Vr Analysis:* The relationship between the variances (Vr) and the parent-offspring covariances (Wr) is used to provide further information about the distribution of dominance and recessive genes.

*(2c). Wr+Vr/P Analysis:* The correlation/regression of Wr+Vr on the parental values (P) is often used to

determine whether the distribution of the dominant allele is correlated with the phenotype of the common parent. No correlation indicates an ambidirection element in the dominance relationship of the genes controlling the character.

*(3). Griffing analysis (4):* The data was also subjected to a modified general and specific combining ability analysis according to Griffing. This again is an estimation of the additive and non-additive genetic components of variance through the use of general and specific combining ability values. A modification of Griffing's analyses Model 3 was used for the present work (Durrant, Pers. Comm.). The modification involves using the reciprocal difference mean square as the residual item for testing GCA and SCA. Estimates of general combining ability for individual parents was also calculated according to Simmonds (11).

## Results

The results for all characters have been summarized in Table 1, 2, 3 and 4. Additive gene action accounted for a large fraction of the genetic variation for most of the characters. The *a* component in the Hayman's analysis (Table 1) and the General Combining Ability component of Griffing's analysis (Table 3) was highly significant for all characters. Although the *bt* component in the Hayman's analysis (Table 1) was significant for most characters, the Wr+Vr component (Table 2) and Specific Combining Ability component of Griffing's analysis (Table 3) was only significant for a few characters.

Overall direction of dominance (b1 component of Hayman's analysis) was significant only for plant height and total plant weight (Table 1). Random gene distribution was found for almost all characters except days to flowering and 1000-seed weight (Table 1). Significant dominance gene interaction was evident for days to flowering, plant height, number of seeds per capsule and 1000-seed weight (Table 1). The analyses, however, does not give any indication of which genotypes are involved.

The *c* item in Hayman's analysis (Table 1) is significant in several instances there are inconsistencies between the results obtained from the analysis of the F1 data and that

Table 1. The Variance of a, bt, b1, b2, b3, c and d components of Hayman's analysis for eight characters of linseed in the F1 and F2 generations.

| CHARACTERS | a | bt | b1 | b2 | b3 | c | d |
|---|---|---|---|---|---|---|---|
| | | | | F1 GENERATION | | | |
| Days to flowering | 98.800*** | 2.849** | 1.952 | 5.740* | 2.102** | 20.440*** | 2.032 |
| Plant height | 25.441*** | 3.205*** | 0.050 | 3.340 | 3.464** | 1.300 | 0.832 |
| Number of basal branches per plant | 65.238*** | 2.556* | 65.943 | 2.780 | 1.825 | 3.218 | 1.226 |
| Number of seeds per capsule | 5.690* | 5.803*** | 12.738 | 6.209* | 5.759*** | 2.665 | 1.456 |
| 1000-seed weight | 231.781*** | 8.438*** | 35.036 | 15.976*** | 4.395** | 3.730 | 1.522 |
| Seed yield per plant | 11.683** | 3.242*** | 28.851 | 1.479 | 3.089** | 2.942 | 1.257 |
| Total plant weight | 20.941*** | 4.013*** | 180.498* | 1.964 | 4.221** | 2.296 | 1.063 |
| Harvest index | 8.512** | 2.120* | 19.216 | 2.715 | 1.090 | 0.971 | 1.877 |
| | | | | F2 GENERATION | | | |
| Days to flowering | 110.025*** | 7.617*** | 26.134 | 7.595** | 7.294*** | 21.745*** | 3.367** |
| Plant height | 17.285** | 3.362*** | 12806.510** | 2.541 | 2.677* | 1.278 | 4.024** |
| Number of basal branches per plant | 40.494*** | 2.493* | 0.067 | 2.086 | 2.983** | 7.086** | 2.317* |
| Number of seeds per capsule | 11.137** | 4.813*** | 6.910 | 1.538 | 12.621*** | 4.071* | 2.299* |
| 1000-seed weight | 321.134*** | 22.533*** | 3.902 | 62.125*** | 19.365*** | 31.335*** | 5.623*** |
| Seed yield per plant | 5.337* | 1.977* | 2.637 | 1.488 | 1.825 | 3.529 | 1.781 |
| Total plant weight | 8.083** | 2.158* | 5.338 | 1.989 | 1.643 | 2.279 | 3.023* |
| Harvest index | 12.498** | 4.062*** | 9.291 | 7.005** | 3.343** | 3.109 | 3.002* |

* Significant (P≤0.05); **Significant (P≤0.01); ***Significant (P≤0.001)

from the F2. The one exception is days to flowering where it would appear that there is a true maternal effect.

The overall regression of Wr+Vr with parenal values was not significant in most cases (Table 2). There are some significant results in both generation, for example, plant height, 1000-seed weight and harvest index. Wr/Vr analysis indicated significant results for plant height, number of basal branches per plant, total plant weight and harvest index in both generations (Table 2). In addition, Wr+Vr/P analysis indicated only significantly results for harvest index in both generation (Table 2).

## Discussion

Although linseed is one of the oldest cultivated plant species the information on the genetic basis of variation of important morpho-physiological characteristics is relatively limited. The present work represents an attempt to address this problem and the results are discussed in terms of the basic genetic control of the characters measured and in terms of the genetic assessment of breeding material.

The overwhelming evidence from the analysis of the segregating populations is that additive gene action accounts for a large fraction of the genetic variation for most of the characters. The *a* component in Hayman's analysis and the GCA component of Griffing's analysis were all highly significant. This points to the importance of additive genetic effects in linseed. Similar additive effects have been reported for plant height (12, 13), days to flowering (14), number of basal branches (13, 15, 16), seed yield (17), number of seeds per capsule (13, 14, 16) and thousand seed weight (13, 14, 17). It is perhaps to be expected that additive effects would predominate in a self-pollinating species such as linseed since the breeding system would inevitably lead to most loci being homozygous and past selection would, therefore, have tended not to involve dominance effects.

Table 2. A summary of the variance of Wr+Vr together with the regression mean squares for Wr on Vr and Wr+Vr on P for the eight characters of linseed in the F1 and F2 generations.

| CHARACTERS | Wr+Vr | | Wr/Vr | | Wr+Vr/P | |
|---|---|---|---|---|---|---|
| | F1 | F2 | F1 | F2 | F1 | F2 |
| Days to flowering | 2.244 | 6.114* | 0.724 | 50.166*** | 0.724 | 0.186 |
| Plant height | 9.403* | 6.672* | 17.076** | 205.073*** | 0.003 | 5.279 |
| Number of basal branches per plant | 1.946 | 3.487 | 22.243** | 178.246*** | 2.574 | 5.113 |
| Number of seeds per capsule | 1.873 | 5.788* | 0.408 | 15.378** | 0.721 | 8.830* |
| 1000-seed weight | 6.769* | 76.714*** | 38.056** | 62.407*** | 4.396 | 15.681** |
| Seed yield per plant | 3.265 | 1.383 | 4.818 | 58.887*** | 0.060 | 7.345* |
| Total plant weight | 2.017 | 1.277 | 12.181* | 59.862*** | 2.316 | 0.162 |
| Harvest index | 7.644** | 10.673** | 48.200*** | 14.680** | 82.066*** | 19.943** |

* Significant (P≤0.05); **Significant (P≤0.01); ***Significant (P≤0.001)

Table 3. Estimates of general and specific combining ability variances for eight characters of linseed in the F1 and F2 generations.

| CHARACTERS | General Combining Ability | | Specific Combining Ability | |
|---|---|---|---|---|
| | F1 Generation | F2 Generation | F1 Generation | F2 Generation |
| Days to flowering | 29.265*** | 23.390*** | 0.706 | 1.553 |
| Plant height | 31.321*** | 15.369*** | 2.411* | 0.949 |
| Number of basal branches per plant | 25.447*** | 12.019*** | 1.796 | 0.635 |
| Number of seeds per capsule | 7.701*** | 6.838*** | 5.011*** | 1.879 |
| 1000-seed weight | 122.552*** | 45.497*** | 2.153* | 1.631 |
| Seed yield per plant | 18.818*** | 6.204*** | 1.730 | 0.598 |
| Total plant weight | 29.552*** | 7.885*** | 2.916** | 0.522 |
| Harvest index | 10.401*** | 5.589*** | 1.468 | 1.503 |

* Significant (P≤0.05); **Significant (P≤0.01); ***Significant (P≤0.001)

Table 4. Estimates of general combining ability (and their ranking) for eight characters of individual parents in the F1 and F2 generations.

| PARENTS | Days to flowering | Plant height | Number of basal branches per plant | Number of seed per Capsule | 1000-seed weight | Seed yield per plant | Total plant weight | Harvest index |
|---|---|---|---|---|---|---|---|---|
| | | | | F1 GENERATION | | | | |
| L | -2.933(2) | -3.816(2) | -0.305(5) | 0.041(4) | 0.268(2) | -1.329(7) | -5.806(7) | 3.573(1) |
| D | -3.033(1) | -7.302(1) | -1.243(8) | -0.115(6) | 1.599(1) | -2.152(8) | -6.739(8) | 0.146(3) |
| C | 0.742(6) | 3.455(7) | -1.202(7) | 0.157(2) | 0.095(5) | -0.514(4) | -0.845(4) | -1.149(8) |
| A | -0.108(4) | -1.420(3) | 0.544(3) | 0.099(3) | -0.414(6) | -1.286(6) | -3.009(6) | -1.025(7) |
| B | -2.405(3) | 0.051(4) | -0.465(6) | 0.032(5) | 0.214(3) | -0.922(5) | -2.038(5) | -0.961(6) |
| P | 0.225(5) | 0.980(5) | -0.107(4) | -0.375(8) | 0.153(4) | 2.355(1) | 7.316(1) | -0.178(4) |
| N | 3.142(7) | 3.182(6) | 1.628(1) | -0.148(7) | -0.727(7) | 1.925(2) | 4.712(3) | 0.169(2) |
| G | 4.371(8) | 4.872(8) | 1.152(2) | 0.309(1) | -1.188(8) | 1.923(3) | 6.408(2) | -0.574(5) |
| | | | | F2 GENERATION | | | | |
| L | -1.811(2) | -2.726(2) | -0.015(5) | -0.034(6) | 0.216(3) | -0.362(6) | -2.449(6) | 2.350(1) |
| D | -2.753(1) | -6.517(1) | -0.730(7) | -0.291(7) | 1.611(1) | -1.233(8) | -4.364(8) | 0.838(3) |
| C | -0.424(4) | 2.178(6) | -1.294(8) | -0.021(4) | 0.130(4) | -0.203(5) | -0.096(5) | -1.619(7) |
| A | 0.104(5) | -0.740(3) | 1.046(1) | 0.343(1) | -0.207(6) | -1.133(7) | -2.915(7) | -0.499(6) |
| B | -1.559(3) | 0.432(4) | 0.083(4) | -0.052(5) | 0.334(2) | -0.011(4) | 0.181(3) | 0.034(4) |
| P | 1.500(7) | 2.299(7) | -0.323(6) | -0.304(8) | 0.127(5) | 1.208(2) | 5.078(1) | -1.798(8) |
| N | 1.322(6) | 1.042(5) | 0.808(2) | 0.137(3) | -0.913(7) | 0.253(3) | 0.140(4) | 0.843(2) |
| G | 3.621(8) | 4.034(8) | 0.425(3) | 0.222(2) | -1.298(8) | 1.480(1) | 4.425(2) | -0.150(5) |

Earliest to flower and lowest height ranked (1); highest values ranked (1) for all other characters.

Despite the fact that the breeding system of inbreeders tends to favor a genetic system where additive gene action predominates, dominince gene action can still be present. The evidence relating to dominance effects in this present work is less clear. Although the *bt* item in Hayman's analysis was significant for most characters in both generations, the Wr+Vr and SCA item of Griffing's analysis were only significant for a few characters. It would appear that there is no clear pattern of directional dominance. The *bt* item in Hayman's analysis tests for overall dominance effects while Wr+Vr in particular tests only for directional dominance. Confirmation of lack of directional dominance comes from the *b1* item in Hayman's analysis.

Overall directional dominance effects (Component *b1*) were detected for only two characters (total plant weight in the F1 and plant height in the F2 generation) but only in one generation each. Where specific combining ability analysis indicated some significant genetic effects it did so in the F1 generation but not in the F2 generation. This is in agreement with the expectation that overall dominance in the F2 is half that in the F1. In the few examples where dominance effects are shown it is in the direction of previsous selection i.e. in a positive direction except for days to flowering where previous selection has presumably been towards earlines. Similar dominance effects for some characters in linseed have been reported in the past. For example, plant height (18), shoot production, seed yield per plant, number of branches and number of capsules per plant (13, 14, 15, 16), number of seeds per capsule (19), and 1000-seed weight (13, 17) were all demonstrated to be influenced by dominant gene action.

Random distribution of genes constitutes an essential assumption in a diallel analysis. In this study, it was found that, generally, random gene distribution was involved. However, there were some exceptions where this was not so. Typical examples are days to flowering and 1000-seed weight. There was also some evidence from Hayman's analysis that significant dominant gene interaction between specific genotypes was present in relation to the expression of some of the characters (days to flowering, plant height, number of seeds per capsule and 1000-seed weight). The analysis, however, does not give any indication of which genotypes are involved.

The evidence for maternal effects in this germplasm is also questionable. Although the *c* item in Hayman's analysis is significant in several instances there are inconsistencies between the results obtained from the analysis of the F1 data and that from the F2. The one exception is days to flowering where it would appear that there is a true maternal effect.

The inescapable conclusion from all these analyses performed on both data sets is that additive genetic effects predominate and that dominance effects, non allelic gene interaction and maternal effects play a relatively minor role in conditioning the phenotypes of the linseed germplasm pool used in this research. The implications for devising breeding strategies is also clearly evident. Progress should be possible using the well tried standard schemes of hybridization followed by selection of superior homozygous (pure lines) in advanced generations. It would be excepted that a high proportion of the superiority of selected early generation segregants would be transmitted to later generations through selfing. The practical problems of identifying superior early generation progeny would still remain. Nevertheless, the pedigree method, doubled haploid or single seed descent schemes should all be relevant in terms of linseed breeding.

There is very little prospect of utilizing superior F1 hybrids in linseed. The evidence from the present work suggests that the non additive fraction is so low for most traits that very little would be gained from attempting such a breeding scheme. This is apart from the technical problems associated with the production of large amounts of F1 seed. This conclusion is reached despite some suggestions that such a breeding scheme might be appropriate for improving some characteristics in linseed. For example, the earlier report of Patil and Chopde (15) suggesting that selection of crosses based on heterotic response would be more effective for seed yield in linseed does not appear to be appropriate here.

The quesiton of which crosses are likely to give the best progeny still remains to be answered. The diallel design is not necessarily the best for solving this problem although the estimates of individual GCA's give some indication of which parents are likely to combine to produce superior progeny. The estimates of GCA given in Table 4 show the relative values for each trait. These values represent an average prediction for each parent and for each trait separately. However, the breeder has to consider all characters together in designing and executing a breeding program. In this context, the relationship between traits becomes important. Negative relationships can adversely affect the overall response to selection.

In general, breeders aim for early flowering, early maturing, short strawed, large seeded cultivars with good standing power, high harvest index, fertility per capsule and oil content. Although standing power and maturity were not measured in the present study they are related to other characters which were measured. Standing power is related, although not completely, to height while maturity is incompletely related, although not completely, to height while maturity is incompletely related to flowering date. On average, it is clear that the high yielding progenies were late flowering, tall and smaller seeded. This is borne out by an examination of the individual GCA values and their rankings in Table 4. None of the parents were good general combiners for all characters. Cultivars such as Blue-Chip (P), McGregor (G) and Norman (N) which, on average, produced high yielding progenies are also the ones which produced the latest and tallest progeny. The progeny of McGregor (G) and Norman (N) also had the smallest seed (low thousand seed weight). The pattern deviates slightly in that the progenies of Blue-Chip (P) were of medium seed weight. The converse is also true. Linda (L) and Lidgate (D) produced the shortest, earliest and largest seeded progenies but, unfortunately, produced the lowest yielding ones.

It is apparet from this experiment that the pleiotropic effect of short stem in linseed is totally different from that of the dwarfing genes in cereals. In linseed a shorter stem leads to lower biomass and lower seed yield because the polygenes for short stem do not seem to facilitate a change in distribution of photosynthate. The main conclusions from this work can be summarized as follows.

(a). Most of the traits relating to yield in linseed are, predominantly, subject to control from genes of additive effects.

(b). The low levels of dominant gene action which was detected was often ambidirectional.

(c). Head to row selection schemes following hybridization of relevant parents should, therefore, be successful in producing superior pure line cultivars of linseed.

(d). Breeding for heterotic effects has little relevance to the material available at the present time.

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