BREEDING FOR QUANTITATIVE CHARACTERS IN LINSEED. II. GENETIC CORRELATIONS AND CORRELATED GENETIC RESPONSE WITH SPECIAL REFERENCE TO TILLERING AND EARLINESS

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The existence of correlated responses in the form of alterations in unselected characters as a result of selection pressure exerted on a particular character has been recognised for a long time by evolutionists and geneticists. Thus, Darwin in his 'Origin of Species' writes "Hence, if man goes on selecting and thus augmenting any peculiarity, he will almost certainly modify unintentionally other parts of the structure owing to the mysterious laws of correlation." With the developments in our understanding of heredity that followed the re-discovery of Mendel's work in 1900, we are now in a position to have some idea of the reasons behind these mysterious laws. Human or natural selection is based on the phenotype as a whole and not on any particular character in isolation. Such selection, is, therefore, based to a large extent on the preservation of the complete genotypes of individuals having the favoured phenotype. It follows that, consequent on such selection, genes not affecting the particular character being selected for will also be exposed to a selection pressure, the magnitude of which will depend on the contribution of these unselected genes towards the fitness of the organism as a whole. The existence of such an indirect selection, as a result of the physical and biochemical relationship between the gene or gene-complex being selected and others, is responsible for what Darwin terms the "mysterious laws of correlation". The mechanism underlying such correlated responses has become much clearer following the formulation of the theory of polygenic control of continuous variation by Mather (1949) and has been considered in great detail by Wigan and Mather (1942) and Mather and Harrison (1949). The literature on this aspect has been reviewed extensively by Haskell (1954) and Sisodia (1960).

In this paper the relationship existing between earliness, tillering and yield as well as a number of yield components in linseed has been analysed with a view to predicting the probable response in these characters when selection is exercised for either tillering or earliness.

Materials and Methods

The experimental data used in the present study were obtained from a cross between a provincial type, T. 477 and an exotic type, Afghanistan-2, of *Linum usitatissimum*. The object of the cross was to incorporate the high-tillering capacity of the exotic parent into the agronomically desirable variety, T. 477. The cross was made in 1956-57 and the F_1 and F_2 populations grown and studied during 1957-58 and 1958-59. The plantings in 1959-60 consisted of parents, F_2 and F_3. For growing the F_3, fourteen plants from the F_2 population of 1958-59 were selected at random and their F_3 progenies grown out along with the parents in a randomised block layout with 4 replications. One 15′ long row with the plants spaced 9″ apart in the row was assigned randomly to each parent or progeny in each replication. Additional F_2 populations were grown in a separate layout with four replications. In each replication, there were eight parental and eight F_2 rows, the rows being assigned completely at random. Data were recorded on individual plants on (1) first flowering date as a measure of earliness,

(2) number of effective tillers, i.e., those which bore capsules, (3) number of capsules, (4) average number of seeds/capsule from 10 capsules selected at random, (5) seed size, as measured by 200-seed weight and (6) yield per plant. Standard statistical procedures were adopted in calculating the genotypic, phenotypic and environmental correlations in the F_2 and F_3 generations.

Experimental Results

The association existing between the different characters studied was estimated by working out the genotypic and phenotypic as well as environmental correlations between these various characters in the F_2 as well as in the F_3 generations of the cross T. 477 × Afghanistan-2.

1. *Association between different characters in the F_2:*

Correlations, at the three levels, were worked out for the F_2 generation from the two populations grown during the years 1958-59 and 1959-60. Table 1 below gives the correlations obtained in the two years, the figure within the parantheses referring to 1959-60.

TABLE 1

The genotypic, phenotypic and environmental correlation between a number of characters in the F_2 of T. 477 × Afg. 2

Association tested	Genotypic r	Phenotypic r	Environmental r
First flowering date with			
Yield	−0·295	−0·222**	+0·006
	(+0·082)	(−0·188)**	(−0·609)**
No. of capsules	−0·181	−0·169**	−0·043
	(+0·410)	(−0·005)	(−0·501)**
Seeds/Capsule	−0·301	−0·148**	+0·025
	(−0·120)	(−0·065)	(+0·039)
200 Seed weight	−0·784	−0·535**	−0·101
	(..)	(..)	(..)
Tiller number with			
Yield	+0·830	+0·669**	+0·346**
	(+0·681)	(+0·579)**	(+0·484)**
No. of capsules	+0·790	+0·667**	+0·407**
	(+0·711)	(+0·575)**	(+0·490)**
Seeds/Capsule	−0·111	−0·094	−0·088
	(−0·071)	(−0·066)	(−0·059)
200-seed weight	−0·062	−0·057	−0·064
	(..)	(..)	(..)
First flowering date with tiller number	+0·098	+0·065	−0·029
	+0·139	−0·034	−0·361**

No data were recorded on 200 seed weight in the year 1959-60. Appropriate tests for significance of genotypic correlations are not available. In both the seasons, the genotypic as well as other correlations between tiller number and other characters remain more or less constant while there were larger fluctuations in the estimates of association between flowering date and the other characters. The reason for this is not clear but it may be pointed out that the sowing was rather delayed in the second season due to climatic factors. As is well known, onset of flowering is dependent upon length of day and other environmental conditions and it may be that in this season late plants were under a disadvantage. This supposition is to some extent made likely by the fact that the environmental correlation between flowering date and number of capsules and yield are negative and highly significant in 1959-60 unlike in the previous season where they are low and non-significant.

2. *Association in the F_3 generation:*

Family structure in a cross having homozygous parents is not discernible until the F_3 generation. Therefore, to determine the degree of the persistence of the association among the characters in the F_3 generation, correlation between these same set of characters were worked out and are presented in Table 2.

TABLE 2

The genotypic, phenotypic and environmental correlation between a number of characters in the F_3 of a cross between T. 477 and Afg. 2

Association tested	Genotypic r	Phenotypic r	Environmental r
First flowering date with			
Yield	−0·394	−0·282	−0·005
No. of capsules	+0·796	+0·139	+0·070
Seeds/Capsules	+0·146	+0·072	+0·015
200 seed weight	−0·634	−0·590*	−0·304**
Number of tillers with			
Yield	−0·226	+0·011	+0·644**
No. of capsules	+1·061	+0·382	+0·608**
Seeds/capsules	+0·758	+0·333	−0·033
200-seed weight	−0·367	−0·323	−0·085
First flowering date with tiller number	+0·487	+0·541*	−0·045

A comparison of the data presented in Tables 1 and 2 suggests that the association among most of the characters in the F_3 is not in agreement with the association observed in the F_2 generation. For instance, the correlation at the genetic level between flowering date and tiller number is fairly low in the F_2 but much more pronounced in the F_3. Similarly, the genotypic correlation between flowering date and yield has been intensified while that between tillering and yield shows a low negative value in the F_3 instead of the high positive value observed in the F_2. On the basis of these results, it is evident that association in the F_2 among characters which show heterosis or dominance is likely to be much disturbed and may not give us a good estimate of the true association. The estimates obtained in the F_3, where mean plot values and not individual plant observations are used and where the masking effect of heterosis or dominance becomes much less pronounced, are probably more realistic estimates. In the present case, however, only 14 F_3 families were available and this necessarily reduces the precision of the estimates. The reliability of these F_3 estimates, therefore needs further confirmation by studying a large number of F_3 or even F_4 families.

3. *Correlated response to selection for earliness and tiller number:*

An attempt was made to study whether correlated changes could be detected as a result of selection for one generation for flowering date and tiller number. The material available for such a study in the present case is somewhat inadequate and further, selection has been applied for one generation only. These drawbacks have to be kept in mind in considering these results but, all the same, some indication can perhaps be obtained of the direction, if not the extent, of such correlated responses.

For the purpose of this study, the 14 F_2 plants selected for growing out the F_3 progeny were grouped into early flowering and late flowering classes and, on the basis of tiller number, into a group with high and a group with low tiller number (" selected groups "). Genetic correlations were worked out among the different characters within each of these groups and also when all the fourteen plants were pooled together into one group (" unselected group "). Comparison of genetic correlation in the " selected " groups with that in the " unselected " group and with the genetic correlation in the F_3 generation should give us some indication of the existence of any correlated change in the unselected characters. The data obtained in the present study are summarised in Table 3. It would be noted that genetic correlation could not be obtained in a large number of cases. In such cases, imaginary numbers were obtained

TABLE 3

The genetic correlation between different characters in the F_2 and F_3 generations in the " unselected " population and in the population where selection has been exercised for one season for flowering and tiller number

Association tested	" Unselected " Group	Group " Selected " for: Early flowering	Late flowering	Low tillering	High tillering
Flowering date and					
Tiller number ..	−0·004	+0·665	+0·289	+0·404	....
	(+0·487)*	(+1·075)	(+0·708)	(+0·909	(+0·364)
Yield	−0·551	−0·402	....	−0·661	....
	(−0·394)	(+0·865)	(−0·271)	(−0·451)	(−0·355)
No. of capsules ..	−0·550	−0·623	+1·052	−0·364	2·085
	(+0·796)	(........)	(+1·253)	(........)	(........)
200 seed weight ..	−0·766	+0·008	−1·494	−2·234	−1·355
	(−0·634)	(+0·040)	(−0·920)	(−0·480)	(−0·830)
Seeds/Capsule ..	....	....	....	....	....
	(+0·146)	(+0·498)	(........)	(........)	(+0·017)
Tillering and					
Yield	+0·639	+0·850	....	+0·638	....
	(−0·226)	(+0·625)	(−0·664)	(−0·078)	(−0·331)
No. of capsules ..	+0·590	+0·618	+1·197	+0·481	....
	(+1·061)	(........)	(+0·467)	(........)	(........)
2C0 seed weight ..	+1·128	+0·455	+0·902	+2·091	....
	(−0·367)	(−0·141)	(−0·742)	(0·287)	(−0·502)
Seeds/Capsule ..	....	....	....	....	....
	(+0·758)	(+0·706)	(........)	(........)	(+0·448)

........Indicates an imaginary number was obtained.

*Figures without parentheses refer to the F_2 and those within parentheses refer to the F_3 generation.

either because genetic correlation was not significantly different from zero or genetic variation within one or both the characters was absent. In such cases, there can obviously be no genetic correlation.

The genotypic correlation in F_3 in the " unselected " group is itself different from the correlation observed in the F_2. This fact has to be kept in mind in assessing the effect of selection on the correlation in the " selected " groups. The situation appears to be the same with regard to most of the characters, though there is a tendency for the association to decrease rather sharply in some of the selected groups. Since the behaviour of the selected populations is more or less similar to that of the group considered as a whole, without any reference to the application of selection pressure, it may be concluded that the selection applied has not had any correlated effect in changing the association between these characters. As has already been pointed out, however, the correlation values obtained in F_2 are likely to be biased by a number of factors while those obtained in the F_3 may prove to be more reliable. It would, therefore, appear more profitable to grow the F_4 generation and then determine whether any correlated response to selection, in respect of the characters studied, occurs or not.

Discussion

A knowledge of the genetic correlation existing between different economically-important characters is very essential to the plant-breeder, if correlated responses in unselected characters are not to erode or nullify the gain achieved by painstaking selection. The problem is all the more important when the breeder is engaged in an attempt to introduce quantitatively inherited characters from an otherwise undesirable variety into an agronomically desirable base. As Haskell (1954) points out, selection carried too far in one direction may prove dangerous for the species or variety which has achieved a delicate adjustment with environmental conditions, built up through a long period of natural, and human, selection. This disadvantage, however, will not be felt if lop-sided selection is not pushed to an extreme.

There appear to be three possible factors which may be responsible for the observed correlated responses. Thus, the same gene or gene-complex which is controlling the character under selection might have a pleiotropic effect on the character(s) showing correlated response. If such is the case, the genetic association between the characters would be rather high, and there may be little possibility of breaking the association. On the other hand, correlated response may also be due to the linkage of genes controlling different characters. As Mather and Harrison (1949) have pointed out, polygenes affecting the same character in different directions, as also those controlling different characters, are most probably intermingled along the chromosomes in balanced combinations, which are held together as units in the absence of recombination. Since, over short periods of time, the units of inheritance may well be entire chromosomes, this would mean that a response to selection in one character will generally be accompanied by a correlated response in another, even when the latter is not itself subject to the direct action of a selective force. Indeed, correlated response could change certain characters even against the apparent trend of natural selection. The closer such linkage between the polygenes concerned, the greater will be the genetic correlation between the two characters. The second type of mechanism differs from the first, however, in one important respect. Since the linkage between genes can be dissolved through recombination, it should be possible to break even very close linkages, provided sufficient population, over a number of generations, is grown, as was demonstrated by Mather and Harrison (1949) for chaetae number in *Drosophila melanogaster*. In their original population, selection for increased or decreased chaetae number was accompanied by a sharp fall in fertility. When selection for chaetae number was relaxed, natural selection for fertility took charge and chaetae number came to the normal level. Interestingly enough, reselection at this stage for high chaetae number did not carry with it a correlated fall in fertility and high-chaetae lines could be selected which maintained their high level, even under mass culture. Apparently, the old linkage between the genes for fertility and chaetae number had been broken and new combinations favouring the coexistence of high chaetae number and high fertility had been built up.

Correlated changes may also occur in the absence of high genetic correlation as a result of the chance association of genes in the parents selected. As Clayton, Knight, Morris and Robertson (1957) have concluded, a major source of correlated response is restricted genetic sampling, as happens when only small populations are available for study. This may not be important under conditions of natural selection for, generally, large populations are available under such conditions. This possibility has, however, to be taken into consideration in plant-breeding programmes, since considerations of economy and space usually restrict the number of individuals which can be handled.

In the present study, genetic correlation has been estimated from the F_2 as well as the F_3 generations. Even if we compare the F_2 generation grown in the same year as the F_3 with the latter, we find that there are considerable discrepancies in the correlations noted at the genetic level in the two generations between most of the character pairs studied. It is not quite clear as to what the reasons for such a discrepancy are. It may be mentioned, however, that the existence of heterosis or dominance with respect to some of these characters has been noted in the F_1 (Sisodia, 1960) and it is likely that these effects have been carried over to the F_2 also to some extent.

The existence of such factors, would, of course, result in phenotypically alike but genotypically different plants being grouped together and may conceivably result in biased estimates of the association. In the F_3, however, these distracting features will be considerably reduced. Furthermore, the F_2 observations are based on individual plant data while the F_3 data are based on plot means. Because of all these considerations, it appears more desirable to rely on the F_3 estimate than on the F_2 values.

Considering, then, the genetic correlations obtained in F_3, (Table 2), it is seen that the genetic correlation between number of tillers per plant and capsule number as well as between first flowering date and capsule number are rather high. Of course, it is possible that these correlations are due to pleiotropic action of a gene or gene complex or to physiological correlation. Thus, fewer tillers may mean fewer flowers and hence fewer number of capsules per plant. On the other hand, earlier start of flowering could result in less vegetative growth, which would ultimately mean that the plant would be capable of supporting only fewer capsules. However, it may be noted that the correlation of first flowering date and tiller number is not so very high, though still about 50 per cent. It is, therefore, likely that the correlation here may be due to linkage and it may be possible to select out combinations of genes giving both earliness and high tillering and the large number of capsules associated with the latter. The genetic correlations between the other combinations studied is rather low and so it should be possible to select early strains without losing the high seed number per capsule or seed weight.

As has already been pointed out, the F_2 estimates of genetic correlation may not give us a true measure of the association actually present. In view of this uncertainty, it is difficult to say whether there has been any correlated response to the selection exerted for one year on flowering date and tiller number. However, the fact that, in general, the trend of change has been in the same direction when all the plants and progenies were grouped together as when they were separated into groups on the basis of F_2 phenotypes, would suggest that there has not been much correlated response, though the extent of association is rather markedly different in the case of some character combinations in the group selected for early flowering. In view of the small number of progenies available, however, it is rather difficult to estimate the significance of this differential behaviour. Perhaps, one should not expect any marked change in the association within one generation and perhaps, such changes may become more apparent in later generations of selection. Especially in view of the complicating factors in the F_2, it would appear desirable to study this aspect in later generations, say F_4 or even F_5, before coming to any definite conclusions. The fairly high positive association shown between flowering date and tillering need not, however, lead to pessimism. For, as the experiments of Mather and Harrison described above show, over a period of time, recombination with selection may break this unfavourable linkage and allow the breeder to obtain early, high tillering and high yielding varieties. Such a possibility is, however, contingent on the observed genetic correlation being due to intermingling of polygenes and consequent linkage and not to pleiotropy or physiological correlation. It would appear, therefore, desirable that comprehensive studies should be taken up to elucidate the exact nature of the correlations observed in the present study.

Summary

The present study was undertaken to investigate the genetic association existing between flowering date and tiller number as well as between these characters and yield as also a number of yield components, in the F_2 and F_3 generations of a cross between two varieties of linseed, T. 477 and Afghanistan 2. A major objective of this cross was to transfer the high tiller number of Afg. 2 to the agronomically desirable parent, T. 477. It was also sought to predict the correlated response to be expected in the characters as a result of selection for earliness or high tiller number. It has been found that the F_3 estimates of correlation, at the genetic level, of a number of character pairs are different from the estimates obtained in the F_2 and it has been suggested that, for a number of reasons, the F_3 estimates might be more reliable. Very high positive genetic correlation was seen to exist between flowering date and tillering on the one hand and number of capsules/plant on the other in the F_3. Since capsule number is an important component of yield, this association will prove disadvantageous to the breeder. However, the association between flowering date and tiller number, though positive, is not very high and hence may be due to linkage. It may be possible, therefore, that over a period of time, through recombination and selection, the breeder might be able to select varieties combining earliness and high tiller number as well as high yield.

The extent of correlated response which would actually be met with in the F_3, if selection for flowering date and tiller number had been practiced in the F_2, has been studied. No correlated response could be convincingly demonstrated in the "selected" group as compared to the "unselected" group. However, it is likely that such responses may become visible if selection is carried on for two or three more generations.

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