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Early Generation Selection for High Oil Content and High Oil Quality in Flax

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CONTENTS

page

Introduction ... 3

Materials and methods ... 4

- Genetic materials ... 5
- Chemical analyses ... 5
- Statistical analyses ... 6

Experimental results ... 7

- Variation and heritability of oil content ... 7
  - Oil percentage of F_2 plants ... 7
  - Oil percentage of F_3 bulked lines ... 9
  - Oil percentage of F_3 plants ... 10
  - Heritability estimates of oil content ... 11
- Variation and heritability of iodine value ... 13
  - Iodine value of F_2 plants ... 13
  - Iodine value of F_3 bulked lines ... 13
  - Iodine value of F_3 plants ... 14
  - Heritability estimates of iodine value ... 15
- Variation and heritability of seed weight ... 16
  - Seed weight of F_2 plants ... 16
  - Seed weight of F_3 plants ... 17
  - Heritability estimates of seed weight ... 18
- Associations between characters ... 18
  - Flower color and seed color with oil content, iodine value, and seed weight ... 18
  - Oil content with iodine value ... 21
  - Oil content with seed weight ... 21
  - Iodine value with seed weight ... 22

Discussion and summary ... 23

Literature cited ... 25

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V. E. Comstock[1]

FLAX is grown in the United States to produce linseed oil of high quality. High oil content and improved oil quality are two important objectives of flax-breeding programs. During recent years, increased competition from other drying oils has focused attention on the need for attaining these objectives.

In order to develop an efficient and dependable breeding program to incorporate high oil content and improved oil quality into commercial flax varieties, information is needed on heritabilities of these characters and on associations between them and with other characters. Possibilities of developing flax varieties with high oil content and high oil quality would be greatly enhanced if effective selection for the two characters could be practiced in early generations. This would depend, to a large extent, on the proportion of total phenotypic variance observed in segregating populations that was caused by environmental factors, and that attributable to genetic diversity.

Both genotype and environment have a marked effect on oil content and oil quality of flaxseed. Paatela (1947), Painter, *et al.* (1944), Dillman and Hopper (1943), and Johnson (1932) have reported significant seasonal effects upon oil content and oil quality expressed as iodine number. Weather conditions were the most important variables and conditions favorable for high seed yields were also favorable for large seed size, high oil content, and high iodine number. Painter, *et al.* (1944), Dillman and Hopper (1943), and Paatela (1947) found an inverse relationship between temperatures during the period of seed development and oil percentage and particularly iodine number. Other environmental factors that can influence the oil content and iodine value of flaxseed are soil moisture (Dillman and Brinsmade, 1938), date of sowing (Culbertson, 1956; Johnson, 1932; Manner, 1956; Paatela, 1947), soil fertility (Johnson, 1932), plant spacing (Dillman and Brinsmade, 1938), and presence of disease (Flor, 1944).

The genotype of flax plays an important part in determining the percent oil, iodine value, and seed size as evi-

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denced by intervarietal differences reported by Dillman (1936), Lemos (1949), and Johnson (1932). Highly significant interannual correlations for the three characters were reported by Lemos and Johnson. Oil content of flax varieties tends to be correlated with seed size (Dillman, 1936; Geddes and Lehberg, 1936; Johnson, 1932; Lemos, 1949; McGregor, 1937) and negatively associated with iodine value (Johnson, 1932; Lemos, 1949; McGregor, 1937).

Results of oil determinations on F_3 lines from flax crosses suggest that oil content is inherited as a quantitative character (Carnahan, 1949; Chu and Culbertson, 1952; McGregor, 1937). Crosses between brown- and yellow-seeded varieties, as reported by Carnahan (1949) and McGregor (1937), revealed that high oil content was associated with yellow seed color within segregating populations.

Several studies have been made of iodine values within hybrid populations derived from crosses of yellow-seeded with brown-seeded varieties (Carnahan, 1949; Culbertson and Kommedahl, 1956; Dillman, 1936; McGregor, 1937; Moseman, 1944). Moseman (1944) and Arny as reported by Dillman (1936) found iodine value to be simply inherited. High iodine value was recessive and was conditioned by a gene closely linked with one that conditioned seed color. Data reported by Carnahan (1949), Culbertson and Kommedahl (1956), and McGregor (1937) suggest that this character, although associated with seed color, is conditioned by multiple genes.

Associations between seed characteristics within hybrid populations of flax have been reported (Carnahan, 1949; Chu and Culbertson, 1952; Culbertson and Kommedahl, 1956; Dillman and Hopper, 1943; Moseman, 1944). In general, oil content is correlated with seed weight and negatively correlated with iodine value. However, Carnahan (1949) and McGregor (1937) found no association between oil content and iodine value. Chu and Culbertson (1952) reported iodine value to be negatively associated with seed weight.

Several workers, including Chu and Culbertson (1952), Moseman (1944), Aurora (1959), Myers (1936), and Carnahan (1949) have studied the inheritance of flaxseed weight expressed in grams per 1,000 seeds. All have concluded that seed size is determined by multiple factors with partial dominance for large seed. There was no evidence for association of seed weight with seed color in crosses studied by Myers (1936), Moseman (1944), or Carnahan (1949); however, Culbertson and Kommedahl (1956) found that the seed weights of yellow-seeded lines were significantly higher than that of brown-seeded lines in a study of paired "isogenic" lines.

MATERIALS AND METHODS

The hybrid populations studied arose from crosses between parents that showed extremes in both oil content and iodine value. The crosses were made primarily to study the inheritance of oil content and iodine value and to determine the degree of association between these two quality characteristics. The F_2 and F_3 generations were chosen for analysis because maximum genetic variance would be expected within such populations. Statistical techniques are available for computing estimates of genetic and environmental variances from F_2 and F_3 plant measurements.

GENETIC MATERIALS

Parent Varieties and F_1 Crosses

Plant materials used in this study were the F_2 and F_3 populations from crosses of Redwood and Marine with C.I. 1455. The latter variety is an introduction from India that is not adapated to the North Central Region. It is short, early-maturing, susceptible to wilt and rust, and very high in oil content. The oil quality, as indicated by iodine value, is poor. This variety has yellow seed color and light blue flowers which result from the recessive genotypes "gg" and "aa" respectively (Barnes, 1958). Redwood and Marine are high yielding, disease resistant varieties grown extensively in the North Central flax growing region. They are medium in height and have brown seeds and blue flowers. Redwood is medium late in maturity and is about average in oil content, iodine value, and seed weight among commercially-grown varieties. Marine is early-maturing with relatively small seeds, average oil content, and is particularly high in iodine value.

Crosses were made in the summer of 1954. Five plants each from Redwood and Marine were used as females in crosses with individual C.I. 1455 plants. Twenty-five F_1 plants from each cross were grown in the greenhouse during the winter of 1954-55 along with selfed progenies from Redwood and Marine. A bulked population of C.I. 1455 was grown because male parents succumbed to wilt before selfed seed had matured in the field.

F_2 Populations

Progenies of approximately 100 F_2 plants from each F_1 plant were grown in the field during the summer of 1955 in single 10-foot rows. Parent varieties were included as checks in every tenth and eleventh row. The F_2 plants were classified for flower and seed color. Approximately 200 plants that were free from disease symptoms were selected at random from each cross. A high prevalence of aster yellows virus, which could not always be detected at harvest time, reduced the number of plants available for quality analysis to 193 from Marine x C.I. 1455 and 173 from Redwood x C.I. 1455. Approximately 50 plants of each variety were selected at random from parent rows; data from which were used to estimate environmental variance. Only a few plants of C.I. 1455 produced enough seed for chemical analysis. Seed weight was determined from a sample of 200 seeds from each F_2 plant. The samples were subsequently used for the determination of oil content and iodine value.

F_3 Populations

F_3 progenies from 132 F_2 plants from the cross Marine x C.I. 1455 and 167 from the cross Redwood x C.I. 1455 were grown in 7-foot rows during the summer of 1956. Approximately 1 gram of seed was sown in each row. Forty of the progenies in each cross were replicated in two randomized blocks. Parent varieties were included at intervals of 20 rows. Several rows were discarded because of poor stands, high incidence of aster yellows and *Fusarium* wilt, or because of poor seed production.

Flower and seed color were each classified as to homozygous dominant, homozygous recessive, or segregating for each row. Individual plants were harvested from 81 lines of each cross. Seed quality data from eight plants selected at random from each row are considered in this study. Approximately eight plants were selected at random from each of seven rows of each parent variety. A bulk sample of seed was obtained from the plants remaining in each row. Additional rows from which individual plants had not been selected were bulked also.

CHEMICAL ANALYSES

Oil content and iodine value of approximately 1 gram of seed from individual plants and of bulk samples from both crosses were determined by the small sample analyses technique described by Comstock and Culbertson (1958). All oil percentages are shown on an 8 percent moisture basis.

STATISTICAL ANALYSES

Associations among seed characteristics—oil content, iodine value, and seed weight—were ascertained by phenotypic correlation analyses. F_2 plant measurements and values obtained from F_3 lines (bulk samples and means of plants within lines) were used to compute correlation coefficients. Associations between factors conditioning seed and flower color and the oil content, iodine value, and seed weight were determined by comparing the means of classes within the F_2 and within F_3 with standard "t" test and by analysis of variance.

Variance and covariance analyses of data obtained from the F_2 and F_3 populations of the two crosses were used to estimate the genetic and environmental components of variance. The methods of statistical analysis employed in this study are patterned after the system given by Horner, *et al.* (1955). From the genetic variance and covariances, individual estimates of the additive genetic variance, σ_g^2, and the dominance variance σ_d^2, were obtained for each character by a least squares technique similar to the method given by Mather (1949). These estimates of genetic variances are subject to the assumptions of no nonallelic interactions and no linkage or cytoplasmic effects upon characters studied. In order to facilitate designation, genetic variances are symbolized by three digit numbers as given in table 1.

The first digit of the variance symbol refers to the generation of the individual plant that is the source of a particular plant or line which is being evaluated. The second and third digits refer to the generation or generations in which plants or lines were grown

Table 1. Variances and covariances used for computing estimates of genetic variance components—showing sources, symbol designation, and expectations

Source	Symbol	Expectation: Additive	Expectation: Dominance
Among F_2 plants	222	σ_g^2	σ_d^2
Among F_3 bulked lines	233	σ_g^2	$\frac{1}{4}\sigma_d^2$
Among F_3 lines from plant measurements	233	σ_g^2	$\frac{1}{4}\sigma_d^2$
Within F_3 lines (plants)	333	$\frac{1}{2}\sigma_g^2$	$\frac{1}{2}\sigma_d^2$
Between F_2 plants and F_3 lines (bulked)	223	σ_g^2	$\frac{1}{2}\sigma_d^2$
Between F_2 plants and F_3 lines (means of plants)	223	σ_g^2	$\frac{1}{2}\sigma_d^2$

and indicate whether the component is that of variance or covariance. For example, "223" symbolizes the genetic covariance between measurements on individual F_2 plants (second digit) and F_3 progeny (third digit), all stemming from individuals selected in the second generation (first digit). Likewise "233" refers to genetic variance among F_3 lines, each of which arose from a single F_2 plant.

The phenotypic variance observed among F_2 plants is composed of the environmental component, σ_e^2, plus the total genetic variance, $\sigma_g^2 + \sigma_d^2$. The latter, symbolized by "222," is estimated by subtracting from the total F_2 variance the environmental variance. The latter is estimated by variance among individual plants within parent varieties. Actually, data were available from but one parent of each cross. Therefore the estimates of environ-

Table 2. General form for the analysis of variance of F_3 bulked line data

Source	df.	MS	Components
Replication	$(r-1)$	M_3	
Lines	$(n-1)$	M_2	$\sigma^2+r(233)$
Error	$(r-1)(n-1)$	M_1	σ^2

where r = number of replications, n = number of lines, and σ^2 = environmental variance among plots in the same replication plus variance among individual F_3 plants in lines, and sampling, and chemical determination variation.

mental variance were not so reliable as they would have been had data been available from both parents of each cross.

Analyses of variance of measurements from F_3 bulked lines give an estimate of the genetic variance "233." The estimate is determined by $(M_2 - M_1)/r$. A general form for the analysis of variance of the F_3 bulked line measurements is given in table 2.

Analyses of variance of individual F_3 plant data provide another estimate of "233" as well as "333." A general form for the analysis of variance is given in table 3.

The variance "333" is equal to $M_1 - V_{P_1}$ where V_{P_1} represents parental variance. The genetic variance "233" is computed as follows: $M_3 - M_2/kr =$ "233."

Covariance of the F_2 plant measurements with F_3 bulked line data and with means of plants within lines gave two estimates of the genetic covariance "223." It was estimated by dividing the corrected sums of products by degrees of freedom.

Heritability in the "narrow" sense was calculated for oil content and iodine value in the F_2 generation by dividing the additive genetic variance, s_g^2, by the total phenotypic variance, $s_e^2 + s_g^2 + s_d^2$. The ratio of additive variance to total variance gives the best estimate of the "fixable" genetic variance present in a population, which is of importance to a varietal improvement program.

Table 3. General form for the analysis of variance of data from individual F_3 plant measurements

Source	df.	MS	Components
Replication	$(r-1)$	M_4	
Lines	$(n-1)$	M_3	$\sigma_e^2+(333)+k\sigma_p^2+kr(233)$
Repl. x lines	$(r-1)(n-1)$	M_2	$\sigma_e^2+(333)+k\sigma_p^2$
Plants in repl. and lines	$(rn)(k-1)$	M_1	$\sigma_e^2+(333)$

where r = number of replications, n = number of lines, and k = number of plants per row, σ_e^2 = environmental variance among individual plants within plots, σ_p^2 = plot-to-plot variance.

Heritability of seed weight was calculated in the "broad sense" in that total genetic variance, $s_g^2 + s_d^2$, was divided by total phenotypic variance. This was done because nearly all total genetic variance for this character was estimated to be dominance variance.

Predicted genetic advance (g_s) was derived from the formula $g_s = k\ \sigma_g^2/\sigma_p$ where σ_g^2 = additive genetic variance, σ_p^2 = phenotypic variance of F_2, and k = number of standard deviation units by which selected individuals are phenotypically superior to entire population. In this case, k has the value of 1.758 which is the expectation in the case of 10-percent selection in large samples (>50).

EXPERIMENTAL RESULTS

VARIATION AND HERITABILITY OF OIL CONTENT

Oil Percentage of F_2 Plants

The oil content of the yellow-seeded parent C.I. 1455, as determined from a bulk seed sample, was approximately 3 percent higher than that of the two brown-seeded parents, Marine and Redwood. There was not a significant difference between the mean oil content of the two F_2 populations nor was the mean of either F_2 population significantly different from its mid-parent mean (table 4).

Frequency distributions of the oil percentage of individual F_2 plants are shown in table 4. The 156 brown-seeded

Table 4. Frequency distribution for oil percentage of two of the parents and individual F_2 plants from the crosses Marine x C.I. 1455 and Redwood x C.I. 1455

Cross and generation	Class center of oil content (in percent)															Total plants	Mean
	34.7	35.2	35.7	36.2	36.7	37.2	37.7	38.2	38.7	39.2	39.7	40.2	40.7	41.2	41.7		
Marine x C.I. 1455																	
P_1 Marine	......	......	1	14	14	11	......	......	......	......	......	......	......	......	......	40	36.6 ± .07
P_2 C.I. 1455 (bulk)	......	......	......	......	......	......	......	......	......	......	(39.7)	......	......	......	......	....	39.7
F_2 Generation																	
Brown-seeded	......	2	2	12	14	18	21	26	28	17	14	1	1	......	......	156	38.0 ± .09
Yellow-seeded	......	......	......	......	2	......	1	1	5	4	7	7	7	2	1	37	39.7 ± .20
Total	......	2	2	12	16	18	22	27	33	21	21	8	8	2	1	193	38.3 ± .09
Redwood x C.I. 1455																	
P_1 Redwood	......	......	......	4	10	4	3	......	......	......	......	......	......	......	......	40	37.1 ± .08
P_2 C.I. 1455 (bulk)	......	......	......	......	......	......	......	......	......	......	(39.7)	......	......	......	......	....	39.7
F_1 Generation	......	......	......	......	3	1	3	2	1	......	......	......	......	......	......	10	37.5 ± .22
F_2 Generation																	
Brown-seeded	1	1	5	8	13	19	16	18	27	10	9	4	......	......	......	131	37.9 ± .10
Yellow-seeded	......	......	......	......	2	3	5	4	6	4	11	2	2	2	1	42	39.2 ± .19
Total	1	1	5	8	15	22	21	22	33	14	20	6	2	2	1	173	38.2 ± .10

Table 5. Variance of oil percentage of individual F_2 and parent plants of two flax crosses

Source	df.	Variance	"222"*
Marine x C.I. 1455 F_2	130	1.5608	1.3864
Redwood x C.I. 1455 F_2	162	1.6420	1.3884
Marine P_1	39	0.1744	....
Redwood P_1	39	0.2536	....

* The genetic variance "222" is estimated by subtracting the parental variance, which is assumed to approximate σ_e^2, from the total phenotypic variance, σ_p^2.

F_2 plants from the cross Marine x C.I. 1455 averaged 38.0 percent oil with a range from 35.0 to 40.5 percent. Thirty-seven yellow-seeded plants from the same cross averaged 1.7 percentage points higher in oil and ranged from 36.5 to 42.0 percent. The total F_2 population averaged 38.25 percent oil, and most of the plants (78 percent) were within the range of the two parents. The standard deviation of the total F_2 population was 1.25 which is 3.27 percent of the mean.

The frequency distribution of the oil percentages of the F_2 plants from the cross Redwood x C.I. 1455 was similar to that of the cross Marine x C.I. 1455. The mean oil content of the yellow-seeded plants was 1.3 percentage points higher than that of the brown-seeded plants. Eighty-three percent of the total F_2 population had oil percentages that were within the range of the two parents. The standard deviation of the total population was 1.31 which is 3.44 percent of the mean.

The phenotypic variances within the two F_2 populations are shown in table 5. These variances are composed of the additive and dominance components, $\sigma_g^2 + \sigma_d^2$, hereafter symbolized as "222," and the environmental variance, σ_e^2. The environmental variances for oil percentage as measured among individual plants of each of the brown-seeded parents are also shown in table 5.

Oil Percentage of F_3 Bulked Lines

The variability of the oil percentage found among 131 bulked F_3 rows of Marine x C.I. 1455 and among 163 bulked F_3 lines of Redwood x C.I. 1455 was comparable to that of their respective F_2 populations (tables 4 and 6). The oil content of the F_3 populations averaged nearly a percentage point higher than the means of the F_2's. This difference may be attributable to seasonal effects as the parent varieties also showed a large difference in oil content between the two years (table 6). The oil content of the bulked samples of Marine x C.I. 1455 averaged 39.1 percent and ranged from 36.4 to 42.4 percent. The standard deviation was 1.07 which is 2.73 percent of the mean. The bulked samples of Redwood x C.I. 1455 ranged from 37.0 to 43.4 percent oil and averaged 40.1 percent with a standard deviation of 1.19 or 2.98 percent of the mean.

The analyses of variance of the oil content data from the bulked F_3 lines

Table 6. Mean oil percent with standard deviations found within two parents, the F_2 and F_3 populations from two flax crosses, 1955 and 1956

Variety or cross	1955 F_2 Generation			1956 F_3 Generation					
	Individual plants			Bulked lines			Individual plants		
	N	Mean	s	N	Mean	s	N	Mean	s
Marine x C.I. 1455	193	38.2	1.25	131	39.1	1.09	928	39.0	1.61
Redwood x C.I. 1455	173	38.2	1.31	163	40.1	1.19	896	39.7	1.62
Marine parent	40	36.6	0.42	....	....	....	58	38.0	0.59
Redwood parent	40	37.1	0.50	....	....	....	50	38.6	0.63

Table 7. Analyses of variance of oil content data from bulked F_3 lines derived from two flax crosses

Cross and source of variance	df.	Variance	"233"
Marine x C.I. 1455			
Replicated lines			
Lines	34	2.4104**	1.1741*
Error	34	0.0622	....
Nonreplicated lines			
Lines	93	1.1755	1.1133†
Redwood x C.I. 1455			
Replicated lines			
Lines	37	2.8493**	1.3949*
Error	37	0.0594	....
Nonreplicated lines			
Lines	123	1.3885	1.329†

** Indicates significance at 1 percent level.

* "233" for replicated lines is estimated as follows: $233 = \frac{V_n - V_e}{2}$, since lines ($V_n$) and error ($V_e$) variances have expectations $\sigma_e^2 + 2(233)$ and σ_e^2, respectively.

† Error variance from replicated lines was used to compute the estimate of "233" for nonreplicated lines.

Table 8. Association between oil content of F_2 plants and that of their bulked F_3 progeny from two flax crosses

Cross	N	Sxy	"223"* (Sxy/df)	r
Marine x C.I. 1455	131	131.50	1.0116	+0.87**
Redwood x C.I. 1455	163	193.20	1.1853	+0.78**

** "r" values significant at 1 percent level.

* Expectation of covariance "223" is $\sigma_g^2 + \frac{1}{2}\sigma_d^2$.

of the two crosses give estimates of genetic variance "233" as shown in table 7. The variance for "lines" was highly significant for both crosses.

The association between the oil content of the F_2 plants and that of their bulked F_3 progenies is shown in table 8. The data from single rows of each F_3 line were used to determine the correlation coefficients between the F_2 and F_3 progenies and to estimate genetic covariance "223." Highly significant "r" values were obtained for both crosses; +0.87 for Marine x C.I. 1455 and +0.78 for Redwood x C.I. 1455.

Oil Percentages of F_3 Plants

The oil content was determined for at least eight individual plants from each F_3 row. There was a total of 16 plants that were analyzed from each of those F_3 lines that were replicated—34 in the cross Marine x C.I. 1455 and 31 from the cross of Redwood x C.I. 1455. The analyses of variance of both crosses are shown in table 9.

There was greater variation among individual F_3 plant measurements in the cross of Marine x C.I. 1455 than in the cross of Redwood x C.I. 1455 as indicated by the variances for "lines" and "plants in lines," and by the genetic variance components "233" and "333." The genetic variances computed from among and within the nonreplicated lines were comparable to those of the replicated lines (table 9).

There were 928 individual F_3 plants from 82 lines of the cross Marine x C.I. 1455 that were analyzed for oil

Table 9. Analysis of variance of the oil determinations of individual F_3 plants from two flax crosses

Cross and source of variance	df.	Variance	Genetic components "233"*	Genetic components "333"
Marine x C.I. 1455				
Lines with two replications				
Lines	33	25.4518	1.4232	....
Repl. x lines	33	2.6803	....	....
Plants within lines	476	1.1958	....	0.9680
Lines with no replication				
Lines	47	10.9457	1.0332*	....
Plants in lines	336	1.0294	....	0.8016
Marine parent	55	0.2278	....	....
Redwood x C.I. 1455				
Lines with two replications				
Lines	30	16.0580	0.8374	....
Repl. x lines	30	2.6593	....	....
Plants within lines	434	0.8421	....	0.5024
Lines with no replication				
Lines	49	10.2345	0.9469*	....
Plants in lines	350	1.0040	....	0.6649
Redwood parent	47	0.3391	....	....

** Significant at 1 percent level.

* The variance of "replication x lines" from analysis of variance of replicated lines was used for computing the estimate of genetic variance "233" for nonreplicated lines.

Table 10. Association between the oil content of F_2 plants and the mean oil content of eight plants selected from F_3 progenies from two flax crosses

Cross	N	Sxy	"223" (Sxy/df.)	r
Marine x C.I. 1455				
Brown-seeded families	73	64.36	.8939	+.76**
Combined families	82	97.52	1.2040	+.78**
Redwood x C.I. 1455				
Brown-seeded families	58	64.63	1.1339	+.75**
Combined families	81	123.87	1.5484	+.80**

** Correlation coefficients significant at the 1 percent level.

content and iodine value. The oil determinations ranged from 35.0 to 45.2 percent with a mean of 39.0 percent for the total F_3 population. The standard deviation of F_3 plant measurements was 1.61, whereas that of the F_2 plant measurements was 1.25 (table 6).

The standard deviation of 896 F_3 plant determinations from 81 lines of the cross Redwood x C.I. 1455 was 1.62. The standard deviation of the F_2 population from this cross was 1.28. The oil percentages of all F_3 plant measurements averaged 39.7 percent and ranged from 35.3 to 43.8 percent (table 6).

There were highly significant positive correlations between the oil percentages of the F_2 plants and the mean oil percentages of selected F_3 plants from each progeny. The correlation coefficients were +0.78 and +0.80 for the two crosses Marine x C.I. 1455 and Redwood x C.I. 1455, respectively (table 10). Covariance "223" was larger from the cross Redwood x C.I. 1455 than it was for the cross Marine x C.I. 1455, which is in contrast to the genetic variances "233" and "333" estimated from the analyses of variance in table 9.

Heritability Estimates of Oil Content

Approximately three-fourths of the total genetic variation observed in the F_2 and F_3 generations of both crosses was additive. The two crosses were similar in respect to the magnitude of

Table 11. Summary of variance components derived from analyses of variance and covariance of oil percent from F_2 and F_3 populations of two flax crosses, with estimates of additive and dominance variances and heritability

Source of variance or covariance	Genetic variance*	Marine x 1455 Estimate		Redwood x 1455 Estimate	
Among F_2 plants	222	1.3864		1.3884	
Among F_3 lines (bulked)					
Replicated lines	233	1.1741		1.3949	
Nonreplicated	233	1.1133		1.3291	
Among F_3 lines (individual plants)					
Replicated lines	233	1.4232		0.8374	
Nonreplicated	233	1.0332		0.9469	
Within F_3 lines (individual plants)					
Replicated lines	333	0.9680		0.5024	
Nonreplicated	333	0.8016		0.6649	
Between F_2 plants and F_3 lines (bulked)	223	1.0116		1.1853	
Between F_2 plants and F_3 lines (mean of plant progenies)	223	1.2040		1.5484	
Estimates of additive genetic variance	σ_g^2	1.0360		1.1028	
Estimates of dominance genetic variance	σ_d^2	0.4172		0.2568	
Estimates of heritability (narrow sense)	....	66.4		67.2	
Estimated genetic† advance in F_3 progenies					
	est.	obs.	est.	obs.	
a) in percent oil	1.46	1.9	1.51	1.5	
b) in percent of F_3 mean	3.74	4.87	3.80	3.78	

* Genetic variances have the following expectations: $222 = \sigma_g^2 + \sigma_d^2$, $233 = \sigma_g^2 + \frac{1}{4}\sigma_d^2$, $333 = \frac{1}{2}\sigma_g^2 + \frac{1}{2}\sigma_d^2$, and $223 = \sigma_g^2 + \frac{1}{2}\sigma_d^2$.

† Genetic advance is predicted on basis of selecting the highest 10 percent of F_2 plants as progenitors of F_3 population.

Table 12. Frequency distributions of iodine values of two of the parents and individual F_2 plants from the crosses Marine x C.I. 1455 and Redwood x C.I. 1455

Cross and generation	Classes of iodine value 150-153	154-157	158-161	162-165	166-169	170-173	174-177	178-181	182-185	186-189	190-193	Total number plants	Mean
Marine x C.I. 1455													
P_1 Marine	......	......	......	......	......	......	2	23	15	......	......	40	181 ± .26
P_2 C.I. 1455 (bulk)	......	......	......	(163)	......	......	......	......	......	......	......	......	163
F_2 Generation													
Brown-seeded	1	1	6	18	33	37	31	20	8	......	1	156	172 ± .50
Yellow-seeded	......	......	......	2	1	8	9	7	7	3	......	37	177 ± 1.0
Total	1	1	6	20	34	45	40	27	15	1	1	193	173 ± .50
Redwood x C.I. 1455													
P_1 Redwood	......	......	......	......	1	8	12	19	......	......	......	40	177.6 ± .41
P_2 C.I. 1455 (bulk)	......	......	......	(163)	......	......	......	......	......	......	......	......	163
F_1 Generation	2	1	3	......	2	......	......	......	......	......	......	10	159
F_2 Generation													
Brown-seeded	......	2	6	24	32	34	21	11	1	......	......	131	170 ± .50
Yellow-seeded	......	......	......	2	4	15	14	5	2	......	......	42	173 ± .70
Total	......	2	6	26	36	49	35	16	3	......	......	173	171 ± .40

both the additive genetic variance, σ_g^2, and the dominance variance, σ_d^2, as shown in table 11.

There was close agreement between the estimates of heritability of oil content within the crosses. It appears that oil content is a highly heritable character, at least in the two crosses under study. The heritability estimates were 66.4 and 67.2 for the crosses Marine x C.I. 1455 and Redwood x C.I. 1455, respectively.

The genetic advance expected by selecting the highest 10 percent of the F_2 plants was computed to be 1.46 units of percent oil or 3.74 percent of the F_3 mean oil content in the case of Marine x C.I. 1455, and 1.51 units of percent oil and 3.80 percent of the F_3 mean from the cross Redwood x C.I. 1455. It was observed that plants selected from F_3 progenies of the highest 10 percent of F_2 plants were superior to the total F_3 mean oil content by 1.9 and 1.5 percentage units; thus the observed genetic advance approximated the predicted. The differences between the mean oil content of F_3 plants grown from "selected" F_2 parents and the mean oil percentages of the total F_3 populations were significant at the 1 percent level.

The genetic advance observed among brown-seeded progenies from the highest 10 percent of brown-seeded F_2 plants was 1.22 and 1.15 oil percentage units for the crosses Marine x C.I. 1455 and Redwood x C.I. 1455, respectively.

VARIATION AND HERITABILITY OF IODINE VALUE

Iodine Value of F_2 Plants

The same individual F_2 plants that were selected from the crosses Marine x C.I. 1455 and Redwood x C.I. 1455 for oil content determinations were also analyzed for iodine values. The frequency distributions of the iodine values determined for the two F_2 populations are shown in table 12.

The iodine values of F_2 plants from the cross Marine x C.I. 1455 ranged from 150 to 190, with a mean of 173 which is one point higher than the mid-parent mean. Ninety-four percent of the values were within the range of the two parents (163 to 181). The standard deviation of the total population was 6.63 or 3.8 percent of the mean.

The 173 F_2 plants from the cross Redwood x C.I. 1455 averaged 171 in iodine value and ranged from 154 to 184. The population mean was one point higher than the mid-parent mean. The F_2 from this cross was not as variable as that from Marine x C.I. 1455 as indicated by a standard deviation of 5.35 or 3.1 percent of the mean.

Total phenotypic variances found among iodine values of individual plants from the two F_2 populations are shown in table 13. The variance for the cross Marine x C.I. 1455 was 50 percent larger than that for the population from Redwood x C.I. 1455. Genetic variance "222" is estimated by subtracting the parental variances from the respective F_2 phenotypic variances (table 13).

Iodine Value of F_3 Bulked Lines

The average iodine value of the two F_3 populations, as determined on bulk samples from F_3 rows, was 10 to 13 points higher than the mean iodine values of the respective F_2 populations. This difference between generations is probably a seasonal effect as indicated by parental means for the two years 1955 and 1956 (table 14). The variances among the 131 samples of bulked F_3 rows of Marine x C.I. 1455 and among 163 bulked F_3 samples of Redwood x C.I. 1455 were somewhat less but com-

Table 13. Variance of iodine values within two parental and the F_2 populations from two flax crosses

Cross or parent variety	df.	Variance	"222"
Marine x C.I. 1455 F_2	130	44.0180	41.3515
Redwood x C.I. 1455 F_2	162	28.6680	21.8475
Marine P_1	39	2.6667	....
Redwood P_1	39	6.8205	....

Table 14. Mean iodine value with standard deviations of F_2, F_3, and two parental populations from two flax crosses

Cross or parent variety	1955 F_2 Generation			1956 F_3 Generation					
	Individual plants			Bulked F_3 lines			Individual plants		
	N	Mean	s	N	Mean	s	N	Mean	s
Marine x C.I. 1455	131	173	6.6	131	183	6.0	928	185	6.6
Redwood x C.I. 1455	173	171	5.4	163	184	4.2	896	185	4.9
Marine	40	181	1.6	......	......	....	42	193	1.5
Redwood	40	178	2.6	......	......	....	50	188	1.9

parable to the variances of the respective F_2 populations.

The iodine values determined on bulked F_3 samples of Marine x C.I. 1455 ranged from 169 to 197 and averaged 183.3. The standard deviation was 6.02 or 3.28 percent of the mean (table 14). The F_3 samples from the cross Redwood x C.I. 1455 ranged in iodine value from 174 to 194 with a mean of 184.4. The standard deviation was 4.18 or 2.27 percent of the mean indicating less variability in this cross than was found among F_3 lines of Marine x C.I. 1455 (table 14).

Analyses of variance of iodine values derived from bulked F_3 lines of both crosses are shown in table 15. Variances for "lines" were highly significant. The much larger values computed for genetic variance "233" and "line" variance from Marine x C.I. 1455 progeny than from progeny of Redwood x C.I. 1455 implies greater genetic diversity in the former population.

Table 15. Analyses of variance of iodine values determined on bulked F_3 lines derived from two flax crosses

Cross and source of variance	df.	Variance	"233"
Marine x C.I. 1455			
Replicated lines			
Lines	34	71.6205**	34.4150
Error	34	2.7879	....
Nonreplicated lines			
Lines	93	36.4194	33.6315*
Redwood x C.I. 1455			
Replicated lines			
Lines	37	27.2000**	11.7200
Error	37	3.7600	....
Nonreplicated lines			
Lines	124	18.2339	14.4739*

** Indicates significance at the 1 percent level.
* Error variance from replicated lines was used to compute the estimate of "233" for nonreplicated lines.

Table 16. Association between iodine values of F_2 plants and that of their bulked F_3 offspring from two flax crosses

Cross	N	Sxy	"223" (Sxy/df.)	r
Marine x C.I. 1455	131	3,874	29.7969	+0.75**
Redwood x C.I. 1455	163	1,879	11.5981	+0.52**

** "r" value significant at 1 percent level.

Associations between iodine values of F_2 plants and that of their bulked F_3 offspring are shown in table 16. Data from single rows of each F_3 line were used to compute the correlation coefficients between F_2 plants and F_3 lines and to estimate genetic covariance "223." Highly significant "r" values were obtained for both crosses; +0.75 for Marine x C.I. 1455 and +0.52 for Redwood x C.I. 1455.

Iodine Value of F_3 Plants

Variability within F_3 lines for iodine value was determined by analyzing 8 plants from each F_3 row which made a total of 16 plants from each line that was replicated. The variance found within F_3 lines is expressed as variance for "plants in lines" in the analyses of variance shown in table 17. There were greater variances among and within F_3 lines of Marine x C.I. 1455 than there were in the F_3 population from the cross Redwood x C.I. 1455. This is indicated by the relative sizes of the vari-

Table 17. Analyses of variance of iodine values determined on seed of individual F_3 plants from two flax crosses

Cross and source of variance	df.	Variance	Genetic components "233"*	"333"
Marine x C.I. 1455				
Lines with two replications				
Lines	33	521.30**	30.5756	....
Repl. x lines	33	32.09	....	....
Plants in lines	476	16.91	....	14.68
Lines with no replication				
Lines	47	200.85	21.095*	....
Plants in lines	336	14.09	....	11.86
Marine parent	39	2.23	....	....
Redwood x C.I. 1455				
Lines with two replications				
Lines	30	169.63**	9.7162	....
Repl. x lines	30	14.17	....	....
Plants in lines	434	11.55	....	8.00
Lines with no replication				
Lines	49	141.29	15.8900*	....
Plants in lines	350	10.21	....	6.66
Redwood parent	47	3.55	....	....

** Significant at 1 percent level.

* The variance of "replications x lines" from the analysis of variance of data from replicated lines was used for computing the estimate of genetic variance "233" for nonreplicated lines.

ance for "lines" and "plants in lines," and by genetic variances "233" and "333" shown in table 17.

The iodine values determined on seed from 928 plants selected from 82 F_3 lines of the cross Marine x C.I. 1455 averaged 184.9 and ranged from 165 to 200. The standard deviation of all F_3 plant measurements was 6.61 or 3.6 percent of the mean, which compares with the standard deviation of 6.63 found among the F_2 plant measurements of this cross (table 14).

Table 18. Association between the iodine value of F_2 plants and the mean iodine value of eight plants selected from F_3 progenies from two flax crosses

Cross	N	Sxy	"223" (Sxy/df.)	r
Marine x C.I. 1455				
Brown-seeded lines	73	1,554	21.5833	+.72**
All lines	82	2,160	26.6667	+.76**
Redwood x C.I. 1455				
Brown-seeded lines	58	403	7.0702	+.42**
All lines	81	781	9.7625	+.53**

** Values of "r" significant at the 1 percent level.

The F_3 plant measurements of the cross Redwood x C.I. 1455 averaged 185.3 points in iodine value and ranged from 168 to 197. The standard deviation computed from data on 896 F_3 plants was 4.89 or 2.6 percent of the mean. The standard deviation of the iodine values determined on the F_2 population was 5.35.

There were highly significant positive correlations between the iodine values of F_2 plants and the mean iodine values of F_3 plants selected from their progenies. The correlation coefficients were +0.76 and +0.53 for the crosses Marine x C.I. 1455 and Redwood x C.I. 1455, respectively (table 18). The genetic covariance "223" was nearly three times as large for the populations from Marine x C.I. 1455 as it was for those from Redwood x C.I. 1455 (table 18).

Heritability Estimates of Iodine Value

Approximately 75 percent of the genetic variation observed in the F_2 and F_3 populations from the cross Marine x C.I. 1455 was found to be additive (table 19). By dividing the additive variance (26.9332) by the phenotypic variance of the F_2 population (44.0180), an estimate of 61.2 percent heritability for iodine value was obtained for this cross. From this it may be concluded that iodine value was nearly as heritable as was oil content within the cross Marine x C.I. 1455.

In contrast to the above, 45 percent of the total genetic variance estimated to be in the F_2 and F_3 populations from the cross Redwood x C.I. 1455 was dominance variance (table 19). The estimate of heritability of iodine value (34.3 percent) was considerably less than was oil content within the latter cross.

The predicted genetic gain from selecting from the F_2 generation of the cross Marine x C.I. 1455 was more than

Table 19. Summary of variance components derived from analyses of variance and covariance of iodine values from F_2 and F_3 populations of two flax crosses, with estimates of additive and dominance variances and heritability

Source of variance or covariance	Genetic variance*	Marine x 1455 Estimate	Redwood x 1455 Estimate
Among F_2 plants	222	41.3513	21.8475
Among F_3 lines (bulked)			
Replicated lines	233	34.4150	11.7200
Nonreplicated	233	33.6315	14.4739
Among F_3 lines (individual plants)			
Replicated lines	233	30.5756	9.7162
Nonreplicated	233	21.0950	15.8900
Within F_3 lines (individual plants)			
Replicated lines	333	14.6800	8.0000
Nonreplicated	333	11.8600	6.6600
Between F_2 plants and F_3 lines (bulked)	223	29.7969	11.5981
Between F_2 plants and F_3 lines (mean of plant progenies)	223	26.6667	9.7625
Estimates of additive genetic variance	σ_g^2	26.9332	9.8235
Estimates of dominance genetic variance	σ_d^2	8.2294	8.1891
Estimates of heritability (narrow sense)	....	61.19	34.27

Estimated genetic† advance	Marine x 1455 est.	Marine x 1455 obs.	Redwood x 1455 est.	Redwood x 1455 obs.
a) in units of I.V.	7.14	6.8	3.23	4.2
b) in percentage of F_3 mean	3.86	3.68	1.74	2.27

* The genetic variances have the following expectations: $222 = \sigma_g^2 + \sigma_d^2$, $233 = \sigma_g^2 + \frac{1}{4}\sigma_d^2$, $333 = \frac{1}{2}\sigma_g^2 + \frac{1}{2}\sigma_d^2$, $223 = \sigma_g^2 + \frac{1}{2}\sigma_d^2$.

† Genetic advance is predicted on basis of selecting the highest 10 percent of F_2 plants as progenitors of F_3 population.

two times as great as that predicted for the cross Redwood x C.I. 1455. The genetic advance actually attained, however, was less than twice as great from the former as it was from the latter (table 19).

VARIATION AND HERITABILITY OF SEED WEIGHT

Seed Weight of F_2 Plants

Seeds of over 100 F_2 plants from each of the two crosses studied were counted and weighed in order to determine their comparative weights. The frequency distributions of the seed weights determined from the two F_2 populations and the parents are shown in table 20.

The small-seeded Marine parent had a mean of 4.9 grams per thousand seeds. C.I. 1455 is larger seeded and averaged 6.7 grams per thousand. The mean seed weight of all F_2 plants was not significantly different from the mid-parent mean. The standard deviation of 114 plant measurements was 0.5136 or 8.9 percent of the mean. Seven percent of the F_2 plants were as small seeded as the Marine parent and 8 percent were as large as C.I. 1455. There was no evidence for transgressive segregation for seed weight within this cross.

The seed weight of Redwood is more nearly like that of C.I. 1455, although greater variation appeared among F_2 plants from the cross Redwood x C.I. 1455 than among F_2 plants of the cross Marine x C.I. 1455. The standard deviation of 132 F_2 plant measurements was 0.6494 or 10.3 percent of the mean. About 10 percent of the plants had seed weights that were beyond the range of the parents. Ten F_1 plants from the cross Redwood x C.I. 1455 had seed weights that were similar to the large-seeded parent, C.I. 1455.

Table 20. Frequency distribution of seed weight of F_2 plants and parents of two flax crosses

Cross and generation	Class centers seed weight (gm./1000) 4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	Total	Mean
Marine x C.I. 1455										
P_1 Marine	7	3	.....	.....	.....	.....	.....	.....	10	$4.94 \pm .025$
P_2 C.I. 1455	.....	.....	.....	2	10	1	.....	.....	13	$6.71 \pm .052$
F_2 Generation										
Brown-seeded	7	20	39	19	5	1	.....	.....	91	$5.74 \pm .054$
Yellow-seeded	1	5	7	7	3	.....	.....	.....	23	$5.84 \pm .106$
Total	8	25	46	26	8	1	.....	.....	114	$5.76 \pm .048$
Redwood x C.I. 1455										
P_1 Redwood	.....	.....	1	10	.....	.....	.....	.....	11	$6.15 \pm .039$
P_2 C.I. 1455	.....	.....	.....	2	10	1	.....	.....	13	$6.71 \pm .052$
F_1 Generation	.....	.....	.....	2	6	2	.....	.....	10	$6.77 \pm .073$
F_2 Generation										
Brown-seeded	2	5	28	32	15	14	2	1	99	$6.31 \pm .067$
Yellow-seeded	.....	6	4	9	12	2	.....	.....	33	$6.22 \pm .106$
Total	2	11	32	41	27	16	2	1	132	$6.28 \pm .057$

Genetic variance "222" estimated from the variance of F_2 populations and parental variances is shown in table 21. The variances within the three parent varieties ranged from 0.0063 in the case of Marine, the smallest-seeded variety, to 0.0347 for C.I. 1455, the largest-seeded parent. Aurora (1959) reported genetic variance for seed size within an F_2 population to be 0.2123 and parental variance as 0.10262.

Seed Weight of F_3 Plants

Seeds from at least eight plants from each selected F_3 row of the cross Redwood x C.I. 1455 were counted and weighed. The seed weights were expressed in grams per 1,000 seeds. Measurements were taken on 16 plants from each of the lines that were replicated. Seed weights of 640 F_3 plants from 56 lines of Redwood x C.I. 1455 ranged from 5.0 to 7.8 grams per 1,000 and averaged 6.17 grams. The standard deviation was 0.4995 or 8.1 percent of the mean, which would indicate that there was less variation among the seed weights of F_3 plants than was found among seed weights of the F_2 population.

The analysis of variance shown in table 22 indicated that variance for "lines" was significant at the 1 percent level. The variances derived from plant measurements of the nonreplicated

Table 21. Variance of seed weight of individual F_2 and parent plants of two flax crosses

Source	df.	Variance	"222"*
Marine x C.I. 1455 F_2	113	0.2638	0.2413
Redwood x C.I. 1455 F2	131	0.4217	0.3951
Marine parent	9	0.0063	....
Redwood parent	10	0.0168	....
C.I. 1455 parent	12	0.0347	....

* Total genetic variance within the F_2 population is estimated by "222," expectation of which is $\sigma_g^2 + \sigma_d^2$. It is computed by subtracting the parental variance $\left(\frac{(N_1-1)V_{P_1}+(N_2-1)V_{P_2}}{(N_1+N_2-2)}\right)$ from the total variance.

Table 22. Analyses of variance of seed weights (grams per 1,000) determined on seed from F_3 plants from the cross Redwood x C.I. 1455

Source of variance	df.	Variance	"233"	"333"
Replicated lines				
Lines	23	1.4035**	0.0762	....
Replication x lines	23	0.1843	....	....
Plants in lines	336	0.1527	....	0.1086
Nonreplicated lines				
Lines	31	1.1777	0.1242*	....
Plants in lines	224	0.1543	....	0.1102
Redwood parent	29	0.0441	....	....

** Indicates significance at 1 percent level.

* Variance of "replication x lines" from analysis of variance of data from replicated lines was used to compute the estimate of "233" for nonreplicated lines.

Table 23. Association between seed weight of F_2 plants and mean seed weight of their F_3 offspring (8 plants from each line) from the cross Redwood x C.I. 1455

Source	N	Sxy	"223" (Sxy/df.)	r
Brown-seeded lines	41	7.61	0.1902	+0.74**
All lines	56	9.19	0.1671	+0.74**

** "r" value significant at 1 percent level.

lines were comparable to the variances computed from data obtained from replicated lines.

Seed weights of F_2 plants were found to be highly correlated with the mean seed weights of their F_3 progeny, as indicated by the correlation coefficients (+0.74) shown in table 23. Genetic covariance "223" was estimated to be 0.1671. Aurora (1959) found that seed weights of F_3 plants were correlated with seed weights of F_2 parents with coefficient of +0.75.

Table 24. Summary of genetic variance components estimated from the analyses of variance and covariance of seed weights determined on individual plants of the F_2 and F_3 generations from the cross Redwood x C.I. 1455

Source of variance or covariance	Component*	Estimate
Among F_2 plants	222	0.3951
Among F_3 lines (means of plants in lines)		
Replicated	233	0.0762
Nonreplicated	233	0.1242
Within F_3 lines (individual plants)		
Replicated	333	0.1086
Nonreplicated	333	0.1102
Between F_2 plants and F_3 progeny means	223	0.1671
Estimate of additive variance	σ_g^2	0.0181
Estimate of dominance variance	σ_d^2	0.3163
Estimate of heritability		
a) Broad sense		79.29%
b) Narrow sense		4.29%

* Genetic variance and covariances have the following expectations: 222 = $\sigma_g^2+\sigma_d^2$, 233 = $\sigma_g^2+\frac{1}{4}\sigma_d^2$, 333 = $\frac{1}{2}\sigma_g^2+\frac{1}{2}\sigma_d^2$, and 223 = $\sigma_g^2+\frac{1}{2}\sigma_d^2$.

Heritability Estimates of Seed Weight

The estimates of the genetic components of variance and the heritability estimate of seed weight shown in table 24 were derived from F_2 and F_3 plant measurements from one cross. Seed weights were not determined on seed of bulked F_3 lines.

A large proportion (90 percent) of the phenotypic variance observed among seed weights of F_2 plants of the cross Redwood x C.I. 1455 was estimated to be genetic variance. In contrast to the proportions of the estimated genetic components computed for the other two quantitative characters studied, nearly all (95 percent) of genetic variance was estimated to be dominance or other "nonfixable" variance.

The estimate of heritability for this character was computed both in the "broad sense," i.e., total estimated genetic variance divided by total phenotypic variance, and in the "narrow sense." Estimates were 79.29 percent and 4.29 percent, respectively. Heritability of seed weight was estimated in the broad sense by Aurora (1959) and found to be 67.7 percent.

ASSOCIATIONS BETWEEN CHARACTERS

Flower Color and Seed Color with Oil Content, Iodine Value, and Seed Weight

Yellow seed color of C.I. 1455 results from the recessive gene "g," and light blue flower color from the gene "a" (Barnes, 1958). Ratios of the flower color and seed color classes observed among F_2 and F_3 populations of two crosses under study indicate that the two genes are inherited independently.

It has been reported from other flax studies that seed color is associated with oil content, iodine value, and to some extent with seed weight (Carnahan, 1949; Culbertson and Kommedahl, 1956; Dillman, 1936; McGregor, 1937; Moseman, 1944). It has not been estab-

Table 25. Comparison of mean oil percentage of F_2 plants and F_3 bulked lines in different flower and seed color classes. Data are combined from two flax crosses Marine x C.I. 1455 and Redwood x C.I. 1455

Flower color	Seed color genotype of F_2 plants or F_3 lines			Mean of total
	Brown	Heterozygous	Yellow	
F_2 plants				
Blue	37.50 ± .19	37.89 ± .21	38.92 ± .31	37.93 ± .14
Number of plants	24	36	12	72
Heterozygous	38.08 ± .18	37.99 ± .13	39.23 ± .23	38.23 ± .11
Number of plants	33	80	37	150
Light blue	38.06 ± .21	38.00 ± .19	39.89 ± .24	38.26 ± .15
Number of plants	22	41	9	72
Mean of total	37.90 ± .11	37.97 ± .09	39.27 ± .17	38.21 ± .07
Number of plants	79	157	58	294
F_3 lines				
Blue	39.27 ± .26	39.19 ± .16	40.40 ± .27	39.42 ± .13
Number of lines	24	36	12	72
Segregating	39.43 ± .19	39.35 ± .13	40.85 ± .21	39.74 ± .11
Number of lines	33	80	37	150
Light blue	39.24 ± .17	39.38 ± .15	41.32 ± .28	39.58 ± .13
Number of lines	22	41	9	72
Mean of total	39.33 ± .11	39.32 ± .09	40.83 ± .16	39.62 ± .07
Number of lines	79	157	58	294

lished whether the association results from close linkage between the seed-color gene and one or more genes that have a major effect upon oil content or iodine value, or whether the association is in some way a pleiotropic relationship between seed color and the amount and manner of oil formation in the seed.

Plants with yellow seeds were found to be higher in both oil content and iodine value than the brown-seeded

Table 26. Comparison of mean iodine value of F_2 plants and F_3 bulked lines in different flower and seed color classes. Data are combined from two flax crosses Marine x C.I. 1455 and Redwood x C.I. 1455

Flower color	Seed color genotype of F_2 plants or F_3 lines			Mean of total
	Brown	Heterozygous	Yellow	
F_2 plants				
Blue	170.4 ± 1.3	171.4 ± 1.0	175.3 ± 1.5	171.8 ± 0.7
Number of plants	24	36	12	72
Heterozygous	170.8 ± 0.8	170.7 ± 0.6	174.3 ± 0.9	171.6 ± 0.5
Number of plants	33	80	37	150
Light blue	168.5 ± 1.1	169.8 ± 1.0	176.7 ± 1.7	170.3 ± 0.8
Number of plants	22	41	9	72
Mean of total	170.1 ± 0.6	170.6 ± 0.5	174.9 ± 0.7	171.3 ± 0.4
Number of plants	79	157	58	294
F_3 lines				
Blue	182.5 ± 1.2	183.6 ± 0.7	189.0 ± 1.0	184.2 ± 0.6
Number of lines	24	36	12	72
Segregating	182.4 ± 0.7	182.1 ± 0.5	189.6 ± 0.5	184.0 ± 0.4
Number of lines	33	80	37	150
Light blue	182.2 ± 1.0	182.4 ± 0.7	190.1 ± 1.4	183.3 ± 0.6
Number of lines	22	41	9	72
Mean of total	182.4 ± 0.5	182.5 ± 0.3	189.6 ± 0.4	183.9 ± 0.3
Number of lines	79	157	58	294

Table 27. Analyses of variance of oil percentage and iodine value of individual F_2 plants and bulked F_3 lines from two flax crosses, showing association of seed color and flower color with these seed characters

		Variance of oil content		Variance of iodine value	
Cross and source of variance	df.	F_2 plants	F_3 bulked lines	F_2 plants	F_3 bulked lines
Marine x C.I. 1455					
Seed color class*	2	21.1925**	12.5317**	379.550**	678.15**
Flower color class†	2	2.5485	0.6585	13.900	13.00
Seed color x flower color	4	0.0425	0.8836	41.600	62.45
Within classes	122	1.2726	0.9664	39.091	25.18
Redwood x C.I. 1455					
Seed color	2	21.170**	35.3450**	215.800**	514.80**
Flower color	2	1.385	1.5500	74.850	56.85**
Flower color x seed color	4	1.015	0.4475	1.100	(−9.22)‡
Within classes	154	1.407	1.0045	26.354	10.92

** Indicates significance at 1 percent level.

* F_2 plants and F_3 lines classified in three classes of seed color; homozygous brown (dominant), heterozygous, homozygous yellow (recessive).

† The three classes of flower color were: homozygous blue (dominant), heterozygous, and homozygous light blue (recessive).

‡ The minus value estimated for variance of first order interaction "seed color x flower color" probably resulted from disproportionate sub-class numbers. This variance was omitted from computations of the other variances.

plants within all populations studied. This is indicated by marginal means in tables 25 and 26 which show combined data from both crosses. The significant effect of seed color character on both seed quality characteristics is shown also by analyses of variance of F_2 and F_3 data in table 27.

A comparison of mean oil percent of the yellow-seeded classes with that of the brown-seeded classes within F_2 and the F_3 populations may be made in table 25. The percent oil in seeds from yellow-seeded F_2 plants and F_3 lines averaged 1.3 and 1.5 percentage points higher than the mean oil percent found in brown-seeded F_2 plants and F_3 lines, respectively. Differences were significant as determined by standard "t" test.

It also was found that seed from F_2 plants and F_3 lines that had yellow seeds were significantly higher in iodine value than those with brown seeds. The means of yellow-seeded and brown-seeded classes within the F_2 and F_3 populations may be compared in table 26. The yellow-seeded class of F_2 plants averaged 4.6 points higher in iodine value than the brown-seeded class. There was an advantage of 7.1 points in favor of yellow-seeded F_3 lines over brown-seeded lines.

There was not a significant association between flower color of F_2 plants or F_3 lines with either oil content or iodine value although there was a tendency for blue-flowered plants and lines to be lower in oil content and higher in iodine value than those with light blue flowers or those that were heterozygous for flower color. Comparisons between mean oil percent and mean iodine value of different flower color classes may be made in the right hand columns of tables 25 and 26, respectively.

Analyses of variance of F_2 and F_3 data, shown in table 27, indicate that flower color did not have a significant association with oil content within either cross or with iodine value within populations from Marine x C.I. 1455. A significant association was observed between flower color and iodine value within the population of F_3 bulked lines from Redwood x C.I. 1455.

The interacting effects of flower color with seed color on oil content or iodine value were not significant within any population analyzed (table 27), further

Table 28. Analyses of variance of seed weights of F_2 plants from two flax crosses

Cross and source of variance	df.	Variance
Marine x C.I. 1455		
Seed color class*	1	0.1863
Flower color class	1	0.0375
Within classes	111	0.2665
Redwood x C.I. 1455		
Seed color class*	1	0.2077
Flower color class	1	0.1359
Within classes	129	0.4266

* Two seed color classes were brown and yellow.

substantiating genetic evidence that the two characters are inherited independently.

Seed color or flower color of F_2 plants did not appear to be associated with seed weight as indicated by means of classes in table 20 and by analyses of variance in table 28.

Neither flower color nor seed color of F_3 lines of the cross Redwood x C.I. 1455 were associated with seed weight. Comparisons may be made between mean seed weights of F_3 plants grouped into classes according to seed and flower color of F_3 lines in table 29.

Oil Content with Iodine Value

It has been reported that oil content is negatively correlated with iodine value (Chu and Culbertson, 1952; Culbertson, 1954; Lemos, 1949). There are many exceptions to this relationship, however, as indicated by the development of varieties that have both high oil content and high iodine value. Examples of such varieties are Bolley, Minerva, Rebu, Bolley Golden, and Viking.

A significant positive association was found between oil content and iodine value of F_2 plants from the two crosses Marine x C.I. 1455 and Redwood x C.I. 1455. The correlation coefficients are shown in table 30. Within seed color classes, there did not appear to be an association between the two characteristics. Since the yellow-seeded plants were significantly higher than the brown- seeded plants in **both** oil content and iodine value, there was a tendency for the combined analyses to show a positive correlation.

Analyses of data from bulked F_3 lines of both crosses revealed little association between the oil percentages and iodine values within seed color classes. When data from all lines, irrespective of seed color, were analyzed together, highly significant correlation coefficients of +0.25 were obtained (table 30).

The same general relationships between oil content and iodine value were observed among the F_3 populations when means of plants within F_3 lines were used to compute correlation coefficients. However, the correlation between the mean oil percentage of F_3 lines (mean of eight plants per line) and mean iodine value within the cross Redwood x C.I. 1455 was nonsignificant.

Oil Content with Seed Weight

It has been reported that oil content of flaxseed is correlated with weight of

Table 29. Comparisons of mean seed weight of F_3 plants grouped into classes according to flower color and seed color of F_3 lines, Redwood x C.I. 1455

Flower color of F_3 lines	Seed color of F_3 lines: Brown	Segregating*	Yellow	Mean of total
Blue	6.17 ± .05	6.03 ± .05	6.24 ± .09	6.12 ± .04
Number of plants	96	64	8	168
Segregating	6.32 ± .06	6.19 ± .05	6.08 ± .04	6.20 ± .03
Number of plants	104	120	96	320
Light blue	6.16 ± .07	6.16 ± .05	6.14 ± .08	6.15 ± .03
Number of plants	40	72	40	152
Mean of total	6.23 ± .04	6.14 ± .03	6.11 ± .04	6.17 ± .02
Number of plants	240	256	144	640

* Only brown-seeded plants were included in means of segregating classes.

Table 30. Association of oil content with iodine value within F_2 and F_3 populations from two flax crosses

Population	Marine x C.I. 1455 N	Marine x C.I. 1455 r	Redwood x C.I. 1455 N	Redwood x C.I. 1455 r
F_2 plants				
Brown-seeded	156	+.0005	131	+.020
Yellow-seeded	37	+.297	42	+.126
Total population	193	+.218**	173	+.160*
F_3 lines (bulked)				
Brown-seeded or segregating	109	+.069	126	−.105
Yellow-seeded	20	−.144	37	−.231
Total population	129	+.249**	163	+.246**
F_3 lines (means of plants)				
Brown-seeded or segregating	73	+.158	58	−.254
Yellow-seeded	9	−.132	23	−.268
Total population	82	+.378**	81	+.080

* Indicates significance at 5 percent level.
** Indicates significance at 1 percent level.

seed (Chu and Culbertson, 1952; Dillman, 1936; Dillman and Hopper, 1943; Johnson, 1932; Lemos, 1949; McGregor, 1937). Correlation analyses were made in order to determine if such an association existed within the progenies from the two crosses under study.

Oil percentages of F_2 plants were related to seed weight as shown by significant positive correlation coefficients in table 31. The association was significant within the brown-seeded classes and within the total F_2 populations of both crosses.

Oil content of F_3 lines, as determined by individual plant analyses, did not show a significant relationship with seed weight. The correlation coefficients were positive, however, and numerically equal to the "r" values obtained in the F_2 generation.

A significant positive relationship was found between seed weights of F_2 plants and oil content of their F_3 progeny (table 31). This relationship was exhibited by populations from both crosses.

Table 31. Association of oil content with seed weight within F_2 populations of two flax crosses and within F_3 population from the cross Redwood x C.I. 1455

Population	Marine x C.I. 1455 N	Marine x C.I. 1455 r	Redwood x C.I. 1455 N	Redwood x C.I. 1455 r
F_2 plants				
Brown-seeded	88	+.374**	99	+.244*
Yellow-seeded	21	+.216	33	+.260
Total population	109	+.274**	132	+.180*
F_3 lines (means of plants)				
Brown-seeded or segregating	....	....	41	+.285
Total population	....	....	56	+.245
F_2 seed weight and F_3 oil content				
Brown-seeded	....	....	96	+.372**
Yellow-seeded	....	....	33	+.135
Total population	63	+.424**	129	+.207*

* Indicates significance at 5 percent level.
** Indicates significance at 1 percent level.

Iodine Value with Seed Weight

There was a tendency for iodine value to be negatively associated with seed weight among F_2 and F_3 populations of the cross Redwood x C.I. 1455 and among the brown-seeded F_2 plants of the cross Marine x C.I. 1455 (table 32).

Seed weights of F_2 plants did not exhibit a significant association with iodine values of their F_3 progeny.

Table 32. Association of iodine value with seed weight within F_2 populations of two flax crosses and within the F_3 population from Redwood x C.I. 1455

Population	Marine x C.I. 1455 N	Marine x C.I. 1455 r	Redwood x C.I. 1455 N	Redwood x C.I. 1455 r
F_2 plants				
Brown-seeded	88	−.211*	99	−.257**
Yellow-seeded	21	−.006	33	−.112
Total population	109	−.156	132	−.236**
F_3 lines (means of plants)				
Brown-seeded or segregating	....	....	41	−.456**
Total population	....	....	56	−.468**
F_2 seed weight and F_3 iodine value				
Brown-seeded or segregating	....	....	96	−.148
Yellow-seeded	....	....	33	+.009
Total population	63	+.007	129	−.121

* Indicates significance at 5 percent level.
** Indicates significance at 1 percent level.

DISCUSSION AND SUMMARY

Oil content data obtained from F_2 and F_3 populations of two flax crosses revealed wide ranges of distribution among plants of both generations. Analyses of variance showed that a large proportion of this variability was due to genetic differences among plants. Oil content was highly heritable with estimates of heritability as high as 67 percent. This indicates that a large proportion of the phenotypic variance was genetic, and that this genetic variance was largely additive. The average oil content of both F_2 populations approximated the mid-parent means, further substantiating the observation that a high proportion of the total genetic variance was additive.

A high proportion of additive genetic variance within the total phenotypic variance of a population enhances the effectiveness of selecting for high oil content. The estimated genetic advance from the F_2 to the F_3 generation was calculated to be about 1.5 oil percentage units if the highest 10 percent of F_2 plants were selected as progenitors of the F_3 population. The observed genetic advance approximated the predicted value (1.9 and 1.5).

A selection procedure which would raise by 1 percent or more the mean oil content of a heterogeneous population would greatly facilitate a selection program designed to increase oil content of flax. The data indicate that it would be a practical and worth-while procedure to select among F_2 plants for high oil content, at least within populations from the two crosses under study.

Seed color appeared to be an excellent criterion for selecting high oil genotypes because of the high degree of association between high oil content and yellow seed color among the F_2 and F_3 populations of both crosses. In actual practice, however, flax breeders tend to select against the yellow-seeded character. This selection seems necessary since several undesirable characteristics have been reported to be associated with the yellow-seeded character by Culbertson and Kommedahl (1956). Yellow-seeded members of paired isogenic lines were lower in germinability; had higher percentages of cracked, split, and blighted seed; lower test weight; and were significantly lower yielding than the brown-seeded lines. Further evidence for the undesirability of the yellow-seeded character in flax is the failure of yellow-seeded varieties to gain general acceptance by flax growers. There are no yellow-seeded varieties being grown on other than limited acreages at the present time.

The yellow-seeded parent used in the two crosses possesses genetic factors for high oil content besides those linked or otherwise associated with the yellow-seeded character. This is indicated by the large proportion of the brown-seeded plants in the F_2 and F_3 populations which were much higher in oil content than the brown-seeded parents. The most likely explanation is that the high-oil, yellow-seeded parent, C.I. 1455, contributed high-oil genes that were inherited independently of the seed color gene.

There were significant positive correlations between the seed weights and oil percentages of individual F_2 and F_3 plants. The associations were of such low order, however, as to make the use of seed weight impractical as a selection criterion for improving oil content.

Although oil content is perhaps the most important seed quality characteristic that concerns flax breeders, high quality of oil, as indicated by iodine value, is a breeding objective. The two characteristics were found to segregate independently within seed color classes. Thus it is possible to combine high oil content with high iodine value. Significant positive correlation coefficients were derived when data from seed color classes were combined, reflecting the higher means of **both** iodine value and oil content in the yellow-seeded class as compared to the brown-seeded group.

The relative ease with which iodine values may be determined on small samples of seed suggests that actual determinations would be the most practical criteria for selecting high iodine value genotypes. Data obtained from the F_2 and F_3 populations of the crosses under study show iodine value to be somewhat less heritable than oil content, particularly in the cross of Redwood x C.I. 1455. Selection for high iodine value among F_2 plants would result in less relative genetic gain in the F_3 than was the case with oil content. Nevertheless it would be a practical breeding procedure.

Progeny from the cross of Marine x C.I. 1455 showed greater total variance for iodine value, both within F_2 and F_3 populations, than did progeny from the cross of Redwood x C.I. 1455. The difference in phenotypic variance was estimated to be largely genetic variance; i.e., there was less heritable genetic variation within the F_2 and F_3 populations stemming from the cross Redwood x C.I. 1455 than there was within comparable populations from the cross Marine x C.I. 1455. This would indicate that Redwood and C.I. 1455 have more alleles in common than do Marine and C.I. 1455 for iodine value. Estimates of the additive genetic variance component within both crosses suggest the factors for iodine value that were segregating in the cross Marine x C.I. 1455 were largely additive in expression. Consequently, Marine would be preferred over Redwood as a parent in a breeding program designed to attain high iodine values because of the additive or "fixable" nature of the factors for high iodine value present in Marine. In support of this conclusion, it may be pointed out that the genetic advance expected in the F_3 generation by selecting from among the highest 10 percent of F_2 plants of the cross Marine x C.I. 1455 was computed to be twice as great as the expected genetic advance from selecting among the F_2 of the cross Redwood x C.I. 1455.

The yellow-seeded F_3 plants of both crosses averaged 4 to 9 points higher in iodine value than did the brown-seeded plants. Some genetic advance in iodine value would be expected by selecting only yellow-seeded F_2 plants. Yellow seed color is not a practical selection index because, as indicated earlier, there are undesirable traits associated with the yellow-seeded character.

High association of yellow seed with high iodine value within populations of both crosses is interesting in that the yellow-seeded parent, C.I. 1455, was 14 to 18 points lower in iodine value than the brown-seeded parents, Redwood and Marine. High iodine value and the yellow seed character came into the crosses in repulsion yet appeared in coupling among the F_2 and F_3 generations. One possible explanation for the association is to assume that there are factors closely associated with the gene-conditioning yellow seed color which result in a certain minimal level of iodine value. Upon crossing, the brown-seeded parents contribute alleles for high iodine value, located at loci independent of the seed color locus, which combine with the yellow seed allele in various recombinations to give different levels of iodine value. All yellow-seeded recombinants would be above or equal to the minimal level of iodine value resulting from the action of factors closely associated with the yellow seed color allele. In support of this explanation, no yellow-seeded F_2 or F_3 plants were observed to be lower in iodine value than the yellow-seeded parent. The iodine values of at least 5 percent of the brown-seeded segregates were less than that of the low iodine value parent.

Highly significant negative associations between seed weights and iodine values observed within F_2 plant populations and among F_3 lines from the cross of Redwood x C.I. 1455 suggest that seed weight is an effective selection criterion for high iodine value. This would be an impractical breeding procedure, however, unless high iodine value was the most important breeding objective. Selection of small-seeded plants would result in phenotypic gain for high iodine value but there would be a tendency to lower the mean oil content of the selected population.

Seed weight was found to be considerably less heritable than either oil content or iodine value when estimated in the "narrow sense." The genetic variance for this character was estimated to be largely dominance variance or other "nonfixable" genetic variance. Highly significant phenotypic correlations were observed, however, between seed weights of F_2 plants and that of their progeny.

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