THE COMBINING ABILITY OF PARENTS OF COCKSFOOT (DACTYLIS GLOMERATA L.) OF MEDITERRANEAN AND NORTHERN EUROPEAN ORIGIN

by

R. Knight

B.Sc.(Lond.) Dip.Agr.Sci. (Cantab.) D.T.A.(Trin.)

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Department of Agronomy
Waite Agricultural Research Institute
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STATEMENT

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except when due reference is made in the text of the thesis.

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INTRODUCTION

This study had two main objectives. One was to evaluate the potential of some newly introduced breeding material of cocksfoot (Dactylis glomerata L.), the second was to obtain information on plant characters that might affect yield.

Dactylis glomerata, of Northern European origin has been grown in Australia since early in the colonisation of the country, but it is only comparatively recently that any material of Mediterranean origin has been deliberately introduced and tested. Over the years 1930-1945 eight seed lots were brought to Australia (C.S.I.R.O. Plant Introduction Inventories) but in 1951 following an increased realisation that the Mediterranean region was a valuable source of germ plasm, the Donald-Miles expedition collected and brought back 31 acquisitions of cocksfoot, along with other species. In 1954 a second expedition (Neal Smith, 1955) brought back a further 103 acquisitions and it is these collections that form the bulk of Mediterranean material at present being investigated in different parts of Australia.

No plant breeding has been carried out in Australia on cocksfoot of Northern European origin, the named varieties, that have been grown, have all been introductions from other countries such as the S strains from Aberystwyth Wales, Danish cocksfoot from Denmark, and Akaroa and Grasslands from New Zealand. (New Zealand cocksfoot is not indigenous but originates from Northern Europe.) Breeding of cocksfoot of Mediterranean origin has been confined to two varieties released in 1955 (Bridgman and Woodward). These were selections from among the eight early introductions mentioned above and their selection was the only breeding practised on them. One of these varieties, Currie is proving to be most successful, but the other Neptune has fallen out of commercial production.

The collections made during 1951 and 1954 were grown at the Waite Institute by the author for several years after 1955 and on a basis of their performance, several strains were selected for further regional agronomic trials. In 1958 the present study, deviating from this previous work in considering only a limited range of material, was started to obtain detailed data on hybrids between some of the introductions and also to evaluate the breeding potential of hybrids obtained from crossing with Northern European material.

A perennial pasture grass for the South Australian environment, with its winter rainfall season, should have the following attributes.

(1) High total productivity, with a premium placed on growth during the autumn and winter, a time when the slow growth of existing pastures is the main factor limiting animal production.

(2) High summer survival to ensure stable pastures and reduce wide year to year fluctuations, characteristic of annual grasses.

(3) Some summer productivity to make use of the erratic summer rainfall provided that such growth is not detrimental to survival.

The Mediterranean and Northern European forms of _Dactylis glomerata_ may to a limited extent be measured against these attributes from data already available (Bridgman and Woodward, 1955; Knight, 1960).

It is known that the Mediterranean forms are winter growing, but that within them there is considerable variation for autumn and winter production. Summer survival is very high but this is apparently achieved by summer dormancy with no production during the summer months.

The Northern European forms are moderately productive during the autumn and winter, this is known from farming practice in areas of irrigation, but the magnitude of this production relative to that of the Mediterranean forms has not been tested. During the summer the Northern European material will grow well if irrigated, but under the natural environment there is still some summer growth through lack of dormancy, despite the severe conditions. The resulting mortality is so high as to preclude the profitable use of this material in pastures under natural rainfall.

It was of interest to find answers to the following questions. (1) Within Mediterranean material, to what extent was it possible to have in one plant high combining ability for growth in autumn, winter and other times of the year? (2) What would be the performance of Mediterranean x Northern European hybrids in terms of seasonal productivity, summer survival and summer dormancy when the parents differed so clearly in these last two characters? (3) What was the magnitude of the differences in growth rhythym of purely Mediterranean, Mediterranean x Northern European, and purely Northern European families?

Answers to these questions might have been obtained using a large number of parents and a relatively simple crossing and testing procedure but it was desired to follow seasonal variation in other plant characters besides top weight and this imposed a limit on the number of families that could be considered.

An important factor in the difficulty of producing grass varieties with increased yields is the lack of knowledge of the growth of grass plants. The relation to yield of characters such as height, tiller production, tiller weight, root size, or top : root ratio remains a matter of conjecture. Also breeders are not fully aware of the effects on yield of changes in growth phases such as the transition from vegetative to reproductive phases. In spite of this, it has been suggested at times that increased yields can be obtained by selection for or against the expression of each one of these characters. Selection can be most inefficient if each character is not making a definite contribution to yield as the overall intensity of selection must be reduced with each additional character selected. An increased knowledge of the importance of these characters as attributes of pasture grasses would be of value in a breeding programme.

The analysis of the data, based on the concept of combining ability, was chosen because of the complex genetic situation in Dactylis glomerata. The somewhat different analysis proposed by Jinks (1954) and Hayman (1954) was originally developed for plants with diploid segregation and although this has been extended to cover a restricted autotetraploid situation (Dessureaux, 1959) it is still unlikely to be suitable for Dactylis glomerata. At present all of the agriculturally important forms of Dactylis glomerata are tetraploid and it is only recently that the range of diploid forms has become evident. (Stebbins and Zohary, 1959). Several studies have been concerned with elucidating the mode of inheritance in the tetraploid group of the species (Myers, 1940, 1941; Brix and Quadt, 1953; Rebischung, 1956; Cuany and Kalton, 1960). Each of these authors has followed single gene characters, mainly chlorophyll deficiencies, and all have concluded that tetrasomic inheritance was the most likely explanation for their results, although Cuany and Kalton consider that disomic inheritance also occurs. It is probable that a mixture of disomic and tetrasomic inheritance is involved; the relative proportions of each depending on the degree of allopolyploidy, which in turn will depend on the origin of the particular race. Tetraploid Dactylis glomerata has almost certainly arisen in several different localities from diploid ancestors. Stebbins and Zohary (1959) consider that gene exchange may still be occurring between the restricted diploids and the widespread tetraploids through triploid intermediaries. In view of this genetic situation in the tetraploids it was more logical to carry out analyses on this important crop using the more statistical approach of combining ability rather than one derived from genetic models and assumptions.

As Dactylis glomerata is a cross pollinated species, plants are genetically different. This results in variation even within an F_1 progeny. If, however, adaptation to local environments results in any fixation of genes the progenies of two different races may not show great variation relative to variation between all progenies. In these circumstances precise experimentation is possible. The matter of precise experimentation and evaluation is an important one in cross pollinated species. Fisher (1949, p. 119) and Falconer (1960, p. 278) have pointed out that the great success of hybrid maize may lie in the precise evaluation of genotypes made possible by the technique of inbreeding to homozygosis and then producing F_1s, rather than in any exceptional value of hybridity. The members of an F_1 family of maize are genetically identical and are replicates of a genotype only present as single individuals in the initial population from which the inbreds were derived. Selection of F_1s is then more accurate and has a much greater chance of success than selection within the initial population. Use of a similar inbreeding technique for grasses has not been successful for a variety of reasons (reviewed by Wexelsen, 1952) and an alternative for some studies may be the use of hybrids between locally adapted races as in the present instance.

Two further problems of technique in relation to grass breeding need to be mentioned. Pasture plants are grown by the farmer in dense swards where there is strong competition between members of the sward. Under these conditions growth is subject to limiting factors such as light, moisture and nutrients; a limitation not met with in the spaced plant conditions customary in many breeding nurseries. It is understandable that selection under the latter environment does not pick out the best genotypes for growth under pasture conditions, (Ahlgren *et al.*, 1945; McDonald *et al.*, 1952; Knight, 1960; Wright, 1960; Akerberg, 1960) nor can it be expected that expression of characters will be similar under the two environments. It is probable that some agronomic characters are affected by daylength, and with these, assessment as spaced plants or as swards must be identical, but these characters are relatively few in number. To obtain a reliable expression of the characters in the present study all the material was grown as swards.

Finally, there was the problem of management of the swards as it was known that the timing of defoliation may differentially affect grass varieties, particularly when there is variation in heading date (Davies, 1956). Scoring of the parents under consideration had indicated that they varied in this character. As a first step in the assessment of the breeding material it was decided to avoid this problem of defoliation, instead obtaining a cumulative yield, later endeavouring to relate this to a particular regime of defoliation. Cumulative yield in the Adelaide environment represents one seasons growth as all top growth is dried off during the summer by hot dry winds and this material rapidly decays with the rains in the autumn.

To summarise the introduction of the experiments, the combining ability of several Mediterranean parents was to be found by crossing within themselves and with Northern European parents the assessment to be in terms of seasonal growth, particularly emphasising periods in which existing pasture species are unproductive, and in terms of survival. A second objective was to follow in detail other plant characters in seeking a fuller understanding of the growth variation. F_1 families would be produced between a limited number of parents by emasculation and controlled pollination, these families would be grown in swards and sampled for their seasonal growth.

REVIEW OF LITERATURE

Concept of combining ability

The concept of combining ability may be traced to a breeding procedure suggested by Shull (1909). Shull had, in his study of inheritance of quantitative characters in maize, been inbreeding, then crossing the inbreds, and was impressed by the restoration of vigour brought about by the crossing. He suggested as a practical breeding procedure that "... it will be necessary to make as many self-fertilizations as practicable, to continue these year after year until the homozygous state is nearly or quite attained. Then all possible crosses are to be made among these different pure strains, and the F_1 plants coming from such crosses are to be grown in the form of an ear to row test ..." On a basis of these tests the most desirable cross would be detected and it would be this cross repeated on a large scale that would provide the farmers seed. It was this breeding programme that led to the production of hybrid maize and the phenomenal increase in corn yields that occurred in the 1930's (Sprague, 1952).

In the years that followed Shull's suggestion, many research studies were devoted to the evaluation of F_1 progenies (Richey, 1924; Hayes, 1926; Jorgenson and Brewbaker, 1927; Jenkins, 1929, 1934). Correlations between an inbred's phenotypic appearance and the subsequent hybrid performance were often too low to be of predictive value and most selection was made on the result of test crosses either among the inbreds themselves or with a standard variety. An inbred was usually saved for further evaluation or discarded on the basis of the mean of its crosses and inbreds were described as having a high or low combining ability as a result of these tests.

In 1942, Sprague and Tatum distinguished two forms of combining ability, general combining ability and specific combining ability, and gave equations - later modified (Federer, 1951; Rojas and Sprague, 1952) - for the calculation of the respective variances. Their definitions were that "general combining ability is used to designate the average performance of a line in hybrid combination ... The term specific combining ability is used to designate those crosses in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved." They mentioned that general combining ability provides an indication of gene effects which are largely additive, and specific combining ability indicates dominance and epistatic gene effects. They did not, however, actually derive the functional relationship between general and specific combining ability and the various classes of gene effects.

Yates (1947) also considered the quantitative analysis of hybrid performance. He gave a detailed account of the application of the analysis of variance to data obtained when parents were crossed in all combinations. In his analysis he considered that each F_1 family inherited a certain effect from it's parents, thus there was an effect due to the female parent and an effect due to the male parent For ease of computation these effects were calculated about the mean of all crosses. The mathematical model was therefore

$$y_{12} = m + a_1 + b_2 + e_{12}$$

where y_{12} is an observed value, m is the mean of all crosses, a_1 is the effect of male parent 1, b_2 is the effect of female parent 2 and e_{12} is a residual or error effect. This analysis was extended to indicate if a specific cross between any two parents was outstanding and also if there were reciprocal differences between crosses. Because incompatibility sometimes prevents the making of certain crosses or selfings the 2-way table of crosses (syn. diallel table) is not fully orthogonal and Yates showed how, utilising least squares estimation, an analysis may be made in these circumstances. Yates' approach to the subject of hybrid performance was statistical and no genetic interpretation was attempted. A similar approach was that of Kempthorne's (1952) except that here emphasis was placed on estimating parameters of a population, from which the parents were a sample, rather than evaluating the parents themselves.

The genetical interpretation of quantitative inheritance is based on concepts elaborated by Fisher (1918). It was shown how the additive and dominance effects of genes contributed to population variances and how covariances or correlations between relatives could be interpreted in terms of gene effects. These concepts were later applied to data on hybrid performance in attempts to evaluate the genetic contribution of parents to hybrids. The genetic analysis of diallel tables was attempted by Hull (1952), Jinks (1954) Hayman (1954) and by Griffing (1956 a). Griffing integrated the combining ability and genetic analyses and showed that under certain prescribed conditions of testing, the general combining ability variance originated from additive gene effects andsome of the additive x additive interactions, whereas the specific combining ability variance originated from dominance effects and all the other epistatic effects. It was then possible to relate combining ability variance to the covariance of relatives put forward by Fisher (1918).

Diallel tables of hybrid data are obtained with one of two objectives. One is to estimate variance components in a population in which case the parents used in the diallel test are a random sample from that population, the second is to obtain data on a selected set of parents and to estimate their value for further breeding. In another paper Griffing(1956b) produced analyses for several different types of diallel crosses considering both these objectives and it is one of these analyses that was used in the present instance.

Other modifications of the diallel cross procedure and combining ability analysis have been made. They include :

(1) The estimation of the combining ability variance components over several years and location. Rojas and Sprague (1952).

(2) The estimation of components when only a sample of the possible crosses among inbreds is made. This economises in the number of crosses enabling a larger number of parents to be used. The efficiency of this procedure is estimating variances was calculated by Kempthorne and Curnow. (1961).

The analysis proposed by Jinks (1954) and Hayman (1954) has been extended by them and by several other authors but as their analysis is based on several assumptions that are not justified in many circumstances (Kempthorne, 1956; Gilbert, 1958), including the present study, this literature is not fully reviewed.

Yield in pasture grasses and its inheritance.

Improvement of yield has been the major objective in all grass breeding programmes, but the methods followed have differed with species, locality and intended use of the improved varieties. Most attempts have aimed at overcoming local limiting factors such as diseases, pests and susceptibility to cold or drought. Other approaches have been to increase persistence to sustain yield at an overall high level instead of showing peaks and troughs, and to be more aggressive in competition with other species when in the seedling stage. Secondary objectives include increased seed production and improved nutritive status. Although breeding for yield has been the main objective, the results have been disappointing in terms of new varieties released. This may have been due to inadequacies in studies of quantitative inheritance or to the special problems associated with the breeding of pasture species. Some of these have already been mentioned in the "Introduction".

In studies on quantitative inheritance in pasture plants the full diallel test has not often been used because of the experimental difficulties of controlled pollination. Many other simpler tests have been tried. All of these tests have had the two objectives mentioned previously; in one, information is required on the breeding value of a selected group of plants and all experiments and inferences therefrom are confined to these plants; in the other, information is sought on a large population and the experimental plants are merely a random sample taken to enable the estimation of parameters in the large population. The information gained on the plants of the sample is incidental. With both objectives the experimental variability is partitioned into environmental and genetic components but in the second the observed mean square is equated to an expected variance derived from genetic models enabling a further partitioning of genotypic variance according to the mode of gene action. The genetic model giving rise to the expected variance is based on several assumptions and it is the failure to meet these assumptions that precludes variability in selected plants from being interpreted in complete genetic terms. In addition there is considerable difference of opinion on the importance of the assumptions and the use of these genetic models to explain experimental results and the subject requires further clarification before it can be profitably used in breeding programmes.

A simple separation of the environmental and genetic components of yield variability has bean made by clonally propagating plants and calculating the between clone and within clone variability. If the plants for propagation are randomly chosen from a population the genetic variability present in that population may be inferred. Burton and De Vane (1953) used this technique to estimate genetic variability for yield in tall fescue but there was some doubt as to the testing environment and randomness of the sample. Their genetic variability was high but this contained variability arising from all forms of gene action, additive dominance and epistatic and the possibilities for genetic advance may not be as good as this component would indicate.

Progeny tests are also capable of providing estimates of components. From inbred populations and polycrosses it is possible to calculate parent offspring regression, from pair-crosses regression of progeny on mid parent, and from the diallel cross half sib and full sib regressions. All of these regressions may be interpreted in terms of additive, dominance and epistatic influences on variability if the genetic models and assumptions are applicable (Fisher 1918; Fisher et al. 1932; Reviews in Mather, 1949; Comstock and Robinson, 1952; Kempthorne, 1957). Cooper (1960) analysed the variability present for yield within three named varieties of Lolium using full sib regressions and found the additive component to be 57%, 46% and 28% of the total variability. These indicate that advances could be made in breeding for yield. Cooper also studied other plant characters in an attempt to find the basis of yield differences but these were not conclusive.

The assumptions underlying the genetic analysis are seldom applicable for most breeding material but regressions can provide a useful measure of the inheritance of a character in statistical terms and have been the major guide in most selection programmes. (Weiss et al. 1951; McDonald et al. 1952; Hawk and Wilsie, 1952; Kalton et al., 1952; Murphy, 1952; Heinricks, 1953; Grissom and Kalton, 1956).

Of a similar nature and purpose are the combining ability estimates of yield in pasture grasses. They are particularly relevant to the present thesis and are considered in some detail in the next section.

Combining ability in pasture species.

In the text that follows general combining ability and specific combining ability have been abbreviated to g.c.a. and s.c.a respectively.

There have been many studies on combining ability in forage species since Sprague and Tatum (1942) first defined the concept and published their results for maize. However, most of these studies did not evaluate s.c.a.

One reason for this is that in forage species the making of controlled pollinations to specific males is difficult. More commonly controlled pollinations are not attempted and pollination takes place with a mixed group of males as in the polycross test. When this occurs the separation of crosses between particular females and males is not possible. Evaluation is restricted to the female parent and only the g.c.a. can be calculated. A second reason for not assessing s.c.a. relates to the practise in breeding of combining several parents into a synthetic variety for release to farmers. With the combination of several parents the s.c.a. is of reduced importance as it is unlikely to be high for all the possible combinations between the plants.

A summary is given in Table 1 of those studies in which pollination difficulties have been overcome and there has been an interest in evaluating s.c.a. The studies are arranged in chronological order.

It is evident that g.c.a. effects were found to be significant

Table 1.

Combining ability studies in pasture species

Authors	Species	Selection of parents	Assessment of progeny	Character	Combining ability significance levels	
					g.c.a.	s.c.a.
Bolton, 1948[+]	Medicago sativa	1) 13 parents inbred for one or two generations. Phenotypically selected for seed yield, agronomic features.	Spaced rows. 5 seeds per foot of row.	1)[≠] Yield Seed yield	*** ***	N.S. *
		2) 13 parents. Outpollinated origin. Phenotypically selected for seed yield.	"	2) Yield Seed yield	*** ***	N.S. *
Corkill, 1950[+]	Lolium sp.	5 parents unselected	Spaced	November Yield March Yield	*** ***	* *
Knowles, 1950[+]	Bromus inermis Agropyron cristatum " desertorum	1) B. inermis. Phenotypic 7 parents	Spaced	1) B. inermis Yield Creeping Habit.	*** ***	*** **
		2) A. cristatum.Phenotypic and self sterility 9 parents		2) A. cristatum Yield	***	N.S.
		3) A. cristatum. Phenotypic and self sterility. Inbred for 1-3 generations. 7 parents.		3) " Yield	***	*
		4) A. desertorum. Phenotypic and self sterility. 7 parents.		4) A. desertorum Yield	***	N.S.
				Aphis damage	***	N.S.
Kalton & Leffel, 1955	Dactylis glomerata	Phenotypic 11 parents	Swards	Yield	**	N.S.
				Panicle no.	**	N.S.
				Spring vigour	**	N.S.
				Leaf dis.	**	N.S.
				Flowering Date	**	N.S.
Oldmeyer & Hanson, 1955[+]	Dactylis glomerata	Phenotypic and polycross for yield. 2 diallel tests (1) 7 early parents (2) 5 late parents	1) Swards	1) Early diallel Yield	*	***
			2) Swards and spaced	2) Late diallel Yield	***	N.S.
Morley, 1957 et al.	Medicago sp.	Parents. Random plants from 10 named varieties	Spaced	Summer Yield	**	**
				Winter Yield	***	*
				Daylength & temp. treatments Yield	**	**

Table 1. (cont.)

Authors	Species	Selection of parents	Assessment of progeny	Character	Combining ability significance levels			
Torrie, 1957	Lolium peranne	1) 5 parents previously selected for high g.c.a. 2) 10 parents unselected	Spaced	1) 5 selected parents Yield	N.S.		**	
				2) 10 random parents Yield	**		**	
Fejer, 1958	Lolium perenne	Selected from old pastures. 1) 3 parents ∅ 2) 4 parents. Above 3 and another.	Spaced	1) Nov. yield	*		—	
				Dec. yield	**		—	
			Spaced	Sept., Jan., Feb., Apr. yield	N.S.		—	
				Nov. tiller No.	**		—	
				Dec. tiller No.	*		—	
				2) Jan., Feb., Apr. yield	**		N.S.	
				Jan., Apr. tiller No.	**		N.S.	
				Jan. tiller wt.	**		N.S.	
				Apr. tiller wt.	**		*	
				Jan. spread	**		*	
				Apr. spread	**		N.S.	
Timothy et al. 1959	Bromus inermis	Phenotype. Contrasting yield leaf %, disease res.	Spaced	Seed yield	**		*	
				Leaf spot	**		*	
				Scald	**		N.S.	
				Bacterial Blight	**		N.S.	
				Height	N.S.		**	
Anderson, 1960	Trifolium pratense	7 parents. Selected on basis of unspecified progeny test.	Spaced	Spring Yield	**		**	
				Summer "	**		**	
				Autumn "	**		**	
				Habit	**		**	
				Persistence	**		**	
				Flowering date	**		**	
Barclay, 1960	Trifolium repens	From Polycross for yield 7 parents	Spaced	February Yield	**		***	
				August "	**		N.S.	
						g.c.a loc.		s.c.a loc.
Carnahan, 1960	Medicago sativa	14 parents. Most promising breeding material from 8 locations	Either sward or spaced at 5 different locations	Seedling vigour	**	**	**	**
				Fall growth habit	**	**	**	**

[+] Combining ability variances were not calculated by the authors but were derived from their data.

[∅] s.c.a. can not be calculated when only 3 parents.

[≠] 2 parents omitted from diallel 1 because of missing values.

more frequently than s.c.a. effects. This may be accounted for by the fact that most forage varieties are relatively unselected, and as pointed out by Sprague and Tatum, g.c.a. variance is greatest with unselected material. As selection progresses, only the better lines remain and s.c.a. becomes of greater importance. In one study of a forage species it was shown (Torrie, 1957) that with selection of the parents s.c.a. alone became significant.

Other possible explanations for the frequent failure to detect s.c.a. are the large experimental errors usually associated with forage crop assessment and the fact that the parents, through not being inbred, are heterozygous lessening the chances of picking out particularly favourable gene combinations.

As so many of the g.c.a. effects were significant, it would suggest that genetic advances were possible, but unfortunately most of these assessments were based on spaced plants. Spaced plants were used instead of swards because of the ease of experimentation and because pollination difficulties prevented the production of the large quantities of seed necessary for the sward test (Timothy _et al_., 1959). It remains to be seen if g.c.a. effects of similar magnitudes will be present in swards in which yield variability is often reduced by limiting factors.

From the literature on yield, dealt with in this and the previous section, it can be concluded that the results have varied widely between experiments; that yield was more influenced by environment than most of the other charactersconsidered, and that few generalisations can be drawn that would serve as a guide for grass breeding programmes.

Information on the other plant characters considered in this study for their relation to yield will now be reviewed.

Stubble weight.

The stubble of a pasture grass may be defined as that part of the plant lying between the photosynthetic tops and the roots. It consists of the non-photosynthetic leaf bases, the apical buds and the very short stems present when the tillers are still vegetative.

As the stubble is an integral part of the grass plant it must affect and be affected by growth of the tops, but the inter-relation of the two would be difficult to determine within the complexities of grass swards. The same is true of the roots which will be considered later.

Recent research has shown that there is an optimal leaf area for maximal top growth under competition for light (reviewed by Donald, 1961). Similarly it might be anticipated that there will be an optimal stubble weight and an optimal root weight for maximal top growth. An excessively large stubble weight or root system may be a disadvantage in that they constitute a respiratory load on the plants' metabolism when it is competing for light. Under other circumstances, such as regrowth from dormancy or when there is a restricted water supply, the optima for stubble and root weight may change drastically. There will therefore be no constant optima for the ratios of tops to stubble or tops to root during the changing climatic conditions of a growing season.

Differences between genotypes in their development of the stubble have been noted (Klapp, 1938) but no studies on the inheritance of this character in grasses is known to the author.

Root weight.

Some evidence is available that the top : root ratio is subject to genetic variation. Cook (1943) found from a study of eight varieties of *Bromus inermis* that the more drought resistant varieties had a greater root weight, a greater rooting depth and a lower top : root ratio. Other work has shown that considerable differences exist between species and ecotypes in the top : root ratio. (Baumann and Klauss, 1955; Troughton, 1956). Species also differ in the perenniality of their roots; some species developing a new root system each year while others retain their roots for many years (Stuckey, 1941; Weaver and Zink, 1946).

Besides genetic differences, variation in root growth and the top : root ratio may arise from environmental conditions such as differing moisture and nutrient supplies, light intensity (Turner, 1922; Richardson, 1953; Troughton, 1956; 1960; Humphries, 1958) and from growth phase. Several workers (Stuckey, 1941; Roberts and Struckmeyer, 1946; Troughton, 1956, 1960) have found that root growth was greatly retarded or ceased when the plants initiated and developed their inflorescences. It is at these times that grass plants show their highest yields (Langer, 1958). A full understanding of the relation between top growth and root growth and their related importance in the physiology of grass swards may be a help in the breeding of productive varieties. As with the variable stubble weight, the author is unaware of any studies dealing with the inheritance of root weight in grasses.

Tillering.

Stapledon (1927) suggested that tiller production was an important attribute of a pasture species. His suggestion arose from the assumption that leaf production was a function of tiller production, and from the observation that some of the more profusely tillering species had a reputation for being good pasture grasses. The evidence that is available does not confirm this view. Langer (1959), using a mower for defoliation, found no relation between tillering and yield except possibly for a short period of the year when defoliation removed the apical buds of elongated tillers. In the author's (1961) assessment of the parents used in the present combining ability study, no relationship between dry matter production and tillering was found, but again the plants were not grazed. Although no constant correlation has been found between the dry matter production and tiller number, for different genotypes, tillering and tiller weight are components of this dry matter.

Several papers have been published on the pattern of tiller production of sward plants. (Langer, 1958, 1959; Mitchell and Glenday, 1958; Smelov, 1959). These studies emphasized the fact that counts of tillers at any one time represent a census of an ever changing population in which new tillers are produced while others decay. Other conclusions were that in Britain there is customarily a decline in tiller number during the summer with a rise towards the end of the year. This decline is less pronounced in wet summers and when the plants are regularly defoliated. (Langer, 1959).

Little is known of the inheritance of tillering. Whitehouse _et al_. (1958) considered that the similar character, ears per plant, in wheat was polygenically inherited and the genetic variance was largely additive. Among the forage grasses, Cooper (1960) considered tillering as under polygenic control and gave a heritability estimate (in the narrow sense) averaging 60 per cent for three varieties of ryegrass. Heritability estimates, to be of value need to be obtained under similar conditions to those in which the selected plants are to be grown and Cooper attempted to simulate sward conditions in his assessments.

Heading date and flowering date.

In perennial pasture grasses an increase in yield occurs at the time of internode elongation and heading. The date at which this takes place is of agronomic importance particularly as varieties may differ widely in this character. In a breeding programme this difference in heading also becomes important when trying to cross varieties. Therefore from both the agronomic and plant breeding points of view, a knowledge of heading date and its inheritance is of value.

In cereals, the majority of studies devoted to the inheritance of heading suggest that very few genes are involved and relatively simple segregation ratios may be expected (e.g. for wheat Allard 1956 and for barley Johnson and Paul, 1958). With pasture grasses, however, all the evidence suggests polygenic inheritance (Burton, 1951; Cooper, 1954, 1959, 1960; Kalton and Lefell, 1955; Breese, 1960).

The most comprehensive studies of the inheritance of heading have been those of Cooper (loc. cit.) in which it was shown that the variability in ryegrass had a large geneticcomponent. His heritability estimates, calculated in the broad sense of including additive and non-additive gene effects were all above 85 per cent and most of this, as indicated by parent progeny regression, was additive. In his studies Cooper did not attempt to make crosses between parents differing greatly in heading date but instead used assortative mating (like to like) at the extremes of the heading distribution, and took recognition of the effect this might have on his results. In subsequent mass selection for this character advances made agree well with predicted estimates of advance based on the heritability values.

Cooper has not attempted to relate heading to increases in yield possibly because of his earlier views on the decline in nutritive value associated with heading. (Peterson, Cooper and Vose, 1958).

Details of experiments

Origin of parents.

In the present study, seven plants of the Mediterranean group of *Dactylis glomerata* and two of the Northern European group were crossed in all combinations but separate analysis were carried out on the within group hybrids and the between group hybrids. In the choice of the parents representative material from different environment was taken with initially no knowledge of their agronomic value in southern Australia. Individual plants were taken from nine representative collections, details of which are given in Table 2. Information was available on the parent material from previous studies (Knight, 1960, 1961). They had been grown, after clonal propagation, under sward conditions and observations had been made on agronomic characters such as tiller number, plant weight, heading data and survival. In addition, the growth of the parent material had been compared under sward conditions, with growth under the spacing conditions of a breeding nursery. It was considered that this information would be of value in the interpretation of hybrid performance.

The first seven parents listed are from collections obtained from uncultivated grazing land and it is assumed that no artificial selection has been practised on them. The last two parents are individual plants of S.37 and S.143 respectively; two strains of cocksfoot bred at the Welsh Plant Breeding station, Aberystwyth, Wales.

Control of flowering.

To cross the parents it was necessary to modify the environment as under natural conditions their flowering times did not overlap. Parent plants, that had been grown in pots in the open were moved on August 28, 1959 to an opensided glasshouse and given a daylength of 16 hours, at a time when natural daylength, including civil twilight, was just under 12 hours. This treatment was continued for six weeks

TABLE 2. ORIGIN OF PARENTS

Parent	C.P.I. No.	Country	Latitude	Longitude	Altitude Ft.	Mean Annual Rainfall (in.)
17	18860	ALGERIA	36° 18' N.	2° 24' E.	300	30
43	18892	MOROCCO	30° 12' N.	8° 26' W.	4800	8
52	18898	MOROCCO	31° 24' N.	8° 00' W.	6000	26
56	18902	MOROCCO	33° 00' N.	8° 00' W.	800	10
63	18910	MOROCCO	33° 48' N.	5° 00' W.	5000	34
80	18942	PORTUGAL	39° 36' N.	9° 04' W.	50	36
82	18931	GREECE	38° 30' N.	22°18' E.	300	28
92	-	U.K.	-	-	-	-
93	-	U.K.	-	-	-	-

by which time inflorescence development was far advanced. The plants were treated by suspending above them a row of incandescent 100 watt bulbs spaced 2 ft. by 2 ft. apart and approximately 2 ft. above the plants.

This treatment was successful in bringing about synchronous development of inflorescences. Further control of flowering was obtained by using a controlled environment room. It had been found that flowering of Dactylis only occurred following a day of high temperatures. A succession of days of low temperature resulted in development of flowers but no anthesis. This phenomenon was utilised by keeping parents in a controlled environment room held at 65°F. The day before it was desired to carry out pollination the room temperature was raised to 85°F for a period of eight hours, dropped to below 65°F overnight, and then raised again on the day of pollination. A high degree of control of flowering was effected in this way.

Emasculation and pollination.

The parents were crossed in all combinations and because they were not fully self sterile they were emasculated. For emasculation a technique was perfected utilising suction to pluck the undehisced anthers from the flower undergoing anthesis. The apparatus consisted of a glass tube drawn at one end to a fine nozzle the other end connected by pressure tubing to a suction pump. Inserted in the line was an air-tight bottle that acted as a suction reservoir and as a trap for the anthers. The nozzle of the glass tube was of such a size that it would fit over three emerging anthers of a flower

Plate 1. The emasculation of a flowering head of *Dactylis glomerata* using a glass nozzle connected to a suction reservoir. Emasculation was usually performed in a controlled environment room or glasshouse where contamination by air borne pollen was prevented.

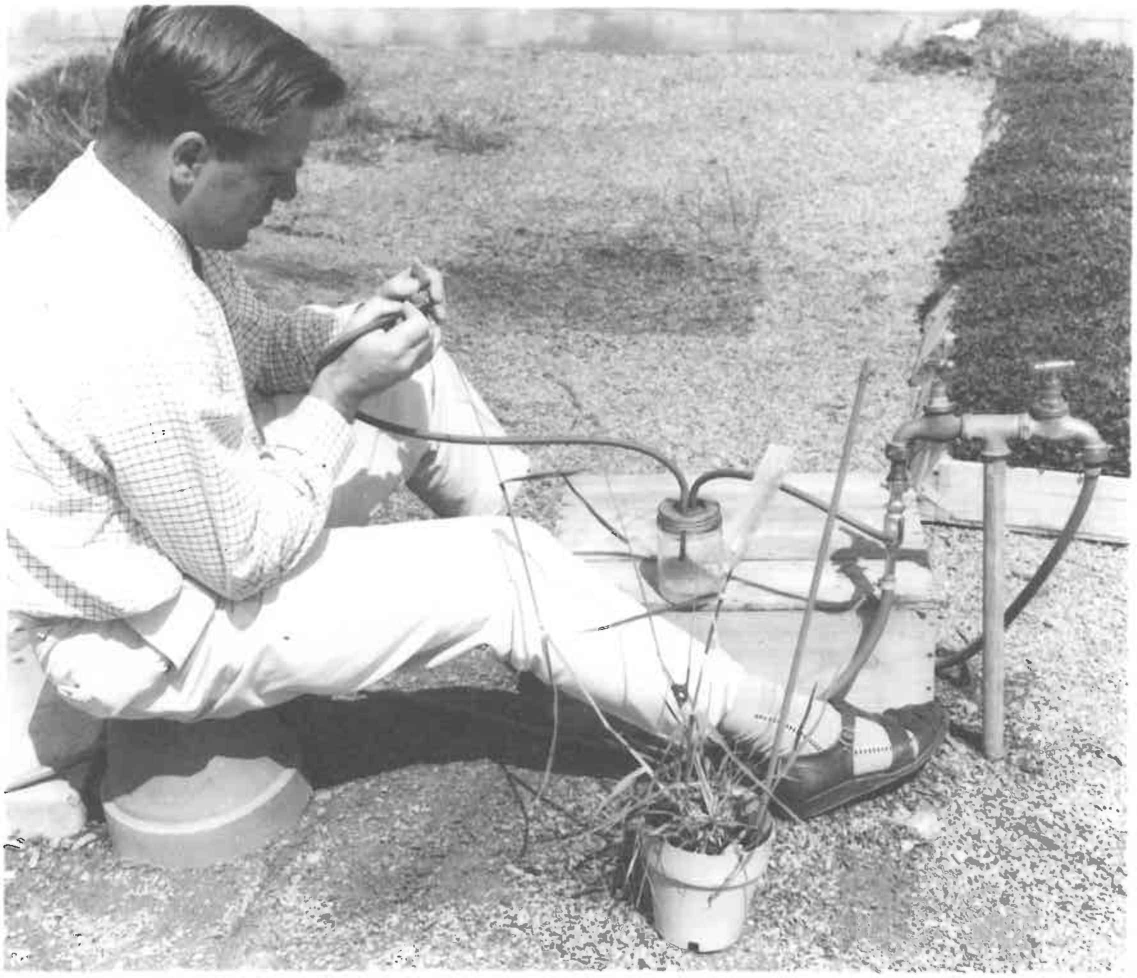


Plate 2.   Detail of a flowering head showing the emerging anthers being removed by suction before they dehisce.

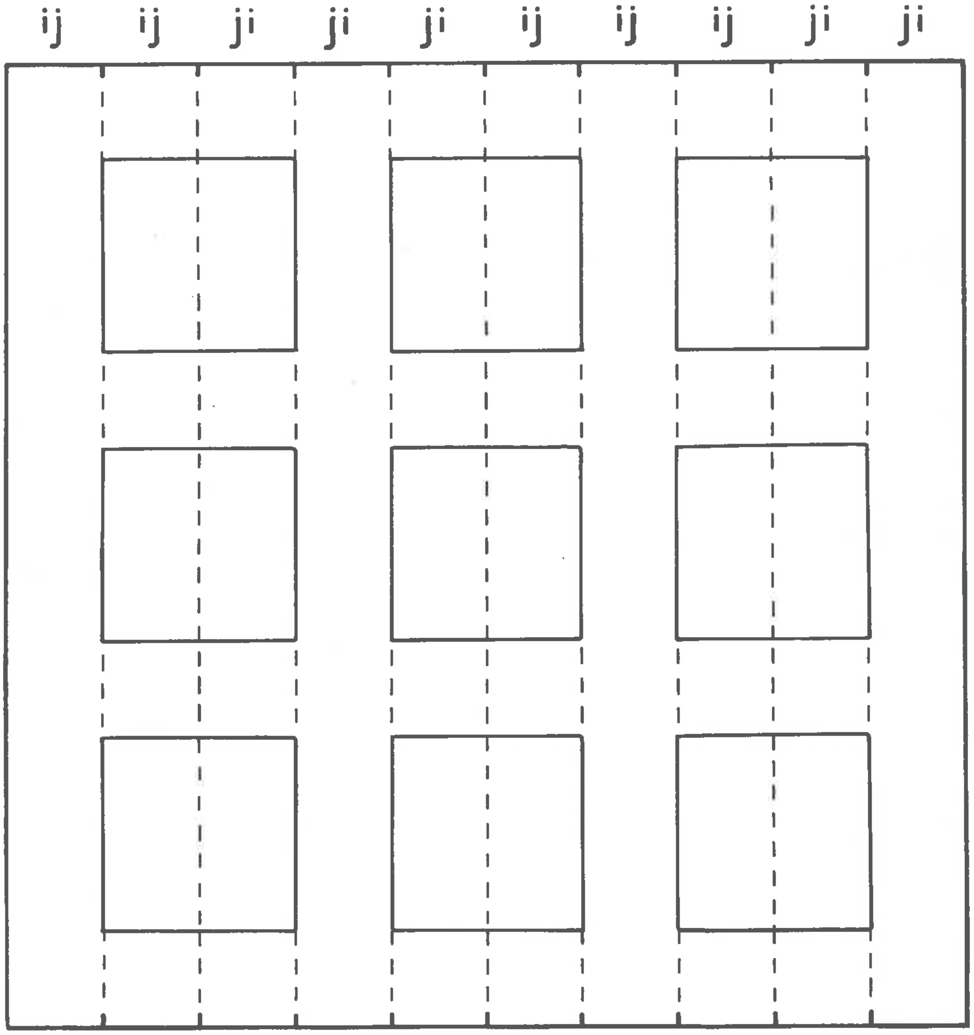
enabling their simultaneous removal. The whole technique was more efficient and less tedious than removing anthers with forceps and much less damaging to the head than a hot water technique (Jodon, 1938; Murakami, 1955) that was tried.

Emasculation of any one head proceeded over several days as the successive waves of flowers matured. Each day after emasculation the flowers were pollinated by dusting with pollen from the male parents. The parents flowered at different times during the day and when a late flowering female was to be crossed with an early flowering male it was found necessary to retard the dehiscence of the anthers of the male. Heads, cut from the male plant were placed in a petri dish containing moist filter paper and under these humid conditions the anthers emerged but did not dehisce and could be kept until required. The removal of the heads from the petri dish for a few minutes was sufficient to cause dehiscence. The emasculation and pollination technique was successful in terms of the number of seeds produced (in excess of 300 per family) and the legitimacy of the hybrids.

Sowing, planting and harvesting.

The seed was sown into seed boxes on June 1, 1959. A field trial of the families was planted out between the 7th and 14th August. A triple lattice layout was used each replicate consisting of 36 plots and each plot containing the two reciprocals, i x j and j x i. In a plot of 100 plants the reciprocals were arranged as shown in Fig. 1.

Fig. 1. The layout of a single plot of 10 x 10 plants, showing the positions of the nine harvest samples and interspersed guard rows, relative to the position of reciprocals ij and ji.


ij
ij
ji
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ji

This arrangement was decided on as being the most efficient in terms of the number of plants taken for a harvest sample in relation to the number of plants needed as guard rows between harvest samples. The planting of the seedlings at a 5 x 5 in. spacing was facilitated by a wiregrid with a mesh of those dimensions. As the planting of each plot was completed, the grid was moved to the next plot.

At each harvest, the four plants in a sample area were taken by cutting the roots just below ground level. Plants were separately labelled and taken to the laboratory for tiller number and dry weight determinations. At any one harvest a total of 432 plants were taken consisting of two plants from each of three replicates for the 72 families.

At six of the harvests the roots were obtained to a depth of 10 inches by hammering into the soil, to that depth, an open ended steel box 10 inches by 10 inches in cross section. The box, containing the cube of soil, was lifted from the ground, the cube was pushed out of the box and taken to a washing cradle where the soil was washed away from the roots by gently rocking in a large trough of water. A more meticulous cleaning of the roots was then carried out in the laboratory before they were eventually dried and weighed.

The individual plants of *Dactylis* remain discrete even after years of growth in sward trials and no difficulty was experienced in the experiment in accurately scoring for survival or in delimiting the plants for harvest.

Explanatory notes of Plant characters.

Stubble.

The part of the plant between the roots and photosynthetic green tops is referred to as the stubble in the present study. It is a part of the plant that is well developed in *Dactylis glomerata*. When the plants are in the vegetative phase the stubble consists of the leaf sheaths and a very short stem as the apical bud is at, or below, ground level. When the plants enter the reproductive phase some of the tillers show stem elongation so that at this phase the stubble will also contain the lower part of the culms. At those harvests taken when reproductive tillers were developed (December, 1959; November, 1960; January, 1961) a separation was made of the stubble of the sterile and fertile tillers. For harvests of the second year the dead culms developed in the first year were removed before weighing the stubble. At later harvests of the second year most of the culms had disappeared through decay.

The term stubble as used here is synonymous with leaf bases used in the study of the parents (Knight, 1960).

Roots.

The root weights were obtained to a depth of 10 inches. It was realised that roots of *Dactylis glomerata* go much deeper than this (Smelov and Ljubskaya, 1940; Jacques, 1943; Kübler, 1954) but that a high percentage were present within this depth (> 80%). The present technique required the removal at each harvest of 108 samples of soil each a cube of side 10 inches and extension of this sampling to a greater depth was not feasible.

Heading.

In both 1959 and 1960 data on heading were obtained. A plant was classified as having reached the heading stage when the distal tips of three inflorescences had emerged from the flag leaves. Heading data were obtained on the guard rows of only the first replicate. It had been necessary in a few plots of the other replicates to complete guard rows with plants of the reciprocal cross.

Single tiller weights.

A sample of 30 tillers per family were taken and individually weighed at each harvest of the second year. The tiller was complete consisting of both top and stubble but did not include any roots.

Climatic observations.

Some climatic data for the two years in which the experiments were being performed are given in Table 3. The data were recorded at the Waite Institute Meteorological Station which was approximately 400 yards from the site of the experiments. The temperatures were recorded in a standard Stevenson screen set at a height of $1^{1}/4$ metres.

The seedlings were planted out into the field from seed boxes between the 7th and 14th August, 1959 and it was necessary to supplement rainfall during establishment, 1959 being the second driest year on record at the Waite Institute. The experimental area was watered

Table 3.

Rainfall in inches and mean maximum and mean minimum temperatures for 1959 and 1960 at the Waite Institute (for intervals of 14 days beginning at date shown)

	Jan. 5	Jan. 19	Feb. 2	Feb. 16	Mar. 2	Mar. 16	Mar. 30	Apr. 13	Apr. 27	May 11	May 25	June 8	June 22	July 6	July 20	Aug. 3	Aug. 17	Aug. 31	Sep. 14	Sep. 28	Oct. 12	Oct. 26	Nov. 9	Nov. 23	Dec. 7	Dec. 21
Rain	0.05	0.04	1.27	0.11	0.07	0.07	1.32	0.26	0.03	0.32	0.30	0.24	0.15	0.22	2.68	1.39	0.02	0.01	1.38	0.70	0.12	0.55	0.00	1.46	0.35	1.76
Max. Temp.	89.4	85.7	78.0	80.0	77.5	80.0	74.1	71.3	69.9	65.8	61.3	60.8	59.8	59.3	57.0	60.6	66.3	70.8	59.3	67.4	69.1	72.5	83.0	76.2	70.2	80.8
Min. Temp.	59.9	65.4	61.5	59.9	59.4	61.5	56.7	56.6	51.7	51.2	48.7	47.4	46.1	45.8	46.8	49.2	52.2	52.6	46.4	52.0	51.0	55.4	60.8	59.4	54.3	60.9

	Jan. 4	Jan. 18	Feb. 1	Feb. 15	Feb. 29	Mar. 14	Mar. 28	Apr. 11	Apr. 25	May 9	May 23	June 6	June 20	July 4	July 18	Aug. 1	Aug. 15	Aug. 29	Sep. 12	Sep. 26	Oct. 10	Oct. 24	Nov. 7	Nov. 21	Dec. 5	Dec. 19
Rain	0.29	0.09	1.98	0.15	0.66	0.25	0.13	0.92	3.42	2.06	3.27	2.10	0.04	1.08	0.73	1.58	0.18	2.28	2.20	0.55	0.64	0.23	3.07	0.17	0.02	0.04
Max. Temp.	90.8	81.2	76.0	80.0	73.9	83.4	75.6	64.7	60.1	57.2	60.9	56.3	56.9	54.5	58.2	54.9	57.5	59.4	60.8	64.6	70.9	71.9	68.4	70.0	79.0	90.2
Min. Temp.	68.8	61.3	58.3	61.5	58.6	66.3	59.0	51.6	49.9	44.8	50.9	45.8	43.3	43.2	46.3	42.9	44.8	47.5	48.9	49.9	54.1	50.3	53.2	53.1	56.7	69.2

with a Pope rainwave spray which is designed to give an even spread over a square area. All supplementary watering ceased at the beginning of October and no further watering was attempted for the duration of the experiment. 1960 was a more normal year although several heavy summer showers were experienced at the beginning of the year and one exceptional shower occurred during the fortnight beginning November 7th.

Analysis of results

All the families were laid out in one field trial in a triple lattice design. A feature of lattice designs is that if the block effects within a replicate are not significantly different the gain in efficiency over a randomised block analysis is negligible and the simpler randomised block analysis may be substituted. The relative efficiency of the two analyses was tested for several characters at several harvests and as the lattice design did not reduce the error below 90 per cent of the randomised block error the latter analysis was adopted throughout.

The complete analysis became:-

		D.F.
Whole plot	Replicates	2
	Families	35
	Error (1)	70
	Total	107
Sub-plots	Reciprocals	36
	Error (2)	72
	Total	108
Plants	Error (3)	216
	Grand Total	431

For those analyses in which reciprocals were found to be non-significant the sub-plots and plants sums of squares were combined to give a pooled error with 324 degrees of freedom. This error, when corrected to be comparable with the mean values in the diallel and topcross tables, was the one used to test significance of the combining ability mean squares.

All data, except where otherwise stated, were transformed to a logarithmic scale before analysis as it was found that the variability increased with the means.

The diallel tables were constructed with a mean value for each particular cross entered in the tables. The combining ability analysis was that proposed by Griffing (1956 b) for a complete set of F_1 families but without the parents. This analysis is based on the mathematical model

$$xij = \mu + gi + gj + sij + rij + \frac{1}{bc} \sum_{k}\sum_{l} eijkl$$

where xij is an observed mean value in the body of a diallel table, μ is the population mean, gi and gj are the g.c.a. effects of parents i and j respectively, sij is the s.c.a. effect peculiar to the crosses ij and ji, rij is the reciprocal genotypic effect and eijkl is an error term peculiar to the ijklth observation.

Data were obtained on reciprocal crosses and although these were found in general to be non-significant they were kept separate in the analysis. The equations used were therefore those given for Griffing's Method 3 with the modifcation that the error included the reciprocal effects. The analysis is given in Table 4.

TABLE 4. ANALYSIS OF VARIANCE FOR COMBINING ABILITY

	D.F.	Sum of Squares*	Expected Mean Square
c.a.	$p-1$	$\frac{1}{2(p-2)}\sum(X_{i.}+X_{.i})^2 - \frac{2}{p(p-2)}X_{..}^2$	$\sigma^2+2(p-2)\left(\frac{1}{p-1}\right)\sum g_i^2$
c.a.	$\frac{p(p-3)}{2}$	$\frac{1}{2}\sum\sum_{i<j}(x_{ij}+x_{ji})^2 - \frac{1}{2(p-2)}\sum(X_{i.}+X_{.i})^2 + \frac{1}{(p-1)(p-2)}X_{..}^2$	$\sigma^2+2\left(\frac{2}{p(p-3)}\right)\sum\sum_{i<j}s_{ij}^2$
rror	m		σ^2

* An individual mean in the diallel table was x_{ij} its reciprocal x_{ji}, the sum for a row (parent i as a mother) was $X_{i.}$, for a column (parent i as a father) $X_{.i}$ and for the whole table $X_{..}$.

The pooled error from the randomised block analysis was divided by 6 (3 replicates of 2 plants) before entry in the above table. The g.c.a. and s.c.a. variance components represented by $\frac{1}{p-1}\sum g_i^2$ and $\frac{2}{p(p-3)}\sum\sum_{i<j}s_{ij}^2$ in the expected mean squares were calculated by equating the observed to the expected mean squares. This aspect of the analysis is less emphasised than the effects.

The effects calculated were

the mean $\hat{\mu} = \frac{1}{p(p-1)}X_{..}$

the g.c.a effect $\hat{g}_i = \frac{1}{2p(p-2)}[p(X_{i.}+X_{.i})-2X_{..}]$

the s.c.a. effect $\hat{S}_{ij} = \frac{1}{2}(x_{ij}+x_{ji}) - \frac{1}{2p(p-2)}(X_{i.}+X_{.i}+X_{j.}+X_{.j}) + \frac{1}{(p-1)(p-2)}X_{..}$

To obtain the g.c.a and s.c.a. contribution, associated with each parent, to total variability the following variances were calculated.

$$\hat{\sigma}^2_{gi} = \hat{g}_i^2 - \frac{(p-1)}{2p(p-2)}\hat{\sigma}^2$$

$$\hat{\sigma}^2_{Si} = \frac{1}{p-2}\sum_j S_{ij}^2 - \frac{(p-3)}{2(p-2)}\hat{\sigma}^2$$

The statistics calculated from each set of data were the g.c.a. and s.c.a. mean squares, and if these were significant, estimates of the corresponding effects given in the model. The effects themselves were compared for significance using Duncan's (1955) multiple range test. This recognises the ranking of effects in the determination of significance, thus two closely ranked effects require a smaller difference for significance than two widely ranked effects. Griffing's equation for the comparing two effect is var $(g_i - g_i) = \frac{1}{p-2}\sigma^2$ where σ^2 is the mean error variance used to test the significance of g.c.a. and s.c.a. in the combining ability analysis. This equation contains a factor of 2 for comparing two variances. As this factor has already been considered in the derivation of Duncan's tables it was necessary to divide by 2 before constructing levels of significance. The steps in the test were therefore to obtain

$$\text{s.e. } (g_i - g_j) = \sqrt{\frac{1}{2} \cdot \frac{1}{p-2}\sigma^2}$$

and to multiply the right hand component of this equation by the respective values given by Duncan for comparing effects that differ by 2, 3, 4, 5 etc. places in their ranking. The effects obtained in the experiments were ranked and any two that exceeded Duncan's significance values corresponding to their difference in rank were considered different. Where the effects are presented in the results any two that are not underscored by the same line are significantly different.

The hybrids between Mediterranean and Northern European parents were analysed for combining ability in a topcross arrangement and corresponding statistics calculated. The error used was the same in both topcross and diallel except on a few occasions when as will be mentioned there were clear cut differences.

In discussion of the results, frequent reference is made to values $\mu + 2gi$. Use of these values needs explanation. The diallel test is one in which parents are assessed on a basis of their progeny performance and it is of interest to compare this assessment with actual phenotypic values for the parents. In the diallel model any observed value is equal to $\mu + gi + gj + Sij + rij$ + error from which is estimated gi and gj as contributions from the parents i and j respectively. As gi is the contribution of parent i to all its progeny the breeding value of parent i may be written as $\mu + gi + gi$ or $\mu + 2gi$. This is a value determined solely from its progeny. Values for $\mu + 2gi$ are presented in the results, being indicative of general combining ability, and for comparison with the phenotypic values for the parents obtained in the previous study (Knight, 1960, 1961). An advantage in presentation of $\mu + 2gi$ as opposed to gi is that it overcomes the negative values of the latter. A graph of gi against time merely varies around one of the axes of the graph whereas $\mu + 2gi$ approximates to a growth curve.

The values entered in the diallel table are mean phenotypic values being made up of genotypic effects and an error. If a regression or correlation is calculated for two characters using the respective mean values xij a measure of the phenotypic association between the characters is obtained. Griffing (1953) has shown that a genotypic regression or correlation may be derived from the g.c.a. and s.c.a. effects. The g.c.a. correlation uses as values $gi + gj$, the g.c.a. effects of the parents. 21 values of gi and gj could have been obtained from the seven parents in the diallel and 14 values from the top cross of Mediterranean x Northern European families,however, it was not necessary to calculate the values $gi + gj$ because of the algebraic identities $\text{dev}^2\ (gi + gj) = (p-2)\ \text{dev}^2\ (gi)$ and

$$\text{cov}\ (gi + gj)_a\ (gi + gj)_b = (p-2)\ \text{cov}(gi)_a\ (gi)_b$$

where p is the number of parents and a and b are two characters such as tiller number and topweight (Gilbert, 1958). As many characters were considered over several harvests there was a large number of possible correlations but only those that were plausible on biological grounds were attempted.

To facilitate the computations much of the data were entered on I.B.M. punch cards and processed on the I.B.M. 7090 computor at the Weapons Research Establishment, Salisbury, South Australia. The author is indebted to Professor E. Remmenga for the programming of this data.

Missing and zero values.

If plants were missing at time of harvest an average of the remaining plants of the cross was used in the diallel table. At no time were there many missing plants and it was possible to complete the diallel table at all harvests.

The fertile and sterile components of plants harvested in the reproductive stage were separately analysed. At these harvests, zero values were obtained mainly for the fertile components in the first year and the November harvest of the second year. They present a problem in analysis in that a zero cannot be transformed to a logarithm. Two alternatives were possible, one was to treat zeros as missing values and use the mean of the remaining plants, the second alternative was to substitute a low value for the zero (Williams, 1947). Use of the second alternative is more correct when comparing components and total plant weights but it results in inflated values of g.c.a. and s.c.a. mean squares. It also increases both the total and heterogeneity of the error. Its main disadvantage, however, was that it had a disproportionate effect on the mean value of a cross. If one or two zeros were recorded among the twelve plants of a cross the substitution of a low value greatly reduced the mean making it less truly representative of that cross. As the number of zeros for a cross at no time exceeded four our of 12 plants, and was usually one or two, zeros in the following analyses were treated as missing values.

RESULTS

Top weight.

At each harvest the plants were subdivided into tops, stubble and roots and the yield of the tops will be the first to be considered (Table 5) In all the analyses, the data were handled in the logarithmic form but in Table 5 the mean weights of the families have been presented as antilogarithms for easier comprehension of the growth changes. The following description relates the growth phases of the plants to the harvest dates. At the first harvest all families had become established while at the second they had passed through the reproductive phase and entered dormancy for the summer or in the instance of the purely Northern European families a period of severely restricted growth. Regenerative growth of the new season had begun by the harvest of April 28, and this growth continued to the harvest of May 24. By June 29 some of the earlier families had begun stem elongation associated with reproduction but this was not evident in all families until September 19. Flower heads of many families had emerged and were far advanced by November 7 while at the last harvest all reproductive plant parts were fully formed and all growth ceased for the summer.

A decline in mean weight was occasionally found for a family between successive harvests. This may sometimes have arisen from experimental variability associated with sampling, but it was also at times a true effect arising from senescence of tillers and leaves.

Attention will now be concentrated on the results for the purely Mediterranean families and their analysis by the diallel combining ability

Table 5. The geometric mean for yield of tops per plant in gm. (twelve plants per family at each harvest).

	5 Oct.	23 Dec.	28 Apr.	24 May	29 June	10 Aug.	19 Sept.	7 Nov.	9 Jan.
17.43	3.79	3.91	.53	2.05	3.43	12.08	14.69	16.94	20.75
52	3.04	7.60	1.19	1.96	2.56	3.92	8.17	21.83	21.14
56	3.67	5.68	.42	1.96	4.63	8.95	13.96	22.23	22.65
63	3.10	6.81	.91	3.20	4.88	8.51	15.56	22.08	30.90
80	3.74	9.04	1.60	2.62	6.38	9.95	21.68	21.63	31.19
82	4.10	7.76	1.03	3.66	6.10	8.28	10.59	21.53	18.58
92	4.19	5.96	.67	2.17	3.27	5.74	13.52	15.92	12.85
93	3.12	4.65	.86	2.71	2.97	6.35	12.88	21.83	15.85
43.52	2.21	5.79	1.27	2.81	3.50	5.21	5.36	16.07	7.15
56	3.01	5.19	.54	1.36	3.81	6.15	12.59	17.26	19.28
63	2.36	4.40	1.11	2.65	4.33	4.74	7.40	13.09	9.89
80	3.74	5.43	1.21	1.47	5.20	7.13	15.00	15.45	16.94
82	3.29	4.46	.88	2.14	3.96	5.65	4.42	8.89	9.08
92	3.16	7.15	1.46	1.26	2.53	3.72	8.61	28.91	14.13
93	2.03	4.68	1.69	2.06	4.42	4.81	15.60	18.54	17.54
52.56	3.01	4.62	.91	3.03	6.22	8.13	16.26	27.61	24.38
63	1.96	2.62	1.35	2.96	5.55	4.93	8.20	13.80	19.72
80	2.48	9.40	.61	2.20	4.30	10.91	17.42	21.58	25.59
82	3.40	4.63	.78	1.99	2.52	6.00	5.09	14.52	17.99
92	3.25	4.36	.85	2.39	2.59	2.27	11.89	16.60	10.91
93	1.88	5.20	.80	2.43	2.69	2.54	5.32	7.43	8.32
56.63	3.50	5.00	1.13	3.15	5.40	7.31	12.39	18.16	18.71
80	5.82	10.50	.66	2.96	5.00	8.97	17.30	25.88	28.45
82	2.39	7.44	.60	2.20	2.60	4.85	8.47	12.85	21.38
92	4.42	6.34	1.48	2.13	7.36	11.35	6.19	15.63	25.06
93	3.06	5.90	1.06	3.19	3.38	7.05	9.35	20.70	32.36
63.80	3.61	5.71	2.40	2.47	4.42	7.23	13.40	31.26	27.99
82	2.42	2.44	1.17	2.34	3.48	4.01	3.09	8.63	14.29
92	1.45	7.38	1.52	2.36	4.70	3.60	7.23	13.80	20.85
93	2.27	3.88	1.30	2.40	4.54	4.29	8.43	9.86	7.19
80.82	1.73	5.60	1.32	2.04	2.39	3.17	7.82	17.22	24.72
92	2.71	8.34	.98	1.60	2.77	6.44	14.00	22.08	27.23
93	2.98	8.65	1.99	1.99	5.12	8.67	7.43	17.95	29.11
82.92	4.33	7.55	1.86	1.39	2.70	7.85	9.40	22.75	22.80
93	2.58	5.51	1.15	2.21	2.65	5.93	9.25	10.26	17.38
92.93	2.50	7.29	.32	1.08	2.56	2.14	7.46	11.30	4.69

procedure. Variation around the generalised growth pattern outlined above was considerable, as shown by family mean weights. At any one harvest differences between families reached several magnitudes and it was the objective of the combining ability analysis to determine the significance of these differences. All further data in this section have been derived from the mean values in the logarithmic form.

One statistic calculated from the diallel population was μ, the mean of all the families. Values of μ in the second year showed a linear increase on a logarithmic scale between the harvests May 24 to November 7 inclusive, indicating that although this was a winter period, many of the families were growing actively.

The combining ability mean squares and their significance are given in Table 6. This shows that the g.c.a. variability was significant at the beginning and towards the end of each growing season. It is believed, and will be further discussed in reference to tiller size that the significant differences for top weight at October 5 of the first season, and August 10 and September 19, of the second are attributable to differences between families in the time of onset of stem elongation associated with the reproductive phase and it will be shown that the significant differences at December 23 and January 9, the last harvests of the two seasons were due to differences between genotype in the proportions of the plants that became reproductive, some tillers remaining vegetative.

A large g.c.a. mean square was obtained at the harvest (April 28)

Table 6.

Combining ability mean squares for total top weight at successive harvests for two seasons (Med. diallel analysis)

	D.F.	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
g.c.a.	6	.0190***	.0515***	.0602**	.0152	.0186	.0343*	.1376***	.0503***	.0750***
s.c.a.	14	.0131***	.0145**	.0223	.0116	.0175	.0203	.0137	.0086	.0096
Error	> 250	.0036	.0056	.0178	.0102	.0108	.0140	.0101	.0114	.0076

Table 7.

Estimates of the g.c.a. effects for total top weight at successive harvests of Med. diallel (the estimates have been multiplied by 1,000 for clearer presentation) and the general mean μ

	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
17	81	96	- 52	36	38	115	147	91	109
43	- 8	-65	- 45	-78	-18	- 6	- 70	-109	-213
52	-75	-12	19	26	-35	- 34	- 65	30	- 36
56	62	34	-177	-27	38	51	135	67	76
63	-52	-138	156	91	58	- 55	- 71	- 36	- 11
80	40	153	107	- 28	35	61	194	106	144
82	-49	-68	- 8	-21	-116	-132	-271	-149	- 69
μ	0.482	0.737	1.975	0.367	0.616	0.816	1.006	1.245	1.284

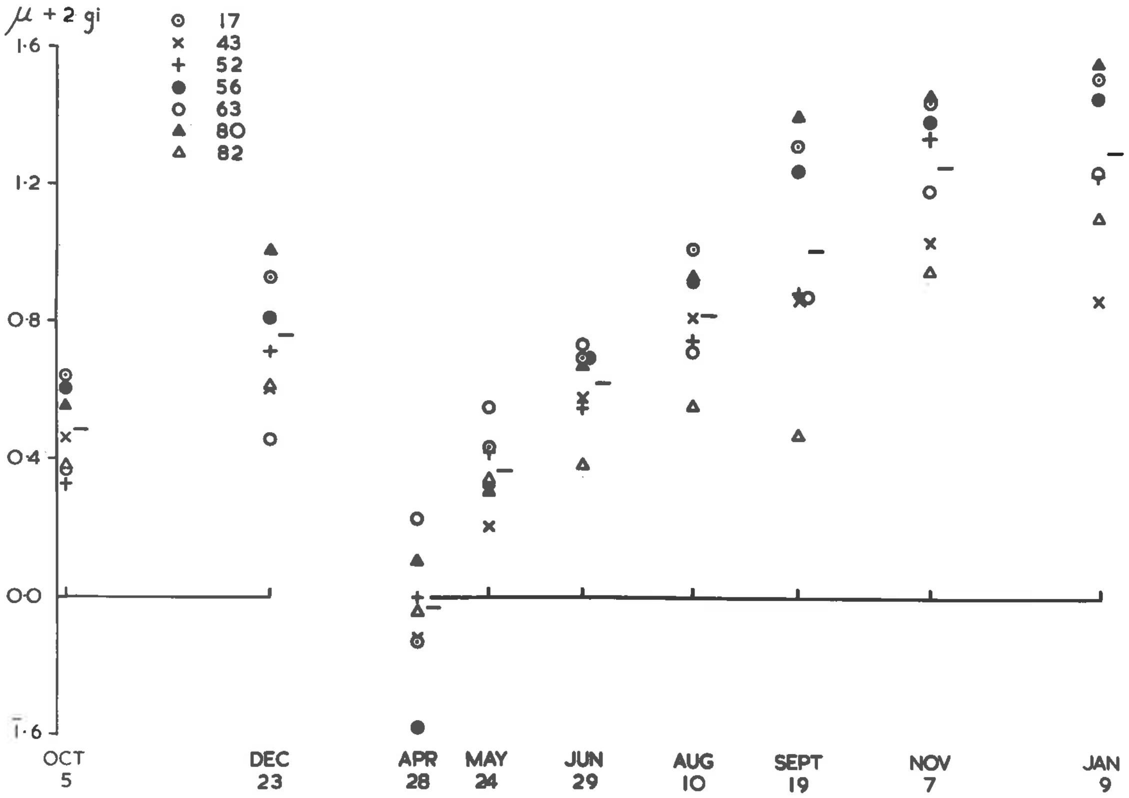
Significant differences between parents as judged by the value of gi.
Parents underscored by the same line are not significantly different. Level of significance used, 5%.

Oct. 5 52 63 82 43 80 56 17
Dec. 23 63 82 43 52 56 17 80
Apr. 28 56 17 43 82 52 80 63
May 24 43 80 56 82 52 17 63
June 29 82 52 43 80 56 17 63
Aug. 10 82 63 52 43 56 80 17
Sep. 19 82 63 43 52 56 17 80
Nov. 7 82 43 63 52 56 17 80
Jan. 9 43 82 52 63 56 17 80

taken soon after regeneration from summer dormancy but was not very highly significant against the large error. This error, like all others in Table 6, was obtained from the whole trial but whereas on all other occasions this error departs very little from an error derived solely from the Mediterranean material on April 28 the discrepancy was quite large. Evidently the variability within the Mediterranean x Northern European families and within the Northern European families was greater than within purely Mediterranean material on this occasion, a difference almost certainly due to the irregular and sporadic growth shown by these families in response to summer showers. The error for the whole trial was 0.0178 and for the Mediterranean material 0.0127. This was the only occasion on which the use of an error from Mediterranean data alone affected the significance of any mean squares. It may be concluded from these results that there were large differences between parents in g.c.a. for the autumnal regeneration as well as later in the season when the plants were reproductive.

The contribution of individual parents to the g.c.a. variability may be gauged from the estimates of the individual parent effects gi (Table 7). Beneath the table these effects have been arranged in ascending order and significance indicated by Duncan's shortest significant range test. No one parent had the highest g.c.a. at each harvest. Parent 80 alone approached this ideal. In general, parents were not consistently high or low in g.c.a. as their seasonal development differed (Fig. 2 contains values of $\mu + 2$ gi). At the important periods of regeneration, April and May, parent 63 was outstanding but this was

Fig. 2. The combining ability values $\mu + 2gi$ for yield of tops, for each Mediterranean parent, plotted against harvest occasion to illustrate seasonal differences. Assessment by Mediterranean diallel test. The diallel mean μ is represented by —.


μ + 2 gi
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× 43
+ 52
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replaced in the second important period, mid winter, by 17, 56 and 80.

At the harvests made when plants were in the reproductive phase, the reproductive or fertile tillers were separated from the vegetative or sterile tillers and the two components weighed separately. These data supplement those for total weight (Tables 8 and 9). Parents differed greatly in their values of gi for the sterile and fertile components of top weight but because there was a negative association between these components for one genotype, differences in gi for total weight were no greater (Fig. 3). One difference between years was in the relative development of the components, the fertile component being much larger in the second year than in the first. In both years the preponderance of the fertile component over the sterile was such that parents were similarly ranked in gi for fertile top weight and total top weight. The figure illustrates that the parents had a great influence on the relative development of the components, that these were consistent between years and that it would be simple to select parents producing extreme types of progenies.

The s.c.a. mean square was significant in October and December of the first season and for the fertile component in December of the first season and January of the second. The s.c.a. effects for fertile top weight and total top weight in December were highlycorrelated; this is understandable as the one is the major part of the other. Apart from this there were no similarities in the s.c.a. effects for the different harvests even for the two reproductive harvests which might have been more constant. This means that the effects,interesting and

Table 8.

Combining ability mean squares for sterile and fertile components of top weight at harvests of the reproductive phase. (Med. diallel)

	D.F.	Dec. 23		Nov. 7		Jan. 9	
		Ster.	Fert.	Ster.	Fert.	Ster.	Fert.
g.c.a.	6	.0635***	.1559***	.1223***	.0776**	.0820***	.1251***
s.c.a.	14	.0085*	.0269***	.0198	.0102	.0125	.0195***
Error	>250	.0040	.0077	.0140	.0113	.0075	.0055

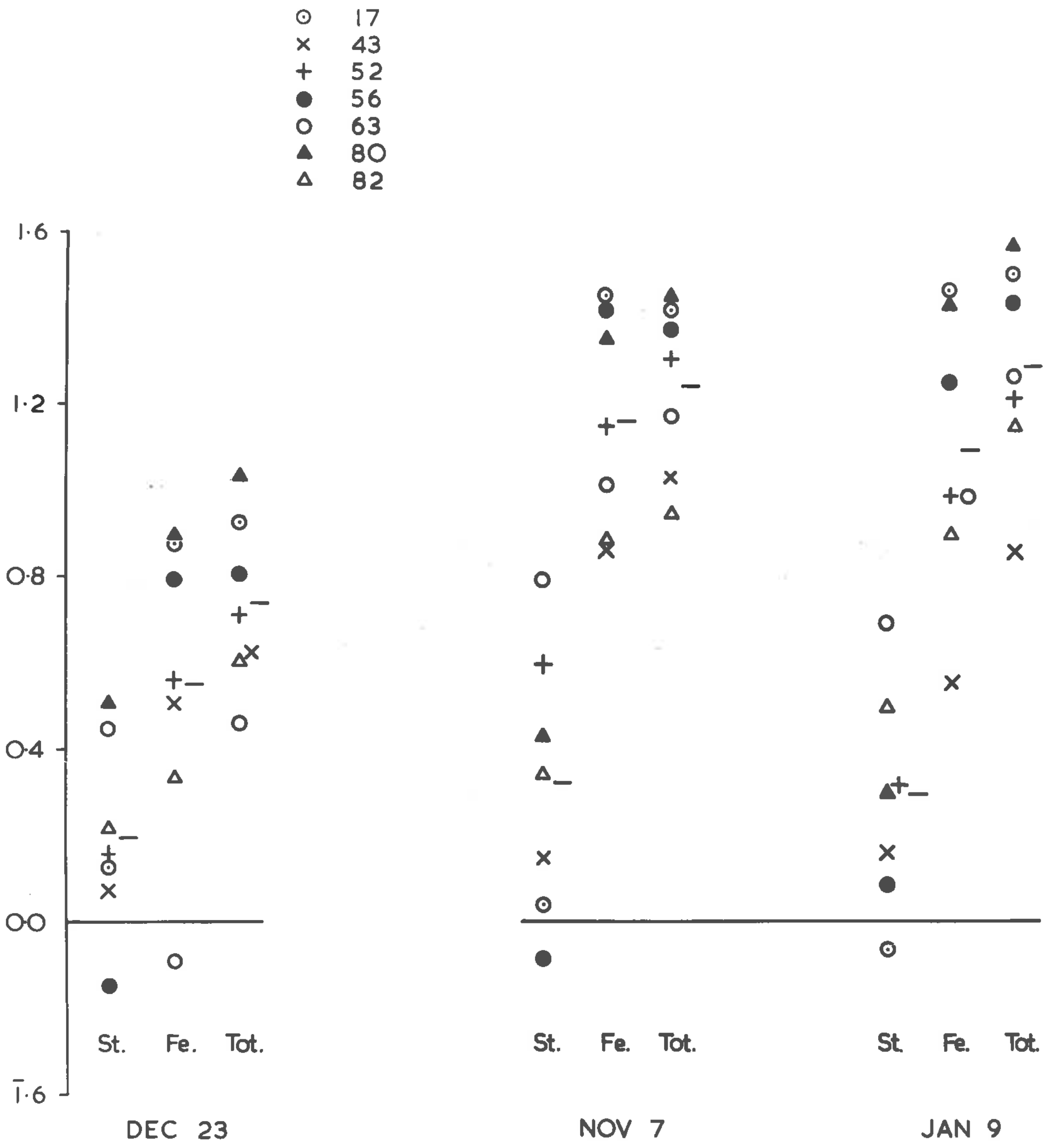
Table 9.

Estimates of the g.c.a. effects for the sterile and fertile components of top weight (the estimates have been multiplied by 1,000 for clearer presentation) and the general mean μ

	Dec. 23		Nov. 7		Jan. 9	
	Ster.	Fert.	Ster.	Fert.	Ster.	Fert.
17	-35	162	-143	144	-175	171
43	-62	- 23	- 89	-148	- 62	-262
52	-20	2	138	- 7	15	- 44
56	-174	120	-204	128	- 99	87
63	124	-323	234	- 75	205	- 45
80	158	172	54	96	8	181
82	9	-110	11	-138	107	- 89
μ	0.198	0.555	0.322	1.165	0.282	1.074

Dec. 23 1959	Ster.	56 43 17 52 82 63 80	Fert.	63 82 43 52 56 17 80
Nov. 7 1960	Ster.	56 17 43 82 80 52 63	Fert.	43 82 63 52 80 56 17
Jan. 9 1961	Ster.	17 56 43 80 52 82 63	Fert.	43 82 63 52 56 17 80

Fig. 3 . The combining ability values $\mu + 2g_i$ for yield of sterile, fertile and total tops for each Mediterranean parent at harvests during the reproductive phase. Assessment by Mediterranean diallel test. The graph shows that the fertile component was the major factor in top weight differences in the second year.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real in themselves, are too transient to be utilised in a breeding programme.

Turning the main attention away from the Mediterranean families to the Mediterranean x Northern European families and purely Northern European families, a comparison was made of their respective means (Table 10). As the means of the categories were derived from 42, 28 and 2 familes, three standard errors for the tests of significance were calculated. Of major interest to a breeding programme is the comparison of the Mediterranean x Northern European values with the purely Mediterranean values, as material of Mediterranean origin is the only material of immediate agricultural importance in this environment. The Mediterranean x Northern European mean only exceeded the Mediterranean mean at the harvest of April 28 but it also fell below at only one harvest, that of August 10. The mean of the purely Northern European families never significantly exceeded the other two means and was significantly less at several harvests in the second year. The exceptionally low value for the Northern European families at the last harvest was undoubtedly a consequence of the sampling, and not a true effect.

An analysis of variance was performed on the topcross of the 14 Mediterranean to the 2 Northern European parents that gave rise to the Mediterranean x Northern European families to determine the Mediterranean parent contribution, the Northern European parent contribution and the interaction contribution to the total variability.

Table 10.

Values of the mean μ for top weight of Med., Med. x N.E., and N.E. families

	Oct. 5	Dec.23	Apr.28	May 24	June 29	Aug.10	Sep.19	Nov.7	Jan.9
Med.	0.482	0.737	$\bar{1}.975$	0.367	0.616	0.816	1.006	1.245	1.284
			*			*			
Med. x N.E.	0.451	0.773	0.079 **	0.330 **	0.544	0.720 ***	0.977	1.212 *	1.232 ***
			***	**		**			***
N.E.	0.397	0.863	$\bar{1}.506$	0.034	0.408	0.331	0.873	1.053	0.228

Values of the mean μ for components of top weight at harvests in the reproductive phase

	Dec. 23		Nov. 7		Jan. 9	
	Ster.	Fert.	Ster.	Fert.	Ster.	Fert.
Med.	0.198	0.555	0.322	1.165	0.282	1.074
	***	***	***	***	***	***
Med. x N.E.	0.521 ***	0.317 ***	0.653 ***	1.006 ***	0.572 *	1.042
	***	**		**	***	***
N.E.	0.780	0.025	0.889	0.623	0.047	0.286

(Table 11). The first two components are equivalent to the g.c.a. mean square of the diallel and the interaction is equivalent to an s.c.a. mean square. The Northern European parents mean square was significant in October of the first year and November of the second, when the influence of the earlier heading parent 92 was most pronounced but for most of the experiment the Northern European effect was the same for both parents of this origin. The enhanced growth, mentioned above, of the Mediterranean x Northern European hybrids at the April 28th harvest was therefore equally expressed irrespective of which Northern European parent was concerned.

The between Mediterranean parents mean square was significant at six harvests, one of which was the one taken on August 10. Fig. 4 clearly shows that at this harvest hybrids involving Mediterranean parents 52 and 63 and the Northern European parent showed a decline in combining ability an effect similar to that shown by the yield of the purely Northern Euoprean families (table 10). Northern European material originating from regions of very cold winters has evolved some degree of winter dormancy and this was evident at thisharvest taken during mid winter. The hybrids having 52 or 63 as one of their parents showed a 10 and 11% decline respectively in yield from June 29 to August 10 while during the same period the Northern European families showed a 19% decline. The remaining Mediterranean x Northern European families showed increases ranging from nearly 20% up to 95%.

Within the diallel considered previously there was little evidence of winter dormancy in the Mediterranean families involving parents 52 and 63. The decline in the g.c.a. effect of parent 63 was more attributable to rapid growth of the other arrays rather than a

Table 11.

Combining ability mean squares for total top weight at successive harvests for two seasons (Med. x N.E. topcross

		Oct. 5	Dec.23	Apr.28	May 24	June 29	Aug.10	Sep.19	Nov. 7	Jan. 9
Between N.E. (g.c.a.)	1	.0356**	.0298*	.0001	.0556*	.0011	.0005	.0016	.0534*	.0099
Between Med. (g.c.a.)	6	.0241***	.0133*	.0317	.0147	.0236*	.0779***	.0171	.0285*	.0644***
Interaction (s.c.a.)	6	.0128**	.0075	.0152	.0051	.0203	.0080	.0248*	.0196	.0210**
Error	>250	.0036	.0056	.0178	.0102	.0108	.0140	.0101	.0114	.0076

Table 12

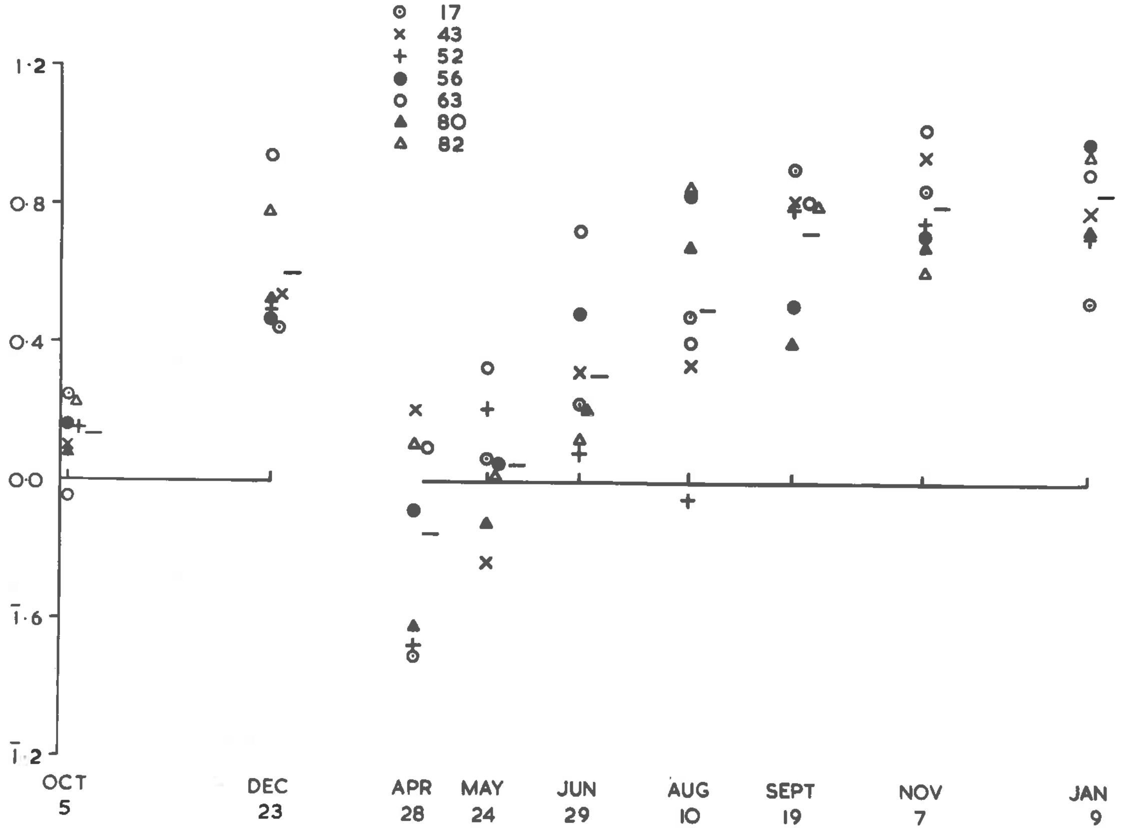
Estimates of the g.c.a. effects for total top weight at successive harvests of Med. x N.E. topcross (estimates are x 1,000 for clearer presentation) and the meanμ

	Oct. 5	Dec.23	Apr.28	May 24	June 29	Aug.10	Sep.19	Nov.7	Jan.9
17	107	- 52	-197	55	- 50	61	144	59	- 77
43	- 48	- 11	117	-122	- 20	-93	87	153	- 35
52	- 57	- 95	-161	52	-123	-339	- 76	-166	-253
56	114	14	18	107	154	232	- 95	43	223
63	-192	- 44	70	47	121	-126	- 84	-145	-144
80	3	156	65	- 78	32	154	32	87	218
82	73	37	86	- 62	-116	114	- 7	- 28	67
92	50	47	- 2	- 63	- 9	- 6	10	62	27
93	- 50	- 47	2	63	9	6	- 10	- 62	- 27
μ	0.451	0.773	0.079	0.330	0.544	0.720	0.977	1.212	1.232

Significant differences between parents as judged by values of gi. Parents underscored by same line are not significantly different at 5% level.

Oct. 5 63 52 43 80 82 17 56
Dec.23 52 17 63 43 56 82 80
Apr.28 17 52 56 80 63 82 43
May 24 43 80 82 63 52 17 56
June 29 52 82 17 43 80 63 56
Aug.10 52 63 43 17 82 80 56
Sep.19 56 63 52 82 80 43 17
Nov. 7 52 63 82 56 17 80 43
Jan. 9 52 63 17 43 82 80 56

Fig. 4. The combining ability values $\mu + 2\ gi$ for yield of tops for each Mediterranean parent when crossed to Northern European parents. One major feature was the mid-winter decline in combining ability of parents 52 and 63. The top cross mean μ is represented by —.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cessation of growth of the 63 array. However, out of the 21 Mediterranean families, the only one that showed a decline in yield between June and August was 52 x 63, which showed a decline of 7%.

Another harvest in which there were significant differences between parents was the last one (January 9) taken during the reproductive phase. In fig. 5 the sterile and fertile components of total top weight (tables 13 and 14) are illustrated for all three harvests in the reproductive phase and this graph shows why there were, or were not, differences in total top weight. The same two factors noted in the Mediterranean families were again operative in determining significance. One factor was the negative association, for any one genotype, of its sterile and fertile components, the other was in the relative development of components, the fertile component for all families being larger than the sterile in the second year. The first effect led to a partial cancelling out of the highly significant component differences resulting in small differences in total top weight at the harvests of December 23 and November 7. The cancelling out did not occur at the last harvest because the fertile component was relatively so much larger than the sterile that a significant difference in total top weight was obtained, exactly following the differences in the fertile component.

A comparison of the components for the Mediterranean families, Mediterranean x Northern European families and Northern European families showed conclusively that the Mediterranean families tended to have a higher proportion of the plant fertile, than the purely Northern European families. (Table 10). The Mediterranean x Northern European hybrids

Table 13.

Combining ability mean squares for sterile and fertile components of top weight at harvests of the reproductive phase (Med. x N.E. topcross)

		D.F.	Dec. 23 Ster.	Dec. 23 Fert.	Nov. 7 Ster.	Nov. 7 Fert.	Jan. 9 Ster.	Jan. 9 Fert.
Between N.E.	g.c.a.	1	.0109	.0342*	.0058	.0139	.0165	.0020
Between Med.	g.c.a.	6	.0183***	.1687***	.1272***	.1057***	.0405***	.0838***
Interaction	s.c.a.	6	.0044	.0368***	.0427***	.0445***	.0320***	.0074
Error		>250	.0040	.0077	.0140	.0113	.0075	.0055

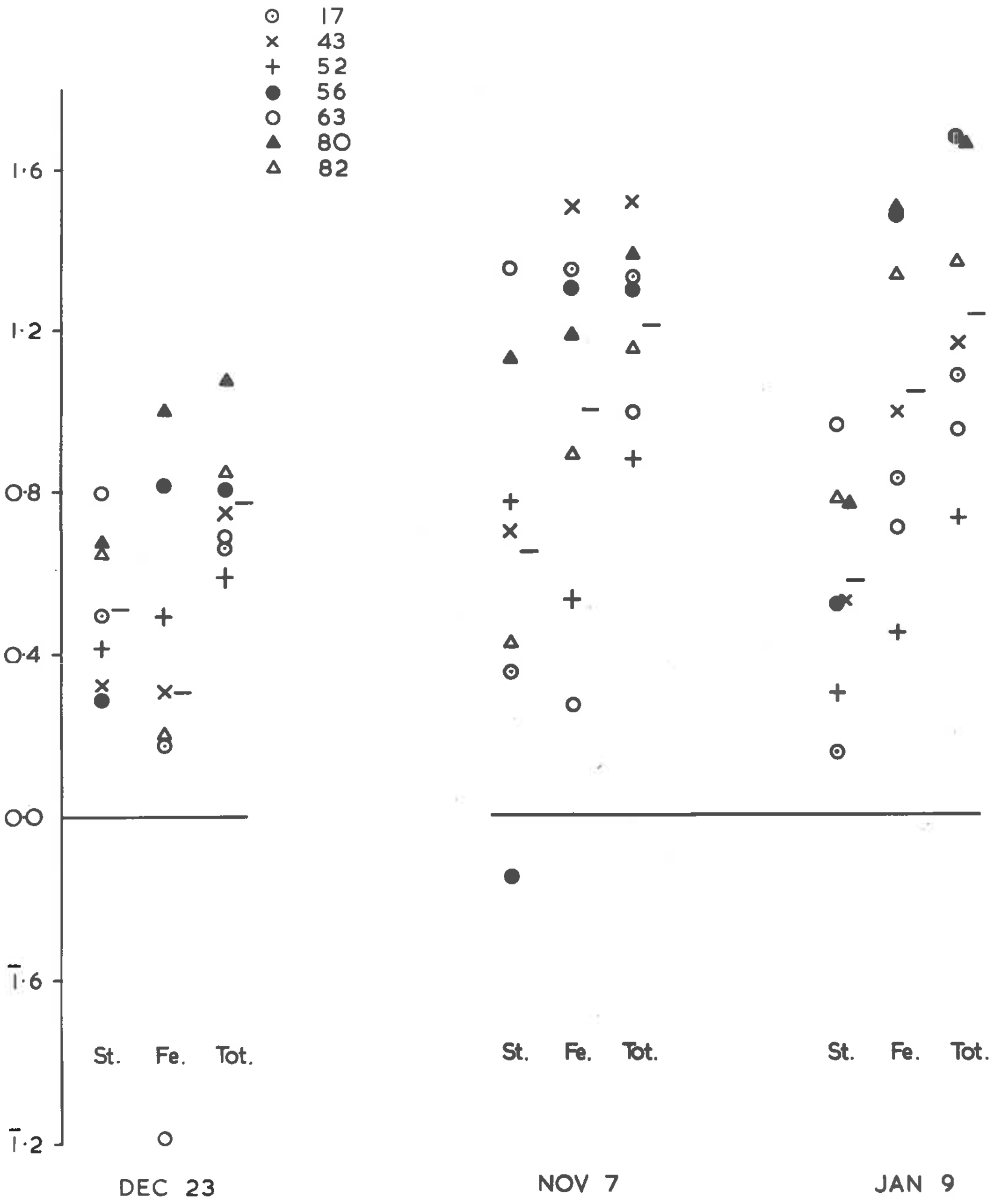
Table 14.

Estimates of the g.c.a. effects for the sterile and fertile components of top weight (estimates are x 1,000 for clearer presentation) and general mean μ

	Dec. 23 Ster.	Dec. 23 Fert.	Nov. 7 Ster.	Nov. 7 Fert.	Jan. 9 Ster.	Jan. 9 Fert.
17	- 14	- 71	-149	170	-210	-108
43	- 97	- 1	19	254	- 20	- 24
52	- 53	87	61	-236	-136	-296
56	-116	247	-404	147	- 25	223
63	138	-552	351	-368	197	-168
80	77	352	236	90	96	229
82	66	- 58	-116	- 55	98	145
92	28	49	20	32	- 34	12
93	- 28	- 49	- 20	- 32	34	- 12
μ	0.521	0.317	0.653	1.006	0.572	1.042

Dec. 23	Ster.	56 43 52 17 82 80 63	Fert.	63 17 82 43 52 56 80
Nov. 7	Ster.	56 17 82 43 52 80 63	Fert.	63 52 82 80 56 17 43
Jan. 9	Ster.	17 52 56 43 80 82 63	Fert.	52 63 17 43 82 56 80

Fig. 5. The combining ability values $\mu + 2\,g_i$ for yield of sterile, fertile and total tops for each Mediterranean parent when crossed to Northern European parents, at harvests during the reproductive phase. The fertile component as in Fig. 3 is the major factor in top weight differences in the second year.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on average were intermediate between the two. Possible reasons for the Northern European material having a lower proportion of the plant becoming reproductive would include that they are inherently later in date of heading in the spring and therefore develop heads in a less equable environment, or secondly that in being bred strains some selection against head production has been practised. The latter has not been specifically stated for these strains but was a general policy for the Welsh Plant Breeding station from where they originate.

The interaction or s.c.a. mean squares were significant in the top cross but again there was no constancy in these effects.

From the top cross analysis, values of gi for both Mediterranean and Northern European parents were calculated. It was then possible to compare two sets of gi values for the Mediterranean parents, one obtained from the purely Mediterranean diallel and the present set where the Mediterranean parents have been crossed to Northern European testers. Correlations were calculated for each parent over the nine harvests. None of these correlations were significant indicating that the two assessments of the parents differed.

Correlations between gi values for each harvest were also calculated but only one of these was significant, the one on June 29. The one for the previous harvest, May 24, was also large but did not reach significance. It was surprising that there was this lack of correlation particularly for those harvests when the g.c.a. mean squares were significant. Different factors contribute to this lack of correlation and mention may be made of some of these. At December 23rd the g.c.a. mean square was significant in the diallel but was not significant in the topcross test. This difference in results has been explained by the negative association between fertile and sterile components, and the relative magnitude of these components which differed in the two test populations. With very little variation in total top weight in the top cross test it is not surprising that there was no significant correlation in gi for the two tests. However, correlations of gi for the components themselves, were relative magnitude has no influence, were highly significant.

The correlation obtained at the June 29 harvest was lost by the next harvest. It was earlier shown that hybrids of parents 52 and to a lesser extent 63 when crossed to Northern European parents showed a decline in yield at August 10, a decline similar to Northern European families. This was not shown in the diallel of purely Mediterranean families. The result indicates that the Northern European parents dominate the hybrids in crosses with 52 and 63 but not in crosses with other Mediterranean parents. This differential in response leads to the lack of correlation for the gi values.

The last two harvests were taken during the reproductive phase but the lack of correlation cannot be explained in terms of the components as was done for the December 23 harvest, for in these even the fertile component was not correlated although the sterile continued to be so. Parents 17 and to a less extent 43 were largely responsible for the lack of correlation in the fertile component and hence total top weight for 17 had a relatively high combining ability value in the Mediterranean diallel but a low value in the top cross and parent 43 was vice versa. The contribution of Northern European parents to a low fertile component in their progenies was more fully expressed in combination with parent 17 than with the other parents, in an analagous way to the mid winter suppression of growth was more fully expressed in progenies with 52 and 63 than other parents.

At the other harvest the g.c.a. in both tests was so low that correlations were not found in gi values.

The diallel and top cross assessments of the parents were derived from progeny performance. A comparison may be made between these assessments and the performance of the parents as clones (Knight, 1960) when the following growth patterns were determined.

(1) 56 as a clone was slow in regenerating during April and May but showed a large mid-winter growth and weight at the end of the season.

(2) 63 was the complete reverse showing rapid regeneration low mid-winter growth and ultimate weight.

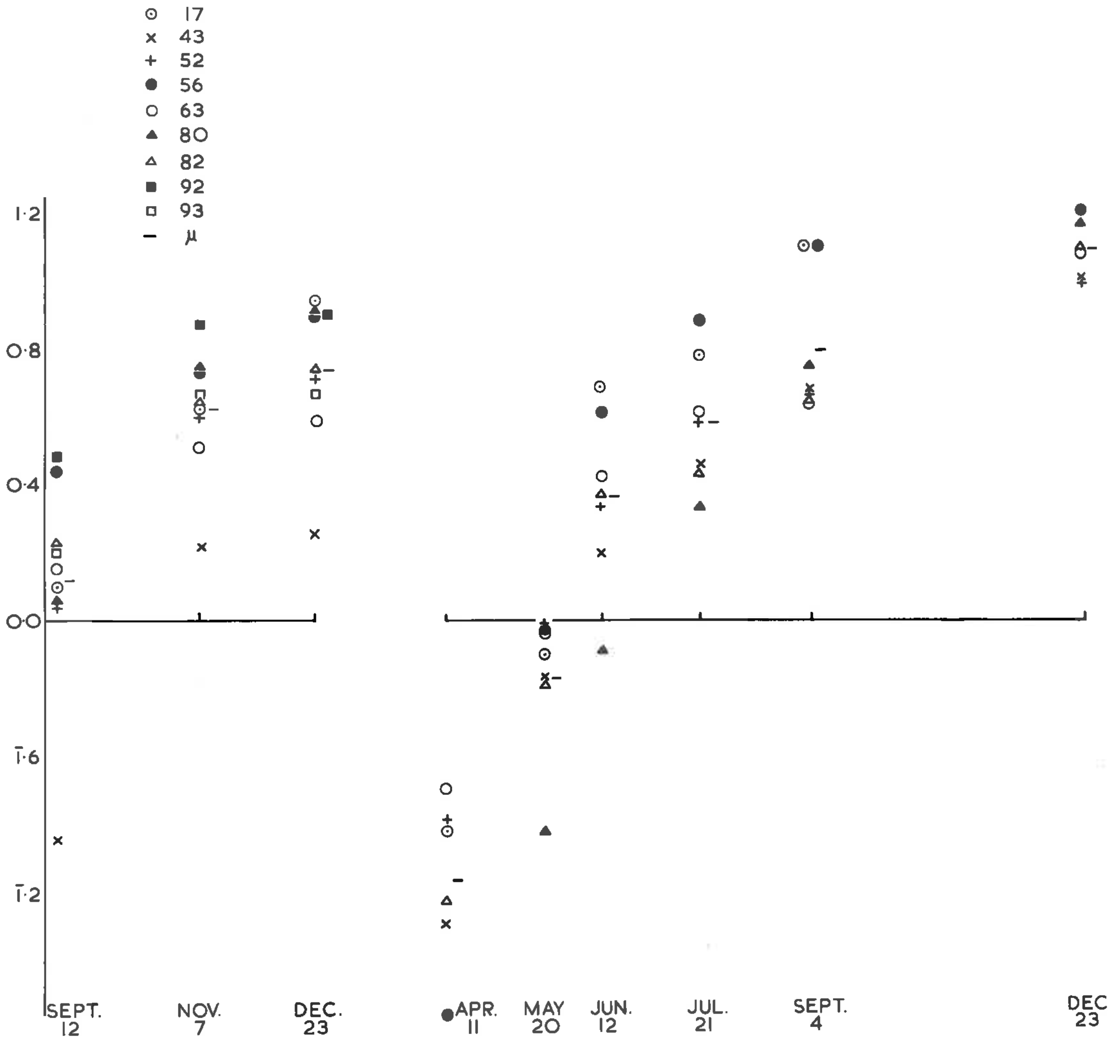
(3) 80 was poor for most of the year but showed a high ultimate weight when it became reproductive.

(4) 92 and 93 moderately productive during their first year died out completely during the first summer.

The other clones were less extreme in their behaviour but 17 could be classed with 56, 52 and 63 and 43 and 82 an intermediate group.

Values for the parents as clones are given in Fig. 6. There

Fig. 6. The top weight per plant of the parents as clones, expressed as a logarithm, and plotted against harvest occasion. Parents 92 and 93 are not represented in the second year because of their low survival.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SEPT. 4
DEC 23

are many resemblances between this graph and that of $\mu + 2gi$ (Fig. 2) derived from the diallel data. The greatest discrepancy between clonal performance and the $\mu + 2gi$ assessment was for 80 which as a clone was by far the poorest for most of the second year but in hybrid performance as measured by the g.c.a. effect was the only outstanding parent.

There were many more dissimilarities in the comparison of the parents as clones and in the topcross test. For instance the superiority of 63 as a clone at regeneration in April is not reflected in the topcross. At this time all the Mediterranean parents showed enhanced growth following hybridisation to Northern European material and 63 was not proportionately larger. Again however, 80 as a parent was relatively better than 80 as a clone.

Discussion of top weight results.

The discussion will cover suggested explanations for the growth pattern shown by the families, comments on the analyses, and possible breeding plans.

Reference has been made to dormancy, which may be defined in the present context as a reduction or cessation of growth, which has evolved to enable survival during periods of stress. From our knowledge of the environment of origin the stresses may be assumed to be extreme cold in the case of winter dormancy or extreme dryness in summer dormancy. Dormancy is to be distinguished from the reductions in growth brought about by limiting factors, and which are not related to survival. From earlier work it was known that the Northern European parents, typical of material of this origin, were not summer dormant and that in the event of a very dry summer complete mortality might result. (Knight, 1960). Very little was known about winter dormancy in these parents, or, for that matter of any other Northern European genotypes. The Mediterranean parents were known to be summer dormant and to show a low or negligible mortality during the summer (loc. cit.) and they gave no indications of any winter dormancy.

Whether or not Mediterranean material was drought resistant, as well as drought escaping, was unknown but in view of the very low annual rainfall of some of the collecting sites it was probable that ecotypes from these localities were also drought resistant.

With this background information it is possible to suggest explanations for some of the patterns of growth. At the regeneration harvest of April 28 the Mediterranean x Northern European hybrids on average gave higher yields than either pure Mediterranean or pure Northern European families and it is suggested that this arose from a combination of drought resistance and lack of summer dormancy from the respective parents. These hybrids were capable of responding to summer showers. Northern European families should also have been capable of responding to showers but had suffered considerably during the summer. The mortality figures to be given later for these families do not completely represent the extent of injury for even where the plants had survived many of its individual tillers had died.

It was interesting to find evidence of winter dormancy in Northern European material in this environment. It is reasonable to assume that in view of the considerable growth shown by Mediterranean and

Mediterranean x Northern European hybrids during the same period that this was not a restriction imposed by a limiting factor but was a true dormancy, an inherent restriction of growth by the plant.

Differences in the pattern of growth at other times of the year have no relation to dormancy but have arisen from differences in the onset of reproduction and in the proportion of tillers that become reproductive.

Several important points of interpretation of diallel analyses have been emphasised by the present data. One of these was that the gi value for a parent was relative to the other parents in the diallel a point exemplified by parent 63 which had a high positive value on June 29 but a negative value on August 10. This change was not so much in the array from parent 63 as in arrays from 17, 56 and 80 which increased considerably during this period. The occurrence of differences in gi, was also illustrated by the diallel topcross comparison which gave two different assessments of a parent depending on the other parents involved in the test. With such lack of agreement, sometimes merely attributable to differences in growth rhythm, considerable caution needs to be exercised before extrapolating from these results to other parents. One could not with certainty predict the outcome of a cross between one of the Mediterranean parents used in the diallel and some other genotype of Mediterranean origin.

Both diallel and topcross showed up another point of breeding interest. Parent 80, which gave a consistently poor performance as a clone, was one of the parents with a high progeny performance in both diallel and topcross. Its breeding value was therefore much greater than would appear from phenotypic data. Other parents, notably 43, showed a similar but less marked trend.

In suggesting breeding plans, on a basis of the results obtained, it must be remembered that this assessment was under only one system of management. It also needs to be recognised that in present day seed multiplication many generations may elapse before the seed is eventually used in agriculture. Any suggested plans are therefore dependent on being able to maintain performance during this multiplication process. This situation may change; the major restriction on producing F_1 seed for farmers being the cost of production. If F_1 seeds are feasible, only two parents need be combined, but if many generations elapse it is customary to combine several parents to avoid inbreeding. The only constant genetic variability found in the test corsses was g.c.a. and this will form the basis of the breeding plans.

To achieve rapid regeneration in the autumn two major approaches are possible. One involving Mediterranean material would be to use parent 63 which had the largest gi value on April 28 and at the two subsequent harvests. The highest yielding family (63 x 80) combining the two parents with the highest gi values in April could be immediately multiplied. As 63 and 80 were single genotypes from two ecotypes it would be possible to combine other members of the two ecotypes thereby reducing the level of inbreeding if there were many generations in the multiplication process. Alternatively parent 63 could be used as a tester in a topcross to screen and select for favourable combinations in a wider range of Mediterranean material. From what has already been said about the change in assessment with different parents there will be some element of doubt in using a particular parent such as 63 in a top cross programme. The more the present parents are a random sample of cocksfoot of Mediterranean origin the greater will be the chances of making a genetic advance with such a topcross.

The second major approach to achieving rapid regeneration, would be to utilise Mediterranean x Northern European hybrids. The two Northern European parents acted equally in producing progeny with high autumn yields through their lack of summer dormancy. A similar effect would possibly be achieved by any parents lacking summer dormancy.

The factor which would most influence the choice between the two approaches would be the incidence of summer rain in the locality for which the improved variety was intended, if the incidence was high the second approach would be preferable.

The harvest of August 10 gave an indication of mid winter yields following the coldest period of the year. Yields at this time were least for Northern European families and highest for Mediterranean families as indicated by their means, with the Mediterranean x Northern European families intermediate. However, within the Mediterranean families there was a significant g.c.a. variation on which to select but parent 63 had by now a lower gi value than the mean. One matter of breeding importance was that if Mediterranean x Northern European hybrids had been selected for their autumn yield, those families involving 52 and to some extent 63 might now be discarded in view of the dominance of the Northern European winter dormancy growth rhythm.

By early spring, (September 19) the effect which had begun to be evident at the previous harvest, led to very large differences in yield among the Mediterranean material. This was the stem elongation associated with the reproductive phase particularly shown by families having 17, 56 and 80 as parents. If it were desired to breed for this period any two of these parents may be combined or their respective ecotypes combined. A harvest in mid September falls at a critical period in terms of seasonal production. High yields just prior to this time are of great value but later in September and October annual grass species are highly productive, and there is less need for high yield from a bred variety. The important question is then can high yields in late winter be achieved by bred varieties of cocksfoot that early exhibit a change to the reproductive phase? If, with further testing, it were found that families from combining 17, 56 and 80 were not early enough in their winter increase in yield, it would be profitable to return and select from the whole collection for additional sources of earliness.

At the end of the growing season the same three Mediterranean parents were still the most important. The high yields from these families comes from their high fertile component and it would be of assistance to final selection to supplement the yield data with quality determinations. Dry matter produced at the beginning of summer has to provide the bulk of feed to sustain stock during the ensuing dry summer months so that both quality and quantity are particularly important, and it is possible that there will be a quality difference between the matured and dry sterile and fertile components as well as within components of the different genotypes. As will be discussed, the question of quality may only be important at this time of maturity and with the emergence of flowering heads.

Among the Mediterranean x Northern European hybrids there was also a significant g.c.a. variation at the last harvest, with 56 and 80 again being the best Mediterranean parents in the combination with the Northern European parents.

High production all the year round is the prime objective of any breeding programme but is not easy to attain and was not shown by any particular cross in these experiments. The next best material is outstanding when feed is scarce, and is average when feed is plentiful. Considering the Mediterranean material for the important periods, autumn, winter and early summer the best crosses were respectively 63 x 80, 17 or 56 x 80 and again 17 or 56 x 80.

Values for these families and harvests are given in Table 15 together with the means of the Mediterranean populations. Within the Mediterranean x Northern European material there were fewer distinctive families, the better ones including 56 x 92 and 80 x 93. These together with the means of the Mediterranean x Northern European families are also included in table15 A discriminant function could be used to pick out the best of these families, weighting the variables in the function with the monetary value of dry matter in each period, but such a step is not warranted without other assessments of the families under different managements. Another necessary step is to attempt to raise the production of 63 x 80 in the winter and summer, and of 17 x 80 in the autumn either by selection within the families, by further crosses between their ecotypes, or else by crossing between the families and selecting within the double cross. The best Mediterranean x Northern European hybrids were not as

Table 15. Log and Antilog values for top weight at three important periods of the year

	63 x 80		17 x 80		56 x 80		μ Med.		56 x 92		80 x 93		μ Med.xN.E.	
Autumn (April 28)	.380	2.40	.203	1.60	$\bar{1}.818$	0.66	$\bar{1}.975$	0.92	.170	1.48	.298	1.99	.079	1.20
Winter (August 10)	.859	7.23	.998	9.95	.953	8.97	0.816	6.55	1.055	11.35	.938	8.67	.720	5.25
Early Summer (January 9)	1.447	28.00	1.493	31.19	1.454	28.45	1.284	19.23	1.399	25.06	1.464	29.11	1.232	17.06

good as the best Mediterranean families but this could alter in years with a greater incidence of summer rains and breeding of the hybrids should be pursued with this in mind.

Stubble weight.

The weight of the stubble was one of the characters assessed for its seasonal variation and its relation to the yield of the tops. The stubble weight of each plant was obtained and the values treated in a similar way to that of the tops. The family means in the antilogarithmic form are given in table 16, where it may be seen that there was considerable variation between families in this character.

Considering first the Mediterranean families and the diallel analysis, an overall picture of changes in the stubble weight for the period of the experiment was obtained from the values of the mean μ in Table 18 and by Fig. 7. The mean showed a curvilinear increase on a logarithmic scale with no abrupt changes in growth so that on average the families showed no mid-winter cessation of growth.

In the combining ability analysis the mean squares for g.c.a. were significant at all harvests, except the first (Table 17), indicating that it would be possible to select for stubble weight. Furthermore, from the g.c.a. effects (Table 18) it may be seen that parents were more constant in this character than they were for top weight; parent 63, consistently having high values, 56 and 80 low values at nearly all harvests. There was also less evidence than in the top weight of seasonal trends (Fig. 7).

At the reproductive harvests of the two seasons (December 23, 1959,

Table 16.

The geometric mean for stubble weight per plant in gm.
(twelve plants per family at each harvest)

	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sept. 19	Nov. 7	Jan. 9
17.43	1.23	1.72	.24	.88	1.27	4.06	3.77	4.39	4.40
52	1.43	3.19	.60	.97	1.50	1.43	4.06	6.67	6.75
56	1.03	1.88	.20	.92	1.45	2.67	3.30	4.24	4.60
63	1.43	4.15	.54	1.33	2.38	3.88	7.82	8.38	8.32
80	1.12	2.81	.53	.86	1.60	2.38	3.84	3.03	4.18
82	1.44	3.59	.47	1.53	2.22	4.72	5.02	6.40	5.35
92	1.82	3.44	.37	.90	2.05	3.08	6.76	5.81	4.70
93	1.34	3.18	.60	1.44	1.68	3.12	6.30	7.62	4.84
43.52	1.04	2.65	.65	1.40	2.38	3.66	2.24	5.30	3.30
56	1.08	1.78	.26	.70	2.08	3.14	3.19	3.64	4.20
63	1.49	3.42	.59	1.70	2.62	5.53	5.38	5.52	5.26
80	1.39	2.31	.49	.65	2.16	2.34	3.21	2.51	3.30
82	1.66	2.48	.54	1.12	2.49	4.46	2.27	2.76	3.33
92	1.48	4.50	.94	.56	1.45	2.66	4.36	7.82	5.77
93	1.17	3.02	1.20	1.17	2.96	2.63	7.87	7.10	7.11
52.56	1.39	2.12	.49	1.48	2.84	2.86	5.36	6.95	5.65
63	1.16	2.73	.80	1.94	4.04	4.60	5.51	6.00	8.05
80	1.12	2.86	.26	1.02	2.25	3.80	5.11	4.16	3.72
82	1.84	2.96	.48	1.36	1.60	4.81	3.67	7.08	6.30
92	1.88	3.30	.45	1.28	1.36	1.34	9.16	9.10	6.11
93	1.05	3.65	.53	1.38	1.82	2.14	3.64	3.92	5.77
56.63	1.48	3.05	.70	1.48	2.77	3.05	5.74	5.97	5.61
80	1.27	2.22	.25	1.12	1.58	2.04	3.24	3.86	4.24
82	1.00	1.96	.26	.79	1.32	2.91	3.01	4.17	5.87
92	1.64	3.44	1.03	.84	4.09	6.47	4.52	4.95	7.78
93	1.22	3.37	.57	1.47	1.55	3.30	3.85	8.12	8.38
63.80	1.56	3.23	1.19	1.03	1.87	2.82	3.04	5.43	4.53
82	1.44	2.79	.59	1.49	2.38	2.93	1.52	4.23	6.89
92	0.95	6.84	.92	1.53	3.52	2.95	5.57	10.23	10.28
93	1.29	4.94	.95	1.57	3.30	2.73	6.25	6.49	5.85
80.82	.74	2.57	.58	1.21	1.44	1.49	3.30	4.71	5.33
92	1.48	3.69	.37	.72	1.40	4.13	4.88	5.94	6.49
93	1.12	3.60	.73	1.15	2.40	3.72	2.85	5.14	5.62
82.92	2.11	5.16	1.19	.76	1.65	5.65	6.14	8.00	9.33
93	1.10	4.60	.76	1.53	1.64	3.77	5.52	3.18	10.05
92.93	1.30	5.65	.21	.76	1.53	1.70	4.88	5.60	1.55

Table 17.

Combining ability mean squares for stubble weight at successive harvests for two seasons. (Med. diallel analysis)

	D.F.	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
g.c.a.	6	.0055	.0225***	.0802***	.0333**	.0316*	.0354*	.0330*	.0428***	.0370***
s.c.a.	14	.0094***	.0054	.0244	.0093	.0106	.0210	.0242*	.0095	.0046
Error	> 250	.0031	.0036	.0173	.0101	.0112	.0146	.0123	.0087	.0054

Table 18.

Estimates of the g.c.a. effects for stubble weight at successive harvests (estimates are 1,000) and the general mean μ

	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
17	- 3	26	- 81	- 41	- 92	- 27	91	45	41
43	8	- 63	- 40	- 63	24	93	- 81	-114	-131
52	12	22	58	76	68	27	54	112	35
56	-35	-106	-186	- 50	- 27	- 66	14	- 14	- 3
63	56	102	223	131	133	86	72	100	118
80	-45	5	18	- 88	- 61	-141	- 24	-116	- 96
82	7	13	7	34	- 45	28	-126	- 12	36
μ	0.105	0.417	$\bar{1}.664$	0.057	0.304	0.494	0.571	0.679	0.699

Significant differences between parents as judged by the value of gi.
Parents underscored by the same line are not significantly different. Level of significance 5%.

Oct. 5 80 56 17 82 43 52 63

Dec. 23 56 43 80 82 52 17 63

Apr. 28 56 17 43 82 80 52 63

May 24 80 43 56 17 82 52 63

June 29 17 80 82 56 43 52 63

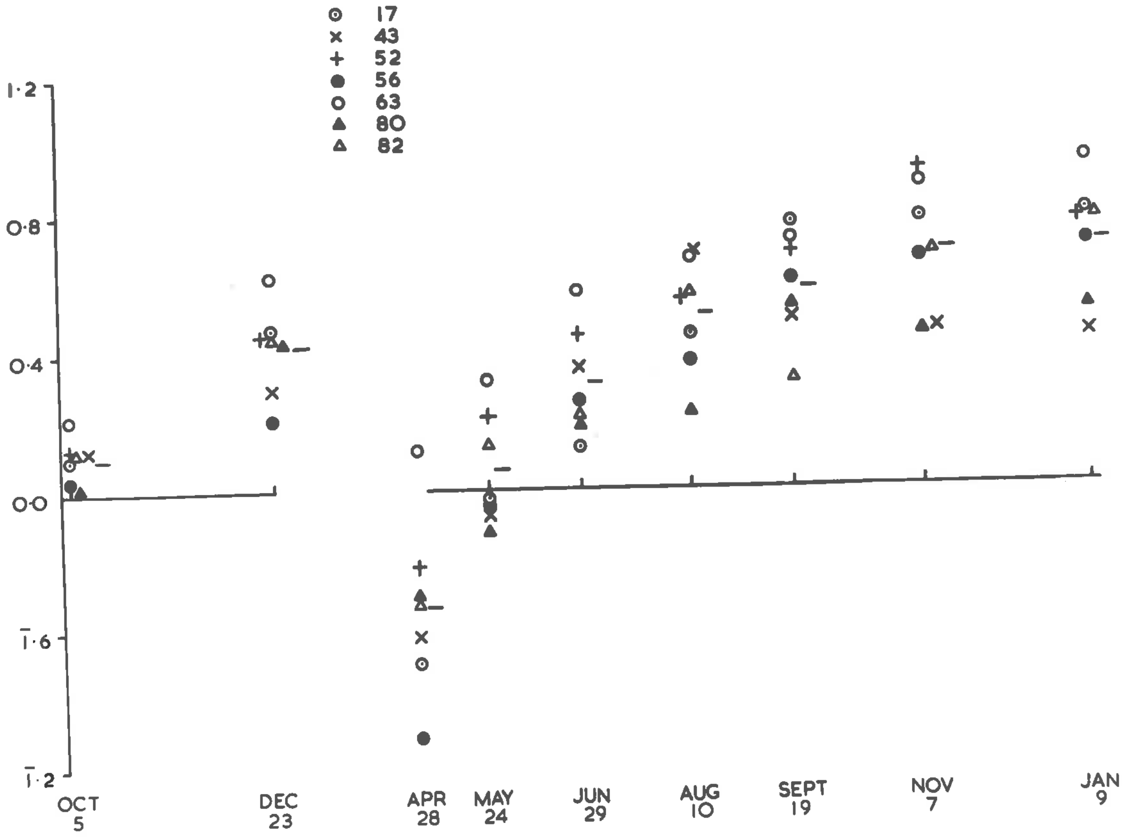
Aug. 10 80 56 17 52 82 63 43

Sep. 19 82 43 80 56 52 63 17

Nov. 7 80 43 56 82 17 63 52

Jan. 9 43 80 56 52 82 17 63

Fig. 7. The combining ability values $\mu + 2gi$ for stubble weight for each Mediterranean parent plotted against harvest occasion. Assessment by Mediterranean diallel test.


⊙ 17
× 43
+ 52
● 56
○ 63
▲ 80
△ 82
1·2
0·8
0·4
0·0
1̄·6
1̄·2
OCT 5
DEC 23
APR 28
MAY 24
JUN 29
AUG 10
SEPT 19
NOV 7
JAN 9

November 7, 1960 and January 9, 1961, in tables 19 and 20) when the sterile and fertile components were separated, the distinctive behaviour of parents for combining ability was maintained (Fig. 8). Variability in the sterile component was particularly large but as this component was smaller than the fertile component, and as there was an inverse association between the two components for most parents, this did not result in a high variability for the total stubble weight.

The performance of the Mediterranean families will now be compared with that of Mediterranean x Northern European and Northern European families. Mean values for these three groups are given in table 21. In general the Mediterranean x Northern European and Northern European families showed a better development of stubble weight, relative to the Mediterranean families than in the weight of tops comparison. The Mediterranean x Northern European mean was higher than the Mediterranean mean at the beginning of the growing season and from September onwards in the second year. The Northern European families with a high mean at the end of the first season were poor at regeneration after the summer, showed a winter cessation of growth (June-August) and it was not until September that they equalled the Mediterranean families.

The analysis of variance of the topcross is given in Table 22. There were significant combining ability differences between the two Northern European parents at three harvests but as these parents do not differ greatly in growth rhythm an explanation in these terms can not be suggested. The Mediterranean g.c.a. was significant at regeneration, mid winter and at harvests of the reproductive phase. The gi values

Table 19.

Combining ability mean squares for sterile and fertile components of stubble weight at harvests of the reproductive phase (Med. diallel)

	D.F.	Dec. 23		Nov. 7		Jan. 9	
		Ster.	Fert.	Ster.	Fert.	Ster.	Fert.
g.c.a.	6	.1500***	.0539***	.2487***	.0481**	.1846** *	.0522***
s.c.a.	14	.0060	.0235***	.0303*	.0101	.0236**	.0081
error	> 250	.0048	.0070	.0147	.0137	.0087	.0055

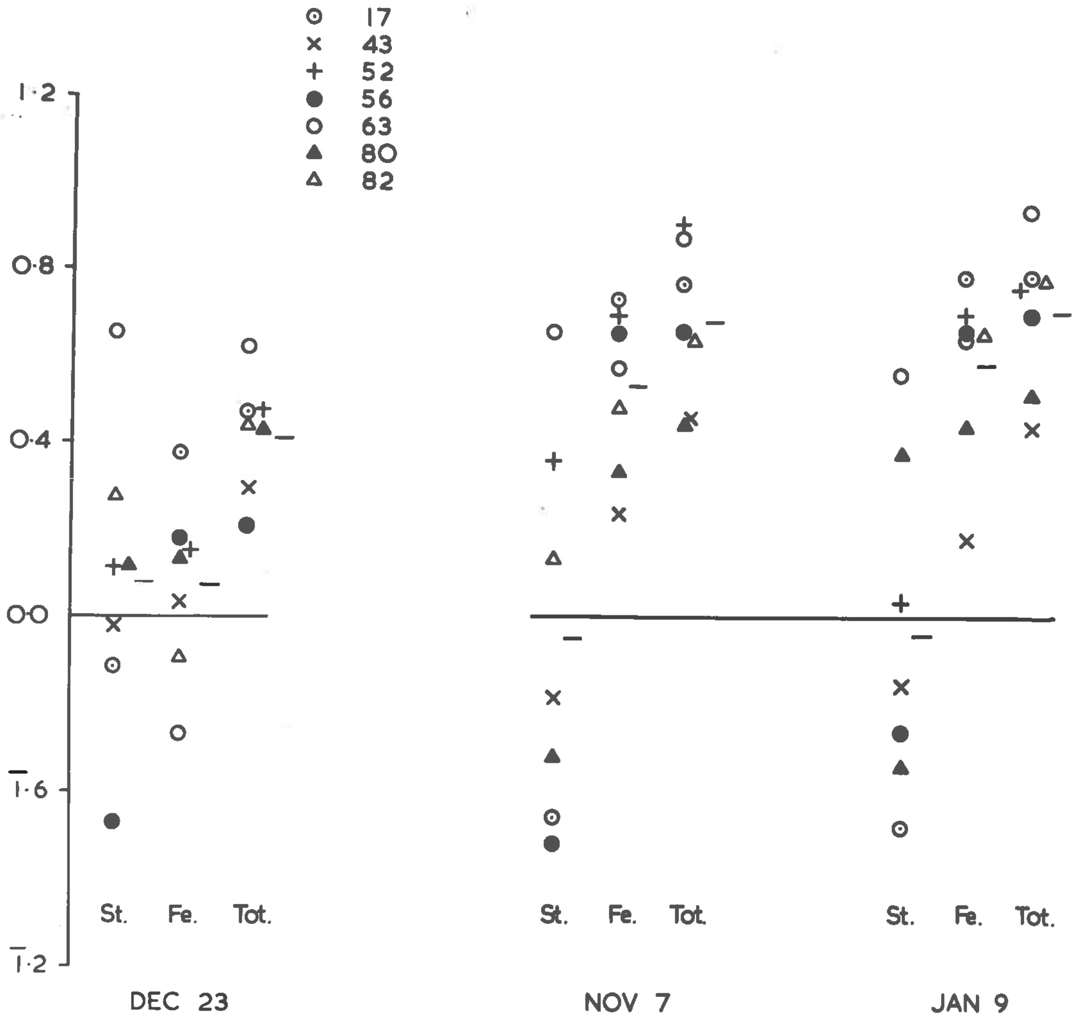
Table 20.

Estimates of the g.c.a. effects for the sterile and fertile components of stubble weight (estimates are x 1000 for clearer presentation) and the general mean μ

	Dec. 23		Nov. 7		Jan. 9	
	Ster.	Fer.	Ster.	Fert.	Ster.	Fert.
17	- 98	150	- 207	120	- 221	101
43	- 49	- 17	- 70	-151	- 57	-199
52	18	42	208	78	36	57
56	-275	51	-237	60	- 113	41
63	287	-171	352	20	299	32
80	19	30	- 136	- 98	- 153	- 72
82	98	- 85	90	- 27	207	40
μ	0.079	0.073	$\bar{1}.952$	0.534	$\bar{1}.960$	0.577

Dec. 23	Ster.	56 17 43 52 80 82 63
	Fert.	63 82 43 80 52 56 17
Nov. 7	Ster.	56 17 80 43 82 52 63
	Fert.	43 80 82 63 56 52 17
Jan. 9	Ster.	17 80 56 43 52 82 63
	Fert.	43 80 63 82 56 52 17

Fig. 8. The combining ability values $\mu + 2gi$ for the sterile, fertile and total stubble weight for each Mediterranean parent at harvests during the reproductive phase. Assessment by Mediterranean diallel test.


⊙ 17
× 43
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1·2
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St.
Fe.
Tot.
St.
Fe.
Tot.
St.
Fe.
Tot.
DEC 23
NOV 7
JAN 9

Table 21.

Values of the mean μ for stubble weight of Med., Med. x N.E. and N.E. families

	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
Med.	0.105	.417	$\bar{1}$.664	0.057	.304	.494	.571	.679	.699
	x	xxx	xxx				xxx	xxx	xxx
Med. x N.E.	0.134	.596 xxx	$\bar{1}$.848 xxx	0.045 x	.314	.503 xx	.723	.797	.832 xxx
		xx	xxx	x		xx			xxx
N.E.	0.144	.752	$\bar{1}$.312	$\bar{1}$.882	.186	.230	.688	.748	.188

Values of the mean μ for components of stubble weight at harvests in the reproductive phase

	Dec. 23		Nov. 7		Jan. 9	
	Ster.	Fert.	Ster.	Fert.	Ster.	Fert.
Med.	0.079	0.073	$\bar{1}$.952	0.535	$\bar{1}$.960	0.578
	xxx	xxx	xxx		xxx	xx
Med. x N.E.	0.449 xxx	$\bar{1}$.934 xxx	0.328 xxx	0.501 xx	0.316	0.631 xxx
	xxx	xxx	xxx	xx	xxx	xxx
N.E.	0.714	$\bar{1}$.675	0.620	0.258	0.053	0.208

Table 22.

Combining ability mean squares for stubble weight at successive harvests for two seasons

(Med. x N.E. top cross)

	D.F.	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
Between N.E. g.c.a.	1	.0579***	.0100	.0043	.1205***	.0013	.0085	.0147	.0498*	.0019
" Med. g.c.a.	6	.0048	.0173***	.0468*	.0177	.0277*	.0481**	.0174	.0112	.0210**
Interaction s.c.a.	6	.0092**	.0030	.0205	.0080	.0292*	.0121	.0211	.0223*	.0059
Error	> 250	.0031	.0036	.0173	.0101	.0112	.0146	.0123	.0087	.0054

presented in Table 23 and Fig. 9 illustrate that the mid winter variability of these Mediterranean x Northern European hybrids was again attributable to combinations involving parents 52 and 63 with Northern European parents. These hybrids ceased growth during the winter, an effect which is accentuated in the combining ability analysis by the continued growth of the remaining hybrids. No cessation occurred with 52 or 63 when crossed to Mediterranean parents in the diallel. One effect of the cessation in 63 was that its record for having high stubble weight was lost at the August harvest and that other parents which were characteristically low in stubble weight have, through continued growth, a high assessment in August.

The illustration of the significance at the reproductive harvests may best be understood from Fig. 10. These data were derived from Tables 24 and 25. Again very large variation in one component was partially compensated for by the negative association of the other component leading to small variability in total stubble weight except where there was a large difference in the magnitude of the components.

To see if the diallel agreed with the topcross assessment a correlation coefficient was calculated from the gi values of each parent over the nine harvests. None of these was significant. Similarly the correlation of the gi assessments at each harvest showed no significance except at one harvest that of May 24. This overall lack of agreement indicates that parents were not always similarly ranked by their progenies performance when crossed to both Mediterranean and Northern European testers. A clear example of this is provided by progenies of parent 63 with their winter cessation of growth when

Table 23.

Estimates of the g.c.a. effects for stubble weight at successive harvests of Med. x N.E. topcross (estimates are x 1000 for clearer presentation) and the mean μ

	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
17	53	- 76	-176	11	- 45	- 11	92	26	-153
43	-15	- 29	180	-136	3	- 80	45	75	- 25
52	13	- 54	-159	79	-117	-274	39	-21	- 58
56	16	- 64	36	1	88	162	-102	-43	75
63	-90	169	124	145	218	- 50	48	114	58
80	-24	- 34	-135	- 85	-51	91	-161	-54	- 51
82	49	92	130	- 11	-97	161	42	-94	154
92	64	27	- 18	- 94	-10	24	33	60	11
93	-64	- 27	18	94	10	- 24	- 33	-60	-11
μ	.134	.596	$\bar{1}$.848	.045	.314	.503	.723	.798	.832

Significant differences between parents as judged by values of gi. Parents underscored by same line are not different at 5% level.

Oct. 5 63 80 43 52 56 82 17

Dec. 23 17 56 52 80 43 82 63

Apr. 28 17 52 80 56 63 82 43

May 24 43 80 82 56 17 52 63

June 29 52 82 80 17 43 56 63

Aug. 10 52 43 63 17 80 82 56

Sep. 19 80 56 52 82 43 63 17

Nov. 7 82 80 56 52 17 43 63

Jan. 9 17 52 80 43 63 56 82

Fig. 9. The combining ability values $\mu + 2gi$ for stubble weight for each Mediterranean parent when crossed to Northern European parents. A major feature is the mid-winter decline in combining ability of parents 52 and 63.

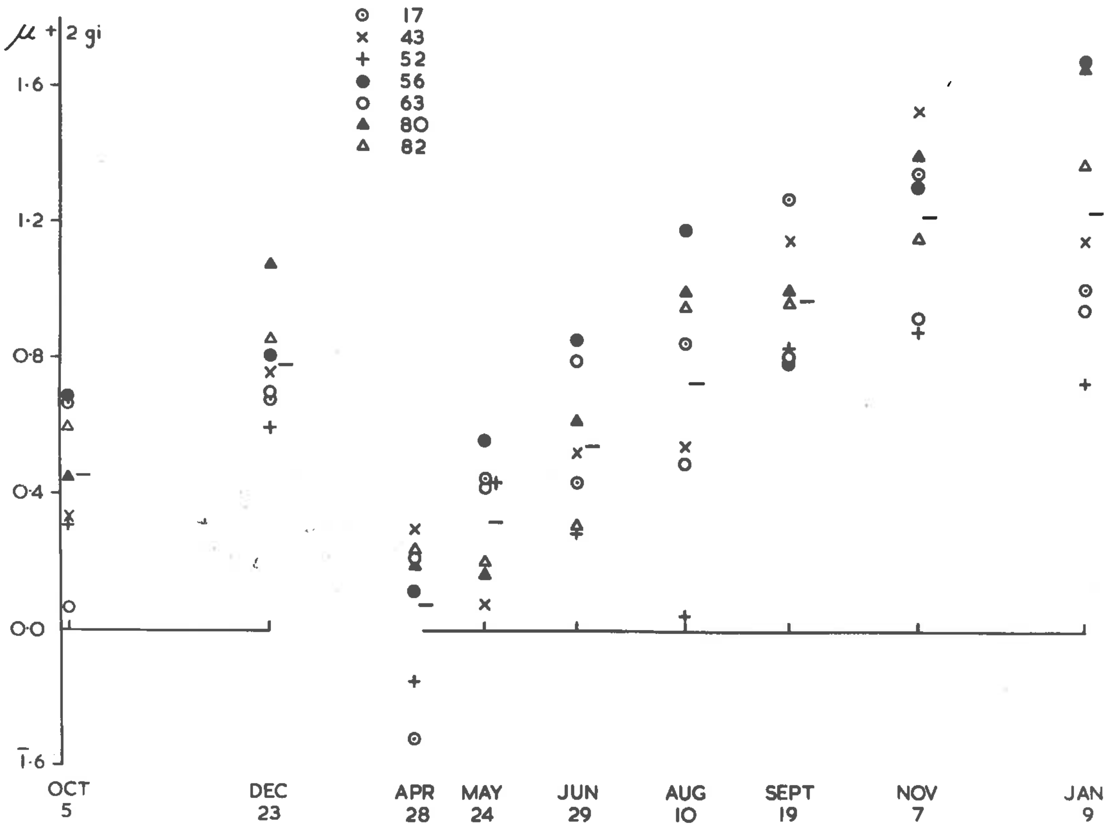

μ + 2 gi
1·6
1·2
0·8
0·4
0·0
1̄·6
⊙ 17
× 43
+ 52
● 56
○ 63
▲ 80
△ 82
OCT 5
DEC 23
APR 28
MAY 24
JUN 29
AUG 10
SEPT 19
NOV 7
JAN 9

Table 24.

Combining ability mean squares for sterile and fertile components of stubble weight at harvests of the reproductive phase (Med. x N.E. topcross)

		D.F.	Dec. 23 Ster.	Dec. 23 Fert.	Nov. 7 Ster.	Nov. 7 Fert.	Jan. 9 Ster.	Jan. 9 Fert.
Between N.E.	g.c.a.	1	.0000	.0548**	.0006	.0445	.0006	.0087
Between Med.	g.c.a.	6	.0442***	.0350***	.1735***	.0401*	.0597***	.0348***
Interaction	s.c.a.	6	.0029	.0120	.0706***	.0418**	.0263***	.0114*
Error		> 250	.0048	.0070	.0147	.0137	.0087	.0055

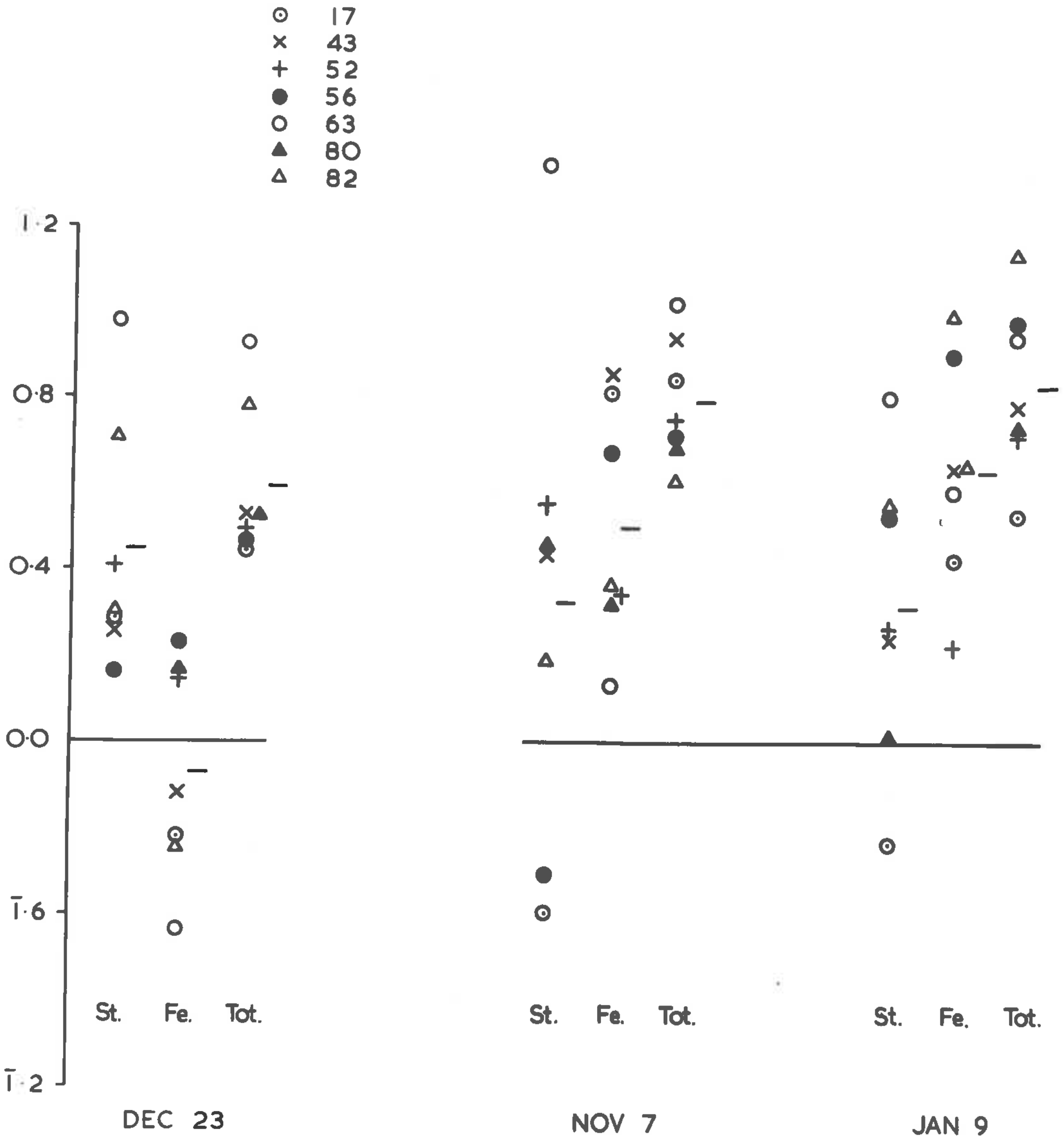
Table 25.

Estimates of the g.c.a. effects for the sterile and fertile components of stubble weight (effects are x 1000) and the mean μ

	Dec. 23 Ster.	Dec. 23 Fert.	Nov. 7 Ster.	Nov. 7 Fert.	Jan. 9 Ster.	Jan. 9 Fert.
17	-78	-80	-363	157	-276	-104
43	-94	-20	59	184	- 38	5
52	-21	107	118	- 77	- 31	-202
56	-143	151	-319	87	105	135
63	267	-186	511	-187	245	- 27
80	-74	118	63	- 90	-125	9
82	141	- 90	- 65	- 75	118	184
92	- 1	62	6	- 58	- 6	- 25
93	1	- 62	- 6	58	6	25
μ	0.449	$\bar{1}$.934	0.328	0.501	0.316	0.631

Dec. 23	Ster.	56 43 17 80 52 82 63
	Fert.	63 82 17 43 52 80 56
Nov. 7	Ster.	17 56 82 43 80 52 63
	Fert.	63 80 52 82 56 17 43
Jan. 9	Ster.	17 80 43 52 56 82 63
	Fert.	52 17 63 43 80 56 82

Fig. 10. The combining ability values $\mu + 2gi$ for the sterile, fertile and total stubble weights for each Mediterranean parent when crossed to Northern European parents at harvests during the reproductive phase.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crossed to Mediterranean parents contributing to an absence of correlation at winter harvests. Progenies of parent 52 had a similar effect. At the reproductive phase harvests parents differed in their combining ability with the tester parents, a notable example being parent 17 whose high combining ability in the Mediterranean diallel and low in the Northern European topcross was a reflection of a major change in the fertile component.

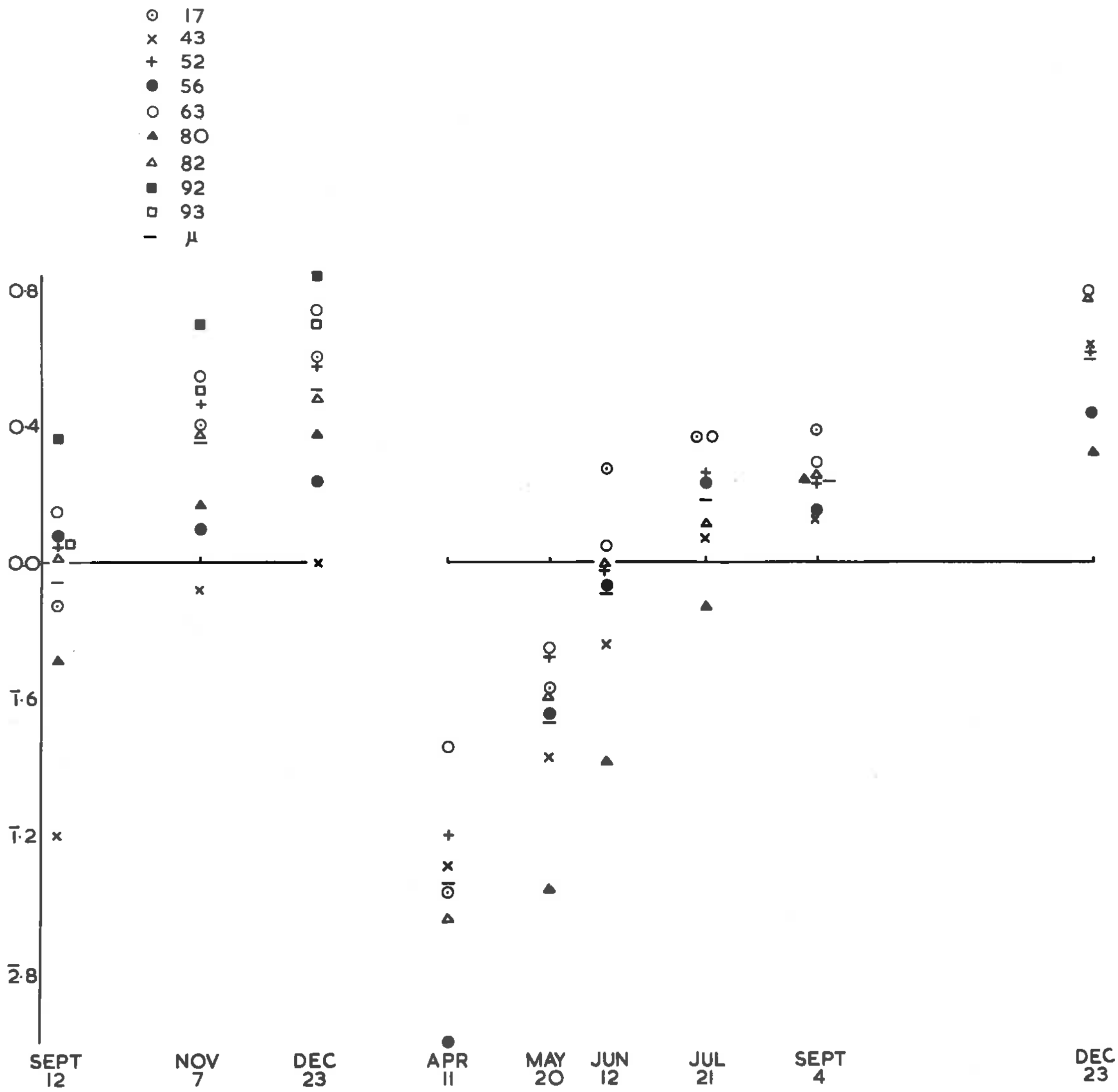
Comparison with parents.

In the study of the parents as clones (Knight, 1960) it had been found that some parents were consistently high for stubble weight while others were low (Fig. 11). High expression was shown by parent 63 and the two Northern European parents for as long as they survived, while low expression was characteristic of 43, 56 and 80. This parental assessment agrees fairly well with the Mediterranean diallel progeny assessment but is poorer with the topcross, because of the striking difference in winter growth of 52 and 63 progenies when crossed to Northern European parents, and with the difference at the reproductive phase shown by 17 x Northern European progenies.

Discussion of stubble weight results

In contrast to the top weights, parents showed a more constant general combining ability for stubble weight and seasonal differences were almost non existent except in the topcross to Northern European parents. Thus in the Mediterranean diallel two parents 52 and 63 were at every harvest of the experiment among the top three parents for high

Fig. 11. The stubble weight per plant of the parents as clones, expressed as a logarithm, and plotted against harvest occasion. Parents 92 and 93 are not represented in the second year because of their low survival.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stubble weight. This evidence, combined with the similarity of results from the parents as clones, indicates that within Mediterranean material a mass selection programme would be successful in making a genetic gain.

It would appear that the Mediterranean x Northern European hybrids would be profitable material from which to select for stubble weight as at many harvests they exceeded the Mediterranean families, however, being less consistent the choice of parents would be more difficult. Parent 63 was the best in combination with Northern European parents, except for the mid winter period, and it would be necessary to know the agronomic significance of this shortcoming.

The association of stubble weight with top weight yield is left to a later section when all the characters under study are considered together.

Root weights

The root weights were not obtained at all harvests because of the great difficulty of obtaining the samples particularly during the summer when the ground was hard. Six harvests were taken one in the first year and five in the second. The root weights were logarithmically transformed and the family means calculated. The antilog. of the mean (Table 26) shows that there were often twofold differences in root weight, but it will be recalled that these differences are not as large as those found in the top, or stubble, weights.

The mean μ of the Mediterranean families in the diallel, together

Table 26.

The geometric mean for weight of roots per plant in gm.

	Oct. 5	May 24	June 29	Sept. 19	Nov. 7	Jan. 9
17.43	1.97	5.01	6.55	8.13	9.33	9.55
52	1.95	6.76	6.97	9.55	10.72	10.00
56	2.00	4.17	5.13	7.76	7.59	11.48
63	1.96	7.94	7.19	10.00	10.47	16.98
80	2.10	5.89	8.18	12.02	9.77	10.00
82	2.05	6.17	7.03	8.51	9.77	11.75
92	2.03	6.03	6.68	12.59	12.88	12.59
93	1.95	6.76	6.38	10.97	15.49	13.18
43.52	1.96	7.76	6.12	7.94	9.12	9.55
56	1.63	3.31	5.58	7.08	8.32	10.23
63	1.90	6.61	7.46	9.33	10.72	11.48
80	1.95	5.50	7.46	10.00	7.94	9.77
82	1.88	4.90	5.41	6.03	6.61	7.41
92	2.19	7.76	9.62	9.12	15.14	12.59
93	1.87	8.32	9.18	13.80	21.38	17.78
52.56	2.00	7.76	6.21	9.33	10.10	12.88
63	1.69	8.51	9.33	12.59	15.85	14.45
80	2.07	6.46	6.92	9.55	11.75	10.72
82	1.92	5.37	7.24	7.94	14.45	16.22
92	2.02	7.41	10.97	10.97	12.88	13.80
93	1.86	6.92	7.29	13.80	12.30	13.49
56.63	1.91	6.31	6.03	8.91	10.72	11.48
80	1.97	5.25	6.56	7.94	9.33	10.47
82	1.90	4.37	6.35	7.94	8.32	12.30
92	1.94	5.50	8.07	10.23	12.88	13.49
93	1.89	7.76	5.75	9.77	9.55	12.59
63.80	2.00	7.41	8.51	8.51	13.80	14.45
82	1.79	6.31	7.13	8.91	13.80	12.88
92	1.97	6.31	8.18	12.59	15.85	10.23
93	1.95	7.41	7.85	7.94	12.02	17.38
80.82	1.82	4.57	9.27	8.91	9.55	11.75
92	2.07	10.97	9.06	16.60	15.49	12.30
93	1.80	7.76	7.82	9.12	18.20	11.48
82.92	2.05	7.41	8.57	9.77	12.02	14.45
93	1.80	7.76	6.87	12.02	12.30	13.49
92.93	1.89	6.61	7.91	8.32	12.02	13.18

with other data are illustrated in Fig. 12. The root weights at the first of the harvests (May 24) of the second year were large and subsequently showed a linear increase, on a logarithmic scale, in weights from May 24 to Nov. 7. Evidently root weights continued to increase throughout the experiment as it may be assumed that the roots formed in the first year were alive and functional in the second. (Stuckey, 1941).

At each of the six harvests (Table 27) the g.c.a. mean squares were found to be significant. It may be seen from the effects (Table 28) and from the graph of $\mu + 2gi$ that there was considerable constancy in these effects, parent 52 and 63 consistently showing high combining ability for root weight and parents 43 and 56 being consistently low. In the previous section which assessed stubble weights, parents 52 and 63 had also been found to be consistently high but not all parents showed a constant association between these two characters. Between the Sept. 19 and Nov. 7 harvests, parents 52 and 63 showed a considerable increase in values of $\mu + 2gi$ resulting in an increase in the variability. The significance of this finding in relation to heading date will be discussed in a later section.

In general the Mediterranean x Northern European hybrids had, as a group, a greater development of roots than the Mediterranean families (Table 29). The Northern European families were not significantly different from either except at the last harvest, which is considered an anomalous result arising from sampling. The greater root weights of the Mediterranean x Northern European hybrids over Mediterranean families

Table 27.

Combining ability mean squares for root weights at six harvests. (Med. diallel analysis)

	D.F.	Oct. 5	May 24	June 29	Sept. 19	Nov. 7	Jan. 9
g.c.a.	6	.0010*	.0270***	.0113**	.0100***	.0246***	.0142***
s.c.a.	14	.0006	.0042	.0021	.0029	.0027	.0042
error	70	.0004	.0047	.0026	.0022	.0048	.0026

Table 28.

Estimates of the g.c.a. effects for root weights at six harvests (Estimates are x 1000 for clearer presentation)

	Oct. 5	May 24	June 29	Sept. 19	Nov. 7	Jan. 9
17	21	1	- 8	25	-31	- 5
43	-13	-49	-40	-50	-87	-95
52	3	95	11	33	77	25
56	- 5	-83	-76	-41	-63	- 3
63	-13	103	46	47	105	83
80	19	- 7	62	35	3	-19
82	- 9	-59	6	-51	- 5	11
μ	.283	.768	.839	.944	1.006	1.061

Oct. 5 43 63 82 56 52 80 17

May 24 56 82 43 80 17 52 63

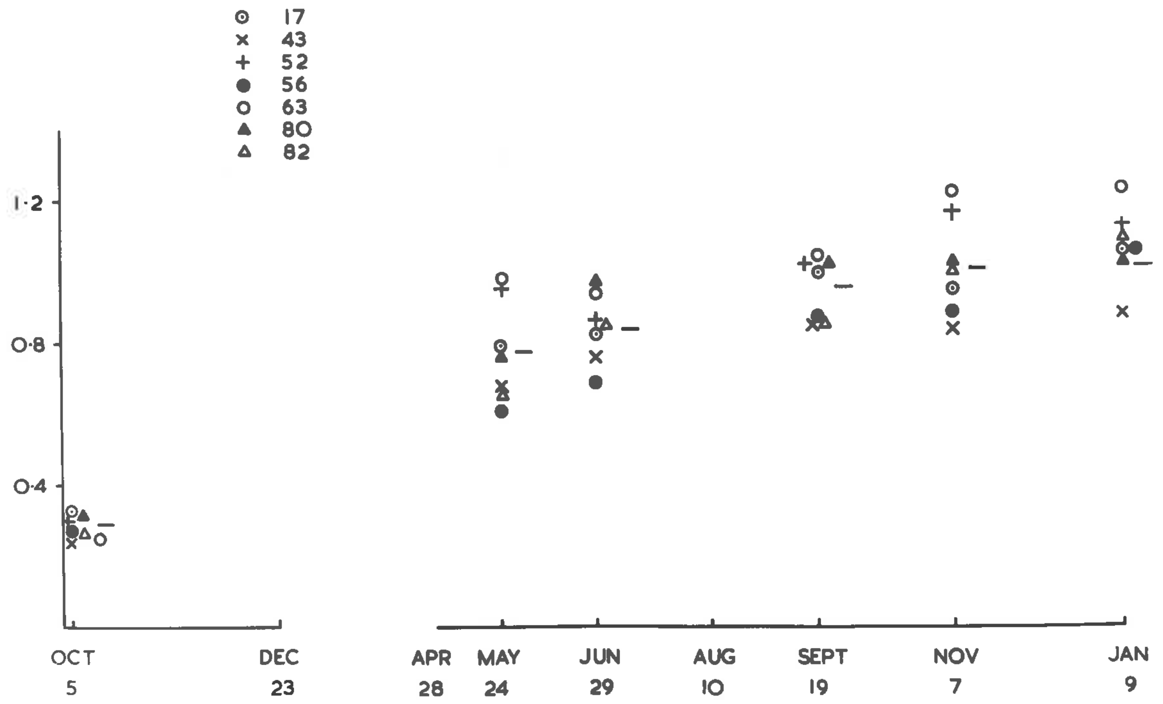
June 29 56 43 17 82 52 63 80

Sept. 19 82 43 56 17 52 80 63

Nov. 7 43 56 17 82 80 52 63

Jan. 9 43 80 17 56 82 52 63

Fig. 12. The combining ability values $\mu + 2g_i$ for root weight of each Mediterranean parent plotted against harvest occasion, illustrating constancy of parents, but overall low variability.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× 43
+ 52
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○ 63
▲ 80
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JAN 9

Table 29.

<u>Values of the mean μ for root weight of Med., Med. x N.E. and N.E. families</u>

	Oct. 5	May 24	June 29	Sept. 19	Nov. 7	Jan. 9
Med.	0.283	.768	.839	.944	1.006	1.061
		***	**	***	***	***
Med. x N.E.	0.291	.866	.898	1.048	1.143	1.126
N.E.	0.277	.820	.898	.920	1.080	1.119

Table 30.

<u>Combining ability mean squares for root weights. Med. x N.E. topcross</u>

		D.F.	Oct. 5	May 24	June 29	Sept. 19	Nov. 7	Jan. 9
Between N.E.	g.c.a.	1	.0045**	.0014	.0210**	.0020	.0001	.0064
Between Med.	g.c.a.	6	.0002	.0063	.0068	.0029	.0114*	.0019
Interaction	s.c.a.	6	.0003	.0043	.0021	.0132***	.0055	.0055
Error		70	.0004	.0047	.0026	.0022	.0048	.0026

was uniformly exhibited by them, for at only one harvest in the topcross was there any significant variation due to differences between the Mediterranean parents (Table 30). This lack of significance in the topcross was not due to a large error term, the coefficient of variation in the roots being no greater than was found in the top weights or stubble weights.

In the trial in which the parents were compared as clones (Knight, 1960) root weights were only obtained for spaced plants and not for the swards. There was however, general agreement between this assessment and $\mu + 2gi$ of the combining ability analysis. Of the Mediterranean material 52 and 63 had heavy root weights and 43 and 56 light root weights.

Tiller number

A tiller number was obtained for the plants at all of the harvests. In addition, a count was made in the field in September of the first year, before the plants had grown too large to make this possible. All the tiller data were analysed in the same way as the previous characters. The magnitude of differences in tiller number may be gauged from values presented as antilogarithms of the mean in Table 31, which shows that on any one occasion some families had two to five times as many tillers as other families.

Seasonal changes in tiller number were very different from the characters so far considered.

For the Mediterranean families the mean of the whole diallel μ rose in both years to a maximum and then declined towards the end of the

Table 31

The geometric mean tiller number (twelve plants per family) at successive harvests.

F1 amily	Sep. 11	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan.9
7.43	14	31	20	17	32	31	33	25	17	25
52	15	35	25	20	29	31	15	21	20	22
56	11	24	18	13	26	26	19	17	17	22
63	18	39	37	20	39	30	28	35	26	31
80	16	34	28	29	28	26	22	29	20	30
82	18	35	32	21	40	42	39	27	21	26
92	13	34	26	9	26	26	25	30	13	18
93	13	35	30	16	24	23	21	26	25	24
3.52	23	50	35	48	74	72	60	36	45	35
56	17	39	30	25	35	63	50	26	27	31
63	22	78	66	49	56	87	50	51	45	54
80	24	69	46	48	43	65	48	46	41	56
82	24	68	35	39	56	85	72	36	31	36
92	25	49	54	27	28	43	54	50	54	47
93	18	40	45	40	50	60	55	78	43	66
2.56	18	44	24	30	56	58	30	34	29	35
63	17	58	56	44	76	72	55	50	34	49
80	20	55	41	25	49	58	55	59	36	39
82	20	71	42	30	50	60	66	40	36	54
92	19	60	37	18	41	37	23	60	32	28
93	14	45	36	17	46	42	28	43	21	28
6.63	21	68	43	38	59	62	37	41	30	58
80	20	47	37	20	47	47	42	35	32	48
82	20	41	29	23	43	46	48	25	28	48
92	22	47	33	26	28	69	51	41	21	45
93	16	34	31	17	42	34	30	28	24	42
3.80	22	72	54	63	49	51	47	49	55	59
82	25	79	69	32	59	89	78	33	30	46
92	22	44	71	30	30	71	54	54	41	49
93	17	58	43	26	43	60	38	58	19	25
0.82	16	46	51	35	55	47	35	49	43	56
92	21	58	45	22	33	39	65	78	50	59
93	16	60	45	30	35	58	74	48	49	60
2.92	24	74	46	30	25	41	71	62	32	50
93	15	50	46	26	41	50	54	47	20	35
2.93	15	46	35	5	17	35	32	52	22	11

growing season. A similar result, when obtained with the parents in swards (Knight, 1961) had been attributed to increased competition as the plants grew larger. If this is the cause, a maximum would or would not occur in an establishment year depending on the sowing or planting density and rapidity of growth. In subsequent years when establishment effects had been lost, the onset of competition would be more uniform. The results were in accordance with this suggestion as the F_1 families showed a maximum in tiller number (μ = 1.69 or 49 tillers) in October of their establishment year and in late June of the second year (μ = 1.71 or 51 tillers). The parents, in the study mentioned above, showed no peak in numbers during their establishment year but rose at all harvests (to μ = 1.30 or 20 tillers) whereas in the second year a maximum value (μ = 1.59 or 39 tillers) was obtained in late June and early July. Among the F_1 families an increase in μ occurred between the penultimate and last harvest. This may have resulted from a reduction in competition as the tops dried off following reproduction and from the unseasonal rain of 2.33 inches on November 12. Values of μ only provide an overall picture and individual families showed deviations around this average behaviour because of their different rates of growth.

The diallel mean squares, and the g.c.a. effects are presented in tables 32 and 33.

The g.c.a. mean square was significant at the 0.1% level on each occasion. Beneath the table of g.c.a. effects the parents have been arranged in ascending order of g.c.a. and Duncan's (1955) test applied. To show how the g.c.a effects change with time a graph of μ + 2gi was plotted against harvest date (Fig. 13). It indicated that some parents

Table 32.

Combining ability mean squares for tiller number at successive harvests for two seasons

	D.F.	Sep. 11	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
g.c.a.	6	.0157***	.0625***	.0794***	.0772***	.0464***	.0882***	.0930***	.0561***	.0587***	.0530***
s.c.a.	14	.0036*	.0042*	.0028*	.0105	.0050	.0036	.0102	.0042	.0044	.0036*
Error	> 250	.0016	.0020	.0014	.0088	.0055	.0069	.0107	.0066	.0059	.0019

Table 33.

Estimates of the g.c.a. effects for tiller number at successive harvests (estimates are x 1,000) and the general mean μ

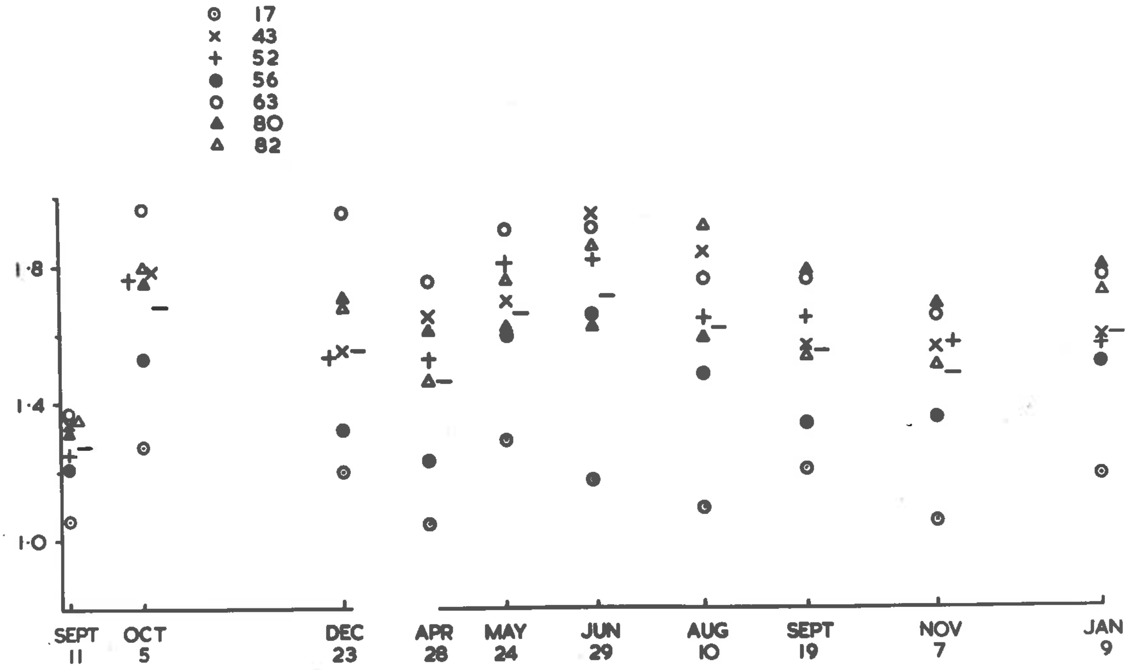
	Sep. 11	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
17	-109	-208	-183	-211	-189	-268	-261	-170	-214	-201
43	34	42	- 5	88	18	117	114	11	40	- 1
52	- 4	22	- 14	28	79	52	13	48	43	- 10
56	- 34	- 80	-122	-118	- 33	- 29	- 67	-104	- 65	- 38
63	50	139	195	143	98	98	70	108	84	87
80	18	34	71	73	- 19	- 44	- 14	116	99	101
82	44	51	59	- 4	46	74	148	- 9	12	60
μ	1.274	1.687	1.561	1.469	1.660	1.709	1.611	1.540	1.475	1.583

Significant differences between parents as judged by the value of gi.
Parents underscored by the same line are not significantly different. Level of significance used 5%.

Sep. 11 17 56 52 80 43 82 63
Oct. 5 17 56 52 80 43 82 63
Dec. 23 17 56 52 43 82 80 63
Apr. 28 17 56 82 52 80 43 63
May 24 17 56 80 43 82 52 63
June 29 17 80 56 52 82 63 43

Aug. 10 17 56 80 52 63 43 82
Sep. 19 17 56 82 43 52 63 80
Nov. 7 17 56 82 43 52 63 80
Jan. 9 17 56 52 43 82 63 80

Fig. 13. The combining ability values $\mu + 2gi$ for tiller number of each Mediterranean parent plotted against harvest occasion. The graph illustrates that values rose to a maximum and then declined in each year. Assessment by Mediterranean diallel test.



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have a tendency to be either high in g.c.a. (parent 63) or low (parent 17) but that the majority did not consistently belong to either category. This occurs because the g.c.a. for each parent moved to a maximum value during the second year and as these maxima did not coincide in time the parents show changes, at one time of the year being relatively high, at another, low. This was therefore quite a different situation from the characters previously considered.

At the reproductive harvests the analysis of the sterile and fertile tiller number (tables 34 and 35) shows clearly the different contribution being made by the parents to these components of total tiller number. The contributions are very consistent as is evident from the graph of $\mu + 2gi$ (Fig. 14) where a similar ranking occurs at each harvest for either one of the components. One exception was parent 63 which developed a relatively greater fertile component in the second year. The components were not as strongly correlated in a negative way as were the top weights, and a parent such as 17 had both low, sterile and fertile tiller numbers.

The sc.a. mean squares were significant at four harvests. In none of them was the mean square very large and because there was very little consistency in the effects, they will not be discussed.

Turning attention to the comparison of the means of Mediterran, Mediterran x Northern European and Northern European families several points may be noted from Table 36. The means behave in a manner already noted for the Mediterranean families, namely to rise to a maximum and then decline. This is most clearly expressed in the second year where the Mediterranean mean reached a maximum by June 29 whereas Mediterranean

Table 34.

Combining ability mean squares for sterile and fertile components of tiller number at harvests of the reproductive phase (Med. diallel)

		Dec. 23		Nov. 7		Jan. 9	
		Ster.	Fert.	Ster.	Fert.	Ster.	Fert.
g.c.a.	6	.1363***	.0350***	.1904***	.0344***	.0989***	.0384***
s.c.a.	14	.0040	.0102**	.0144*	.0033	.0126*	.0096**
error	>250	.0027	.0035	.0079	.0080	.0057	.0035

Table 35.

Estimates of the g.c.a. effects for the sterile and fertile components of tiller number (estimates are x 1000) and the general mean μ

	Dec. 23		Nov. 7		Jan. 9	
	Ster.	Fert.	Ster.	Fert.	Ster.	Fert.
17	-209	- 67	-356	-120	-270	-101
43	- 14	65	113	- 39	56	- 73
52	- 35	23	76	14	25	- 26
56	-171	30	-168	23	- 71	36
63	278	-133	214	7	152	4
80	65	115	35	152	- 9	169
82	87	- 33	87	- 37	118	- 9
μ	1.424	.911	1.097	1.176	1.246	1.242

Dec. 23	Ster.	17	56	52	43	80	82	63
	Fert.	63	17	82	52	56	43	80
Nov. 7	Ster.	17	56	80	52	82	43	63
	Fert.	17	43	82	63	52	56	80
Jan. 9	Ster.	17	56	80	52	43	82	63
	Fert.	17	43	52	82	63	56	80

Fig. 14. The combining ability values $\mu + 2gi$ for the number of sterile, fertile and total tillers for the Mediterranean parents, at harvests of the reproductive phase. Assessment by Mediterranean diallel test.

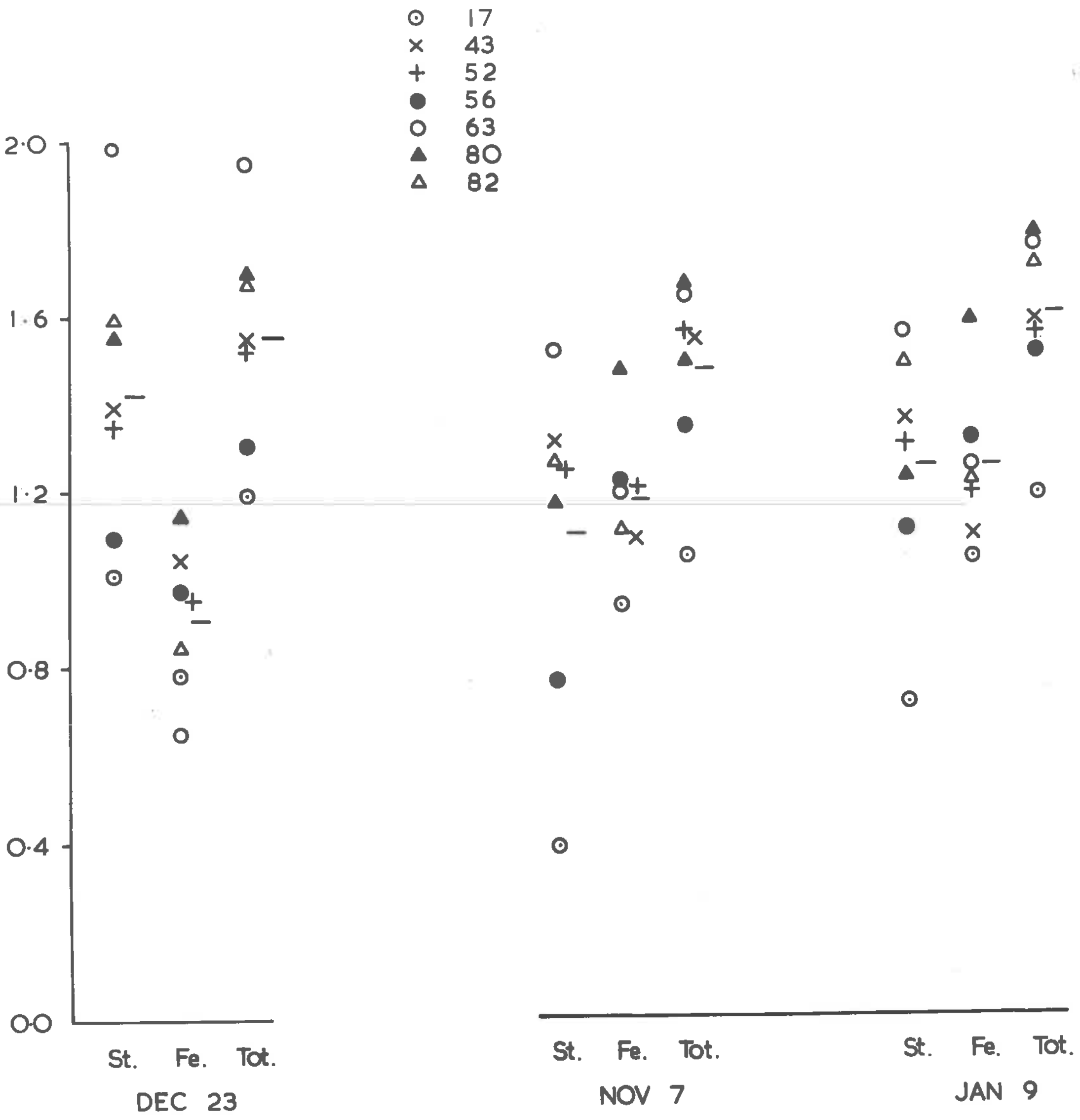
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Table 36.

Values of the mean μ for tiller number of Med., Med. x N.E. and N.E. families

	Sep. 11	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
Med.	1.274	1.687	1.561	1.469	1.660	1.709	1.611	1.540	1.475	1.583
			xxx	xxx	xxx	x		xxx		
Med. x N.E.	1.253	1.679	1.608	1.353 xxx	1.532 xxx	1.646	1.626	1.675 x	1.459	1.582 xxx
				xxx	xxx					xxx
N.E.	1.192	1.657	1.549	.721	1.216	1.543	1.514	1.719	1.347	1.046

Values of the mean μ for components of tiller number at harvests of the reproductive phase

	Dec. 23		Nov. 7		Jan. 9	
	Ster.	Fert.	Ster.	Fert.	Ster.	Fert.
Med.	1.424	.911	1.097	1.176	1.246	1.242
	xxx	xxx	xxx	xxx	xxx	xxx
Med. x N.E.	1.532 x	.676 xxx	1.233 xxx	.988 xxx	1.352 xxx	1.112 xxx
		xxx		xxx	xxx	xxx
N.E.	1.518	.331	1.289	.561	.993	.150

x Northern European and Northern European groups being slower to tiller at regeneration from the summer and showing a mid winter pause did not reach a maximum until September. The maxima were very similar 1.71, 1.68 and 1.72 respectively. Evidently the groups were showing a similar effect, differing only in their timing,

In the topcross analysis the Northern European parents differed significantly at a few harvests while the Mediterranean parents showed a very highly significant variation at all but one harvest (Tables 37 & 38). Thus the great variation for tiller number already noted in the diallel was maintained. Once again a major difference between the diallel and topcross performance was the midwinter decline showed by parents 52 and 63, and this effect superimposed on a curve rising to a maximum results in an erratic curve for these parents (Fig. 15).

Several interesting differences were found in the component analysis. Mention has already been made of the fact that the Northern European parents were later heading and on average less fertile than the Mediterranean parents. This was also evident for the progenies in which there was a progressively smaller fertile tiller number for Mediterranean, Mediterranean x Northern European and Northern European families respectively. Within the Northern European group Parent 93 was less fertile than parent 92 but among the topcross progenies this was mainly evident in the establishment year (Tables 39 & 40). However, there was strong evidence of interaction in both years parent 63 in combination with 92 having a near average number of fertile tillers but extremely low number in combination with 93.

Table 37.

Combining ability mean squares for tiller number at successive harvests for two seasons (Med. x N.E. topcross)

	D.F.	Sep. 11	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
Between N.E. g.c.a.	1	.0518***	.0105	.0058*	.0026	.0504**	.0002	.0122	.0199	.0180	.0027
" Med. g.c.a.	6	.0092***	.0163	.0237***	.0438***	.0107	.0357***	.0680***	.0362***	.0561***	.0546***
Interaction s.c.a.	6	.0015	.0055	.0049**	.0109	.0060	.0143	.0069	.0097	.0207**	.0117***
Error	> 250	.0016	.0020	.0014	.0088	.0055	.0069	.0107	.0066	.0059	.0019

Table 38.

Estimates of the g.c.a. effects for total tiller number at harvests of Med. x N.E. topcross (estimates are x 1000 for clearer presentation) and the mean μ

	Sep. 11	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
17	-137	-141	-169	-268	-133	-263	-260	-231	-213	-268
43	72	-33	85	161	43	61	112	119	220	164
52	- 29	33	- 42	-109	106	- 53	-221	31	- 52	-145
56	20	- 79	-104	- 28	4	40	- 37	-143	-110	53
63	33	22	133	87	15	168	29	72	- 17	- 40
80	15	92	43	58	- 4	38	213	112	236	193
82	30	107	54	100	- 30	10	166	41	- 60	47
92	- 61	- 27	- 20	15	60	4	- 30	- 38	- 36	- 14
93	61	28	21	- 14	- 60	- 3	29	38	36	14
μ	1.253	1.679	1.608	1.353	1.532	1.646	1.626	1.675	1.459	1.582

Significant differences between parents as judged by values of gi. Parents underscored by the same line are not different at 5% level.

Sep. 11 17 52 80 56 82 63 43
Oct. 5 17 56 43 63 52 80 82
Dec. 23 17 56 52 80 82 43 63
Apr. 28 17 52 56 80 63 82 43
May 24 17 82 80 56 63 43 52
June 29 17 52 82 80 56 43 63

Aug. 10 17 52 56 63 43 82 80
Sep. 19 17 56 52 82 63 80 43
Nov. 7 17 56 63 52 82 43 80
Jan. 9 17 52 63 82 56 43 80

Fig. 15. The combining ability values $\mu + 2gi$ for tiller number of each Mediterranean parent when crossed to Northern European parents. Erratic curves are shown by parents 52 and 63 in this assessment due to winter dormancy of their progenies. This also influences μ.

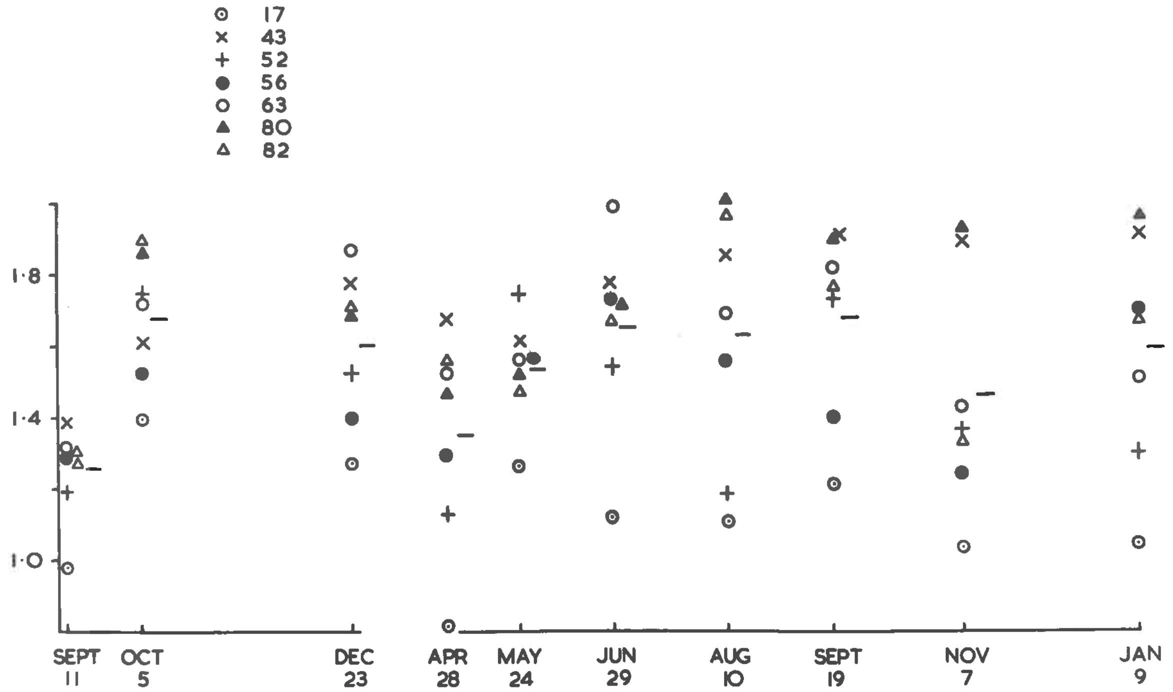

⊙ 17
× 43
+ 52
● 56
○ 63
▲ 80
△ 82
1·8
1·4
1·0
SEPT 11
OCT 5
DEC 23
APR 28
MAY 24
JUN 29
AUG 10
SEPT 19
NOV 7
JAN 9

Table 39.

Combining ability, mean squares for sterile and fertile components of tiller number at harvests of the reproductive phase (Med. x N.E. topcross)

		Dec. 23		Nov. 7		Jan. 9	
	D.F.	Ster.	Fert.	Ster.	Fert.	Ster.	Fert.
Between N.E. g.c.a.	1	.0010	.1414***	.0000	.0329*	.0014	.0106***
Between Med. g.c.a.	6	.0306***	.0946***	.1025***	.0795***	.0573***	.0857***
Interaction s.c.a.	6	.0047	.0172***	.0290**	.0408***	.0161*	.0474
Error	>250	.0027	.0035	.0079	.0080	.0057	.0035

Table 40.

Estimates of the g.c.a. effects for the sterile and fertile components of tiller number (effects x 1000) and the mean μ

	Dec. 23		Nov. 7		Jan. 9	
	Ster.	Fert.	Ster.	Fert.	Ster.	Fert.
17	-166	-211	-303	- 40	-311	-208
43	64	127	212	291	193	55
52	- 37	107	36	-133	-108	-168
56	-136	152	-273	59	- 5	177
63	187	-346	200	-297	42	-249
80	21	252	218	193	150	270
82	71	- 77	- 88	- 73	42	127
92	9	100	0	49	10	28
93	- 9	-100	0 0	- 49	- 10	- 28
μ	1.532	.676	1.233	.988	1.352	1.112

Dec.23	Ster.	17 56 52 80 43 82 63	Fert.	63 17 82 52 43 56 80
Nov. 7	Ster.	17 56 82 52 63 43 80	Fert.	63 52 17 82 56 80 43
Jan. 9	Ster.	17 52 56 82 63 80 43	Fert.	63 17 52 43 82 56 80

In the topcross, as was found in the diallel, there was not a strong negative association between components and some families had both few fertile and sterile tillers while other families had many (Fig. 16).

Throughout the results it has been found that parents and their progenies were characteristic in their tiller number, the extremes having consistently high or low numbers. It is then understandable that the diallel and topcross should give similar assessments of the parents and at eight of the ten harvests there was a significant correlation between the two sets of gi values. One of the harvests at which assessments differed was understandably the mid winter harvest of Aug. 10.

The seasonal variation in tiller number although evident in both assessments was not sufficiently similar to lead to correlations for individual parents over harvests.

Little need be said about the parents as clones as there were no striking differences from the diallel and topcross assessments not already noted in the previous analyses. The parents themselves (Fig. 17) did not show the winter decline shown by progenies of parents 52 and 63 when crossed to Northern Europeans, and parent 80 which was very poor as a clone after the summer showed up much more favourably in the crosses.

Discussion of tiller number

The results have shown that there were large differences in tiller number between parents, and between progenies, the variation exceeding that found for top weight, stubble weight or root weight. At many harvests in both tests the tiller number mean squares were significant

Fig. 16. The combining ability values $\mu + 2$ gi for the number of sterile, fertile and total tillers for the Mediterranean parents when crossed to Northern European parents at harvests of reproductive phase.

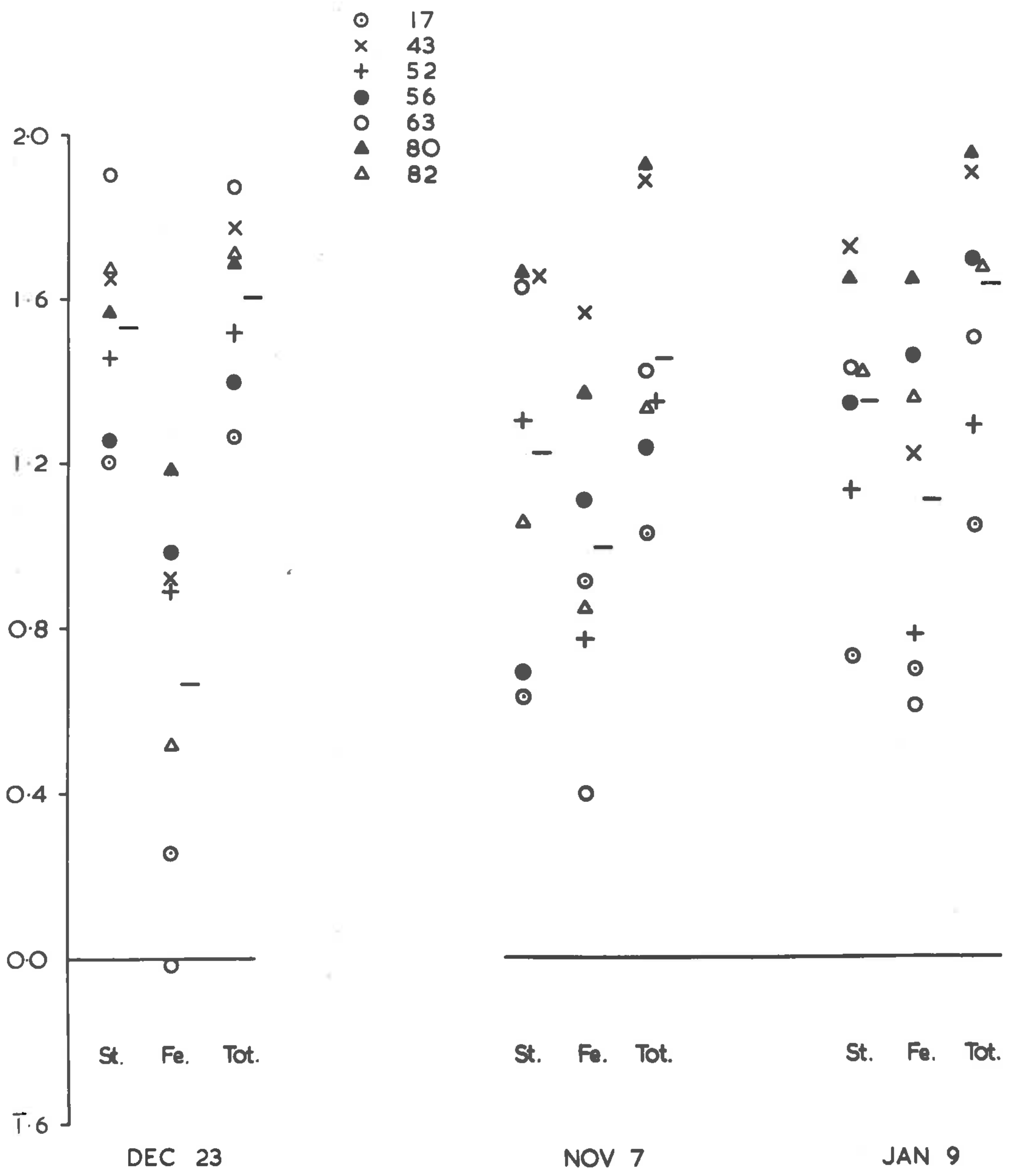
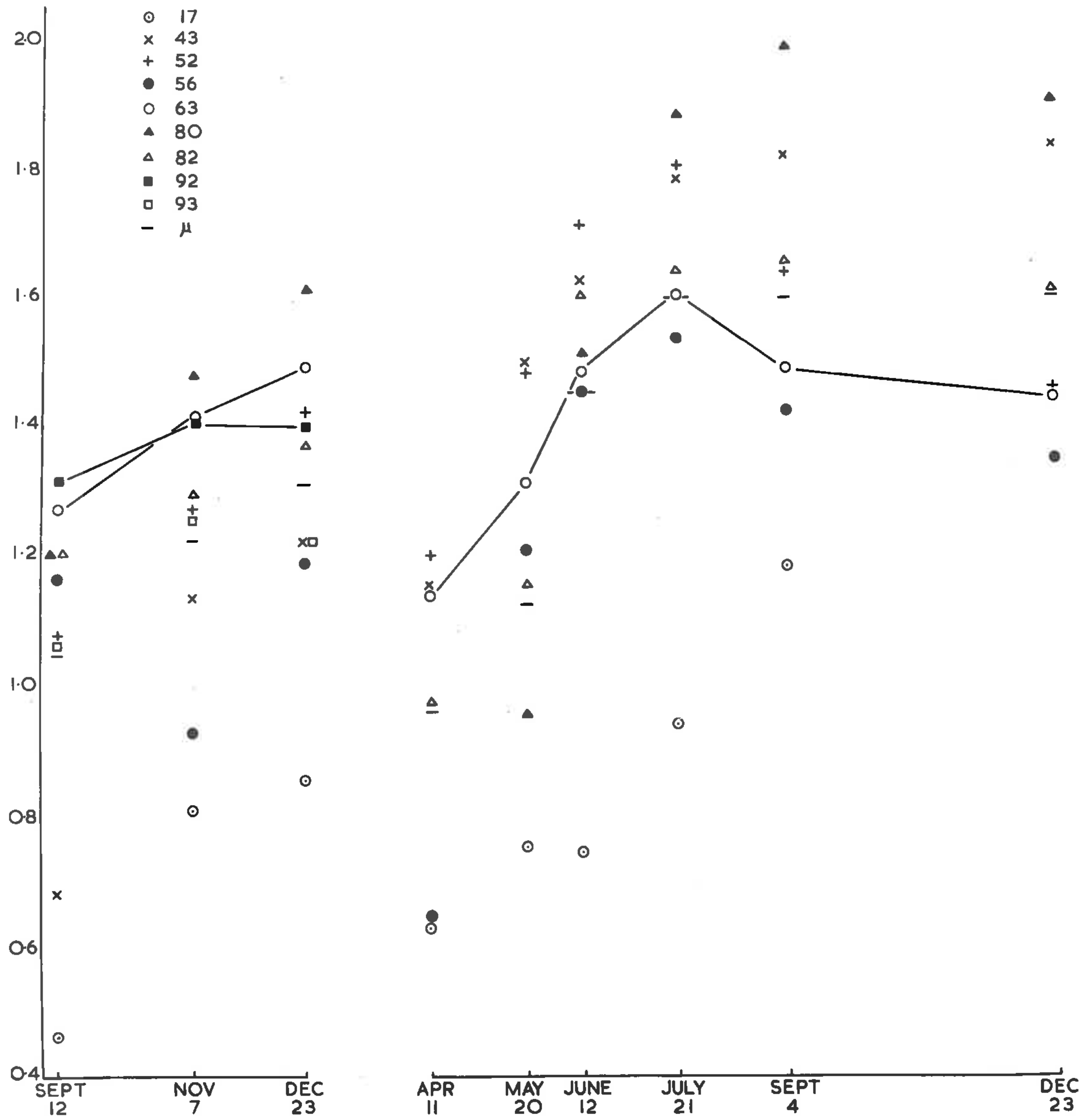

⊙ 17
× 43
+ 52
● 56
○ 63
▲ 80
△ 82
2·0
1·6
1·2
0·8
0·4
0·0
$\bar{1}$·6
St.
Fe.
Tot.
St.
Fe.
Tot.
St.
Fe.
Tot.
DEC 23
NOV 7
JAN 9

Fig. 17. The tiller number per plant of the parents as clones expressed as a logarithm and plotted against harvest occasion. Values for parents 63 and 92 have been connected to show seasonal variation. No values were obtainable for 92 after the summer.


⊙ 17
× 43
+ 52
● 56
○ 63
▲ 80
△ 82
■ 92
□ 93
– μ
2·0
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
SEPT 12
NOV 7
DEC 23
APR 11
MAY 20
JUNE 12
JULY 21
SEPT 4
DEC 23

even when the top weights were not, indicating that similar yields were obtained from genotypes having very different tiller numbers. Evidently tiller weights compensated in this situation and some genotypes had many small tillers, others few large tillers.

Selection for tiller number, either high or low expression would be simple with the present variation. This point is stressed for even if tiller numbers are not related to yield and selection for them will not be practised in the present breeding programme, they may be important if the breeding programme changes its emphasis. Of the characters so far considered this is the only one in which the different testers gave a similar result.

Single tiller weights

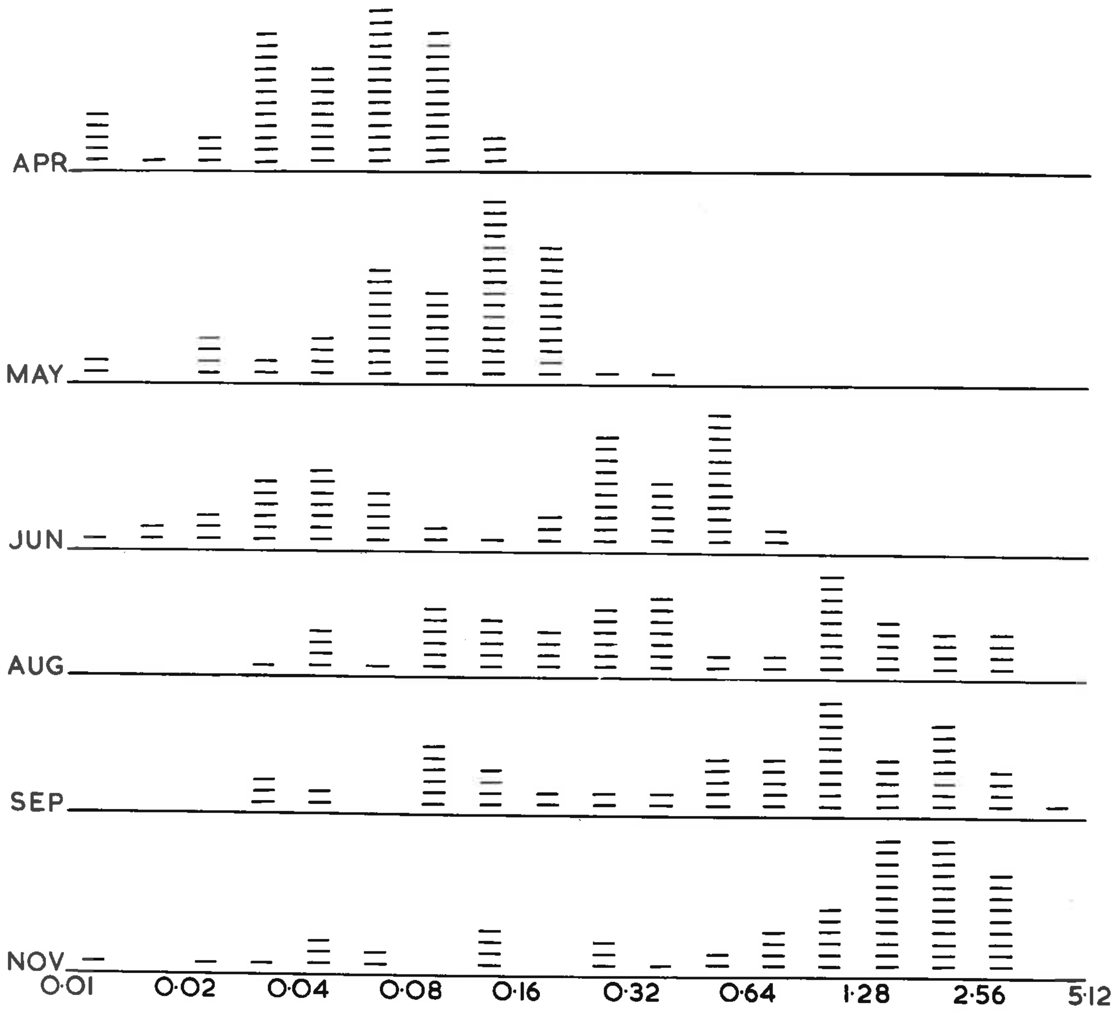
It has already been noted that families having the same top weight could have very different tiller numbers and in these circumstances tiller weights must have been compensating.

The mean weight of a tiller may be calculated by dividing a plants' weight by its tiller number or by taking a sample of tillers, obtaining their individual weights, and then calculating a mean. The latter method is to be preferred in that in addition to the mean the distribution of weights is determined. This distribution when obtained over several harvests may show when tillering has begun or ceased by the presence or absence of very light tillers and when the differentiation begins of the heavier fertile tillers from the lighter sterile tillers. The distribution, as indicated by the within family error, increases sharply at this differentiation.

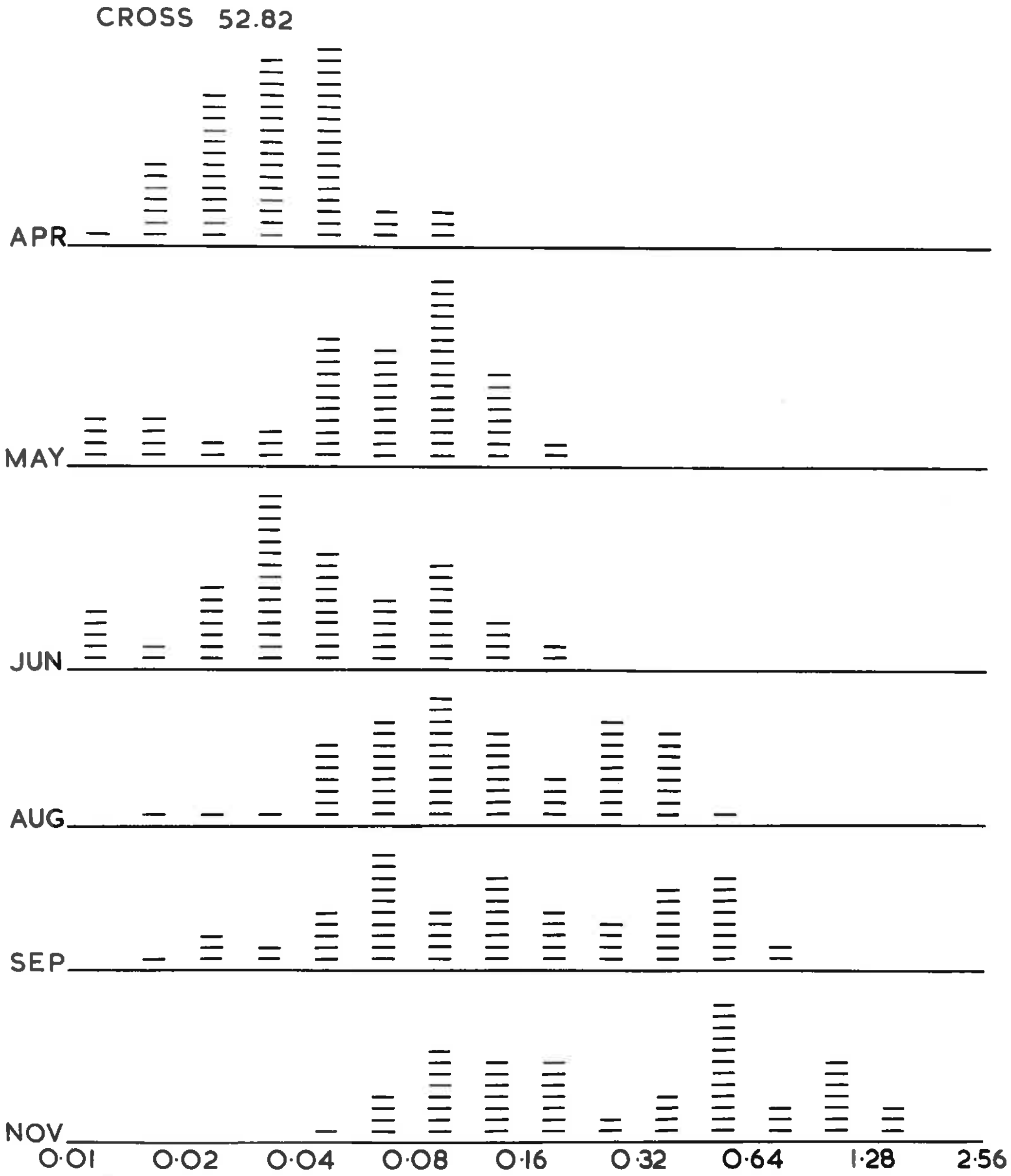
The weights of 30 tillers were obtained for each family at the harvests of the second year. These weights were transformed to logarithms and the family mean (Table 41) and error calculated. At the January harvest when the sterile and fertile tillers formed two almost discontinuous distributions separate means and errors were obtained for these two components. At the November harvest not all families had sufficient fertile tillers differentiated to make these separate analyses although errors were very large by this time.

Tiller weight distributions for the individual families were plotted, of which representative examples are presented in Fig. 18-21. The histogram for the cross between Mediterranean parents 17x56 showed a normal distribution for April and May while new tillers were being formed, followed in June by a bimodal distribution resulting from the differentiation of the reproductive tillers. In Aug. and Sept. there was a progressive development of these tillers but no evidence of many new small tillers. In the cross 52x82 also between Mediterranean parents, newtillers were evident in both May and June but reproductive tillers were not evident until August. Again there were no new tillers in Aug., Sept. or Nov. The histograms for the Mediterranean x Northern European family 17x92 illustrate a difference that was characteristic of the hybrids between the groups, it was the large size of the fully grown tillers in April. This was also shown by the purely Northern European family 92x93 This family being one of the latest in entering the reproductive phase did not have reproductive tillers until September. The histograms for the other families were interpreted in a similar way. In general the demarcation of the reproductive from vegetative tillers was at a weight

Figs. 18 - 21. Histograms of tiller weight (mg) on a logarithmic scale of four families, 17 x 56, 17 x 92, 52 x 82 and 92 x 93, illustrating the differentiation of heavy reproductive tillers.

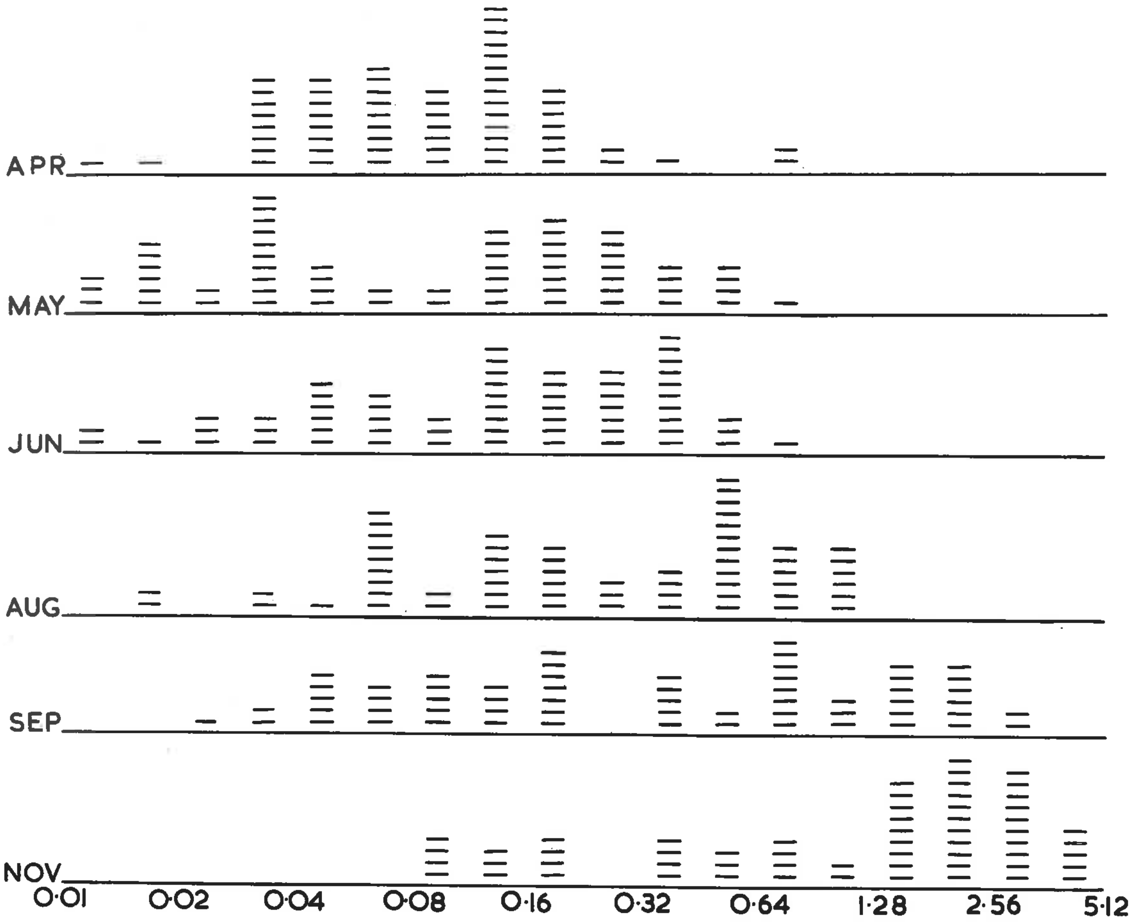


CROSS 17.56



CROSS 52.82
APR
MAY
JUN
AUG
SEP
NOV
0·01
0·02
0·04
0·08
0·16
0·32
0·64
1·28
2·56

CROSS 17.92



CROSS 92.93

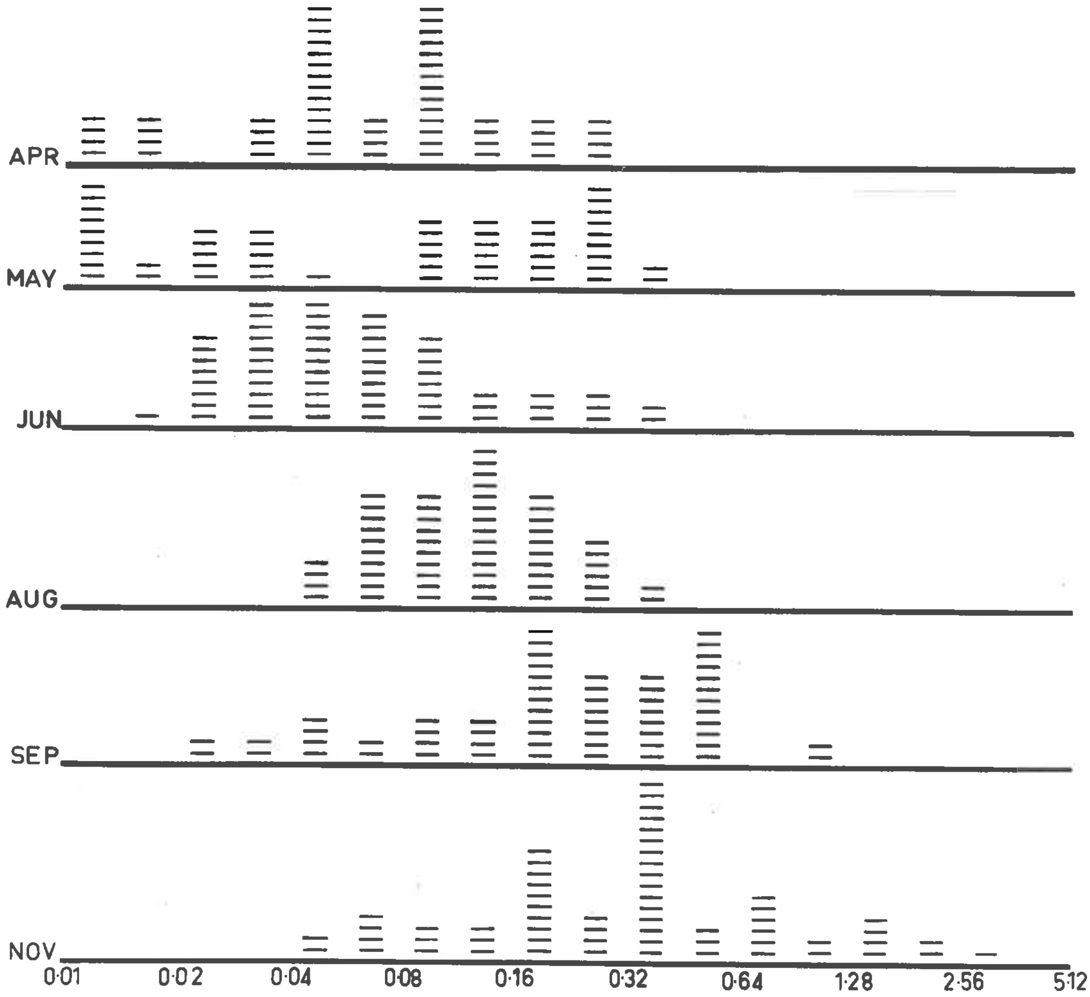


Table 41.

Geometric mean for weight of a tiller in gm. for harvests of the second year

	Apr. 28	May 24	June 29	Aug. 10	Sept. 19	Nov. 7	Jan. 9 Ster.	Jan. 9 Fert.
17.43	.052	.088	.122	.190	.514	1.210	.080	1.824
.52	.064	.083	.106	.214	.454	.646	.113	2.547
.56	.051	.095	.136	.404	.520	.807	.094	1.910
.63	.064	.062	.137	.403	.570	.506	.152	1.811
.80	.061	.124	.247	.415	.841	.935	.076	2.114
.82	.068	.094	.107	.175	.330	.757	.102	.213
.92	.078	.089	.127	.235	.317	1.070	.097	1.538
.93	.095	.101	.090	.337	.234	.631	.216	2.535
43.52	.041	.037	.042	.114	.176	.174	.061	.568
.56	.029	.055	.089	.163	.454	.443	.060	1.156
.63	.029	.066	.062	.177	.242	.155	.112	.551
.80	.026	.041	.114	.205	.346	.172	.043	.719
.82	.029	.058	.045	.132	.322	.142	.052	.759
.92	.132	.030	.055	.074	.267	.259	.085	.804
.93	.068	.064	.071	.057	.254	.337	.060	.804
52.56	.052	.079	.141	.372	.467	.395	.079	1.072
.63	.057	.073	.083	.127	.240	.174	.146	1.026
.80	.119	.066	.057	.208	.248	.305	.053	.900
.82	.034	.058	.051	.125	.145	.245	.134	1.109
.92	.068	.054	.077	.048	.234	.279	.100	1.259
.93	.070	.083	.112	.126	.206	.290	.159	1.125
56.63	.035	.089	.106	.264	.384	.401	.149	.959
.80	.033	.085	.131	.282	.308	.377	.049	.957
.82	.050	.075	.069	.128	.202	.207	.089	1.265
.92	.114	.103	.096	.166	.263	.513	.109	1.340
.93	.098	.074	.123	.191	.762	.481	.111	1.472
63.80	.045	.069	.076	.185	.313	.286	.085	.625
.82	.052	.080	.047	.090	.173	.211	.105	.855
.92	.076	.111	.087	.112	.227	.411	.232	1.143
.93	.081	.078	.093	.050	.172	.406	.281	1.503
80.82	.035	.050	.062	.090	.234	.230	.105	.687
.92	.056	.053	.094	.192	.276	.259	.047	1.104
.93	.056	.065	.060	.133	.144	.202	.137	.689
82.92	.060	.099	.046	.141	.179	.354	.128	1.030
.93	.140	.107	.065	.066	.190	.286	.199	.955
92.93	.064	.065	.065	.129	.187	.352	.240	1.170

of between 0.16 - 0.32 gm. The main features in which the histograms differed between families were in the magnitude and timing of the flush of new tillers, the timing of the differentiation of reproductive tillers and the occurrence of large tillers in April.

These differences in growth phase lead at any one time to a heterogenity between families of their errors, as calculated from the within family variability, even though the data were transformed to logarithms. It was therefore considered that to derive a pooled error from the within-family variability would contravene the condition of homogeneity of variance for the analysis, and an error based on reciprocal differences would be more valid. Such an error has been used throughout this section of results.

The combining ability analysis of the diallel population showed that the g.c.a. mean square was significant at most harvests (table 42 & 43) and Fig. 22 illustrates that the g.c.a. effects were most consistent in their differences. Some of the parents (17, 43, 56, 80) showed a linear increase in their effects parallel to the mean for most of the growing season whereas others (52, 63, 82) showed a drop between May and June. The histograms 17 x 56 and 52 x 82 illustrated why these differences occurred. Crosses such as 52 x 82 continued to have only vegetative tillers until Aug. whereas in crosses such as 17 x 56 fertile tillers had begun development by June. This led to differences between families in tiller weight and to some parents having a relatively lower combining ability for the June harvest. Parent 82 was outstanding in this regard, the presence of many small new tillers and the late

Table 42.

Combining ability mean squares for tiller weight (Med. diallel)

	D.F.	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9 Ster.	Jan. 9 Fert.
g.c.a.	6	.0539*	.0314	.1068***	.1079**	.0974**	.2179***	.0723	.1219***
s.c.a.	14	.0148	.0091	.0125	.0149	.0128	.0176	.0086	.0060
Error	36	.0194	.0229	.0131	.0267	.0228	.0354	.0349	.0068

Table 43.

Estimates of the g.c.a. effects for tiller weight in Med. diallel (estimates are x 1000) and the mean μ

	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9 Ster.	Jan. 9 Fert.
17	141	125	233	201	245	433	77	325
43	-167	-124	- 98	- 90	- 3	-128	-150	-136
52	110	- 46	- 92	- 40	-110	- 86	27	- 7
56	- 60	60	115	138	72	91	- 32	41
63	- 2	19	- 41	- 16	- 44	-135	180	-103
80	11	- 15	71	48	31	- 21	-148	- 97
82	- 33	- 19	-189	-241	-191	-154	46	- 22
μ	.658	.845	.940	1.280	1.510	1.532	.936	2.039

Apr. 28 43 56 82 63 80 52 17

May 24 43 52 82 80 63 56 17

June 29 82 43 52 63 80 56 17

Aug. 10 82 43 52 63 80 56 17

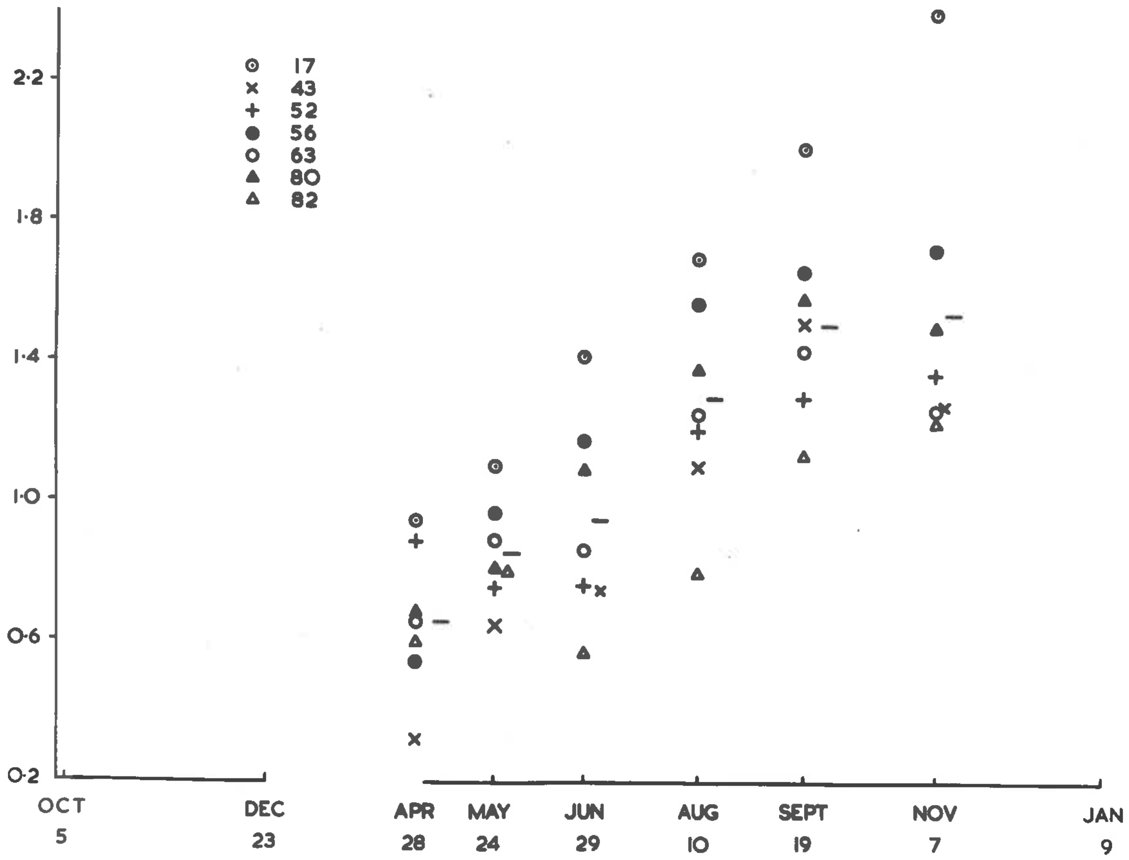
Sep. 19 82 52 63 43 80 56 17

Nov. 7 82 63 43 52 80 56 17

Jan. 9 St. 43 80 56 52 82 17 63

Jan. 9 Fe. 43 63 80 82 52 56 17

Fig. 22. The combining ability values $\mu + 2g_i$ for tiller weight of each Mediterranean parent plotted against harvest occasion. Assessment by Mediterranean diallel test.


⊙ 17
× 43
+ 52
● 56
○ 63
▲ 80
△ 82
2·2
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OCT 5
DEC 23
APR 28
MAY 24
JUN 29
AUG 10
SEPT 19
NOV 7
JAN 9

development of the reproductive tillers lead to an actual decline in average tiller weight.

Clear cut differences in tiller weight were also shown in the contrast between Mediterranean, Mediterranean x Northern European and Northern European families (Table 44). The Mediterranean families had much smaller tillers than either Mediterranean x Northern European or Northern European families in April when regenerating from dormancy, but their average tiller size increased almost linearly from April to Sept. firstly with the increase in size following regeneration and then with the development of fertile tillers. The Mediterranean x Northern European and Northern European families initially with large tillers showed no increase in tiller weight until Aug. by which time the Mediterranean families had reached and surpassed them. By Nov., with the further late development of the Mediterranean x Northern European and Northern European families, the three groups were once again similar. This similarity in mean was due to the overriding effect of the fertile tillers for as the last harvest showed the sterile tillers still showed significant differences, with the Northern European families again having the largest sterile tillers.

Large sterile tillers in January may be accounted for by an effect noted by Stuckey (1942) and commonly observed in Northern European material of Dactylis when grown under long days. Under these conditions large tillers are developed. If tiller weights in this experiment were solely a reflection of daylength, then large tillers should also have been evident in April and May, and smaller tillers in June. This was only

Table 44.

Values of the mean μ for tiller weight in Med., Med. x N.E. and N.E. families

	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9 Ster.	Jan. 9 Fert.
Med.	.658	.845	.940	1.280	1.510	1.532	0.936	2.039
	xxx	x		xxx	xxx		xxx	
Med. x N.E.	.910 x	.912	.914 x	1.104 x	1.386 xx	1.572	1.096 xxx	2.068
							xx	
N.E.	.803	.815	.810	1.110	1.271	1.547	1.380	2.068

Table 45.

Combining ability mean square for tiller weight in Med. x N.E. topcross

	D.F.	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9 Ster.	Jan. 9 Fert.
N.E. g.c.a.	1	.0015	.0563	.0034	.0018	.0011	.0080	.0950	.0006
Med. g.c.a.	6	.0173	.0155	.0265	.1145*	.0352	.0688	.0706	.0390***
Inter. s.c.a.	6	.0192	.0548*	.0108	.0325	.0273	.0061	.0215	.0088
Error	36	.0194	.0229	.0131	.0267	.0228	.0354	.0349	.0068

partly evident in the 92x93 histogram. Tiller weights were not large in April because they were regrowing following the summer. They were quite large in May but simultaneously a flush of new tillers had developed so that the average tiller weights were not large for either of these two months, and any trend in mean weight that might have followed daylength was masked.

The topcross analysis of the Mediterranean x Northern European families did not reveal many significant differences in combining ability (Table 45). At no time did the Northern European parents differ in their combining ability. The Mediterranean parents were significantly different at Aug. 10 when their combining abilities agreed with the diallel assessment, 17, 56 being high 43, 52, 63 low, but with the exception that parent 82 exceeded the mean in this test. In Jan. when the combining ability of Mediterranean parents were again different for fertile tillers, there was good agreement between topcross and diallel, except that parent 63 was better in the topcross.

The picture of tiller development provided by the histograms complements that already obtained from the analysis of the tiller numbers. In particular they illustrate that when numbers decreased between Aug. and Nov. two processes were involved, one being the lack of formation of new tillers, the other the loss of existing tillers.

Tiller length

In the second year an estimate of the depth of the sward was obtained for each family as this could be a factor leading to high yields.

The physiological reasons for this suggestion will be discussed later. The depth was measured as an average tiller length for each plant, the distance between the ground and the top of the canopy, and was therefore a somewhat subjective determination.

Data on tiller length were transformed to logarithms and analysed in a similar manner to the other characters. The antilogarithm for each family is given in table 46. Combining ability mean squares for the Mediterranean diallel are presented in table 47, g.c.a. effects in table 48 and a graph of these effects in fig. 23. It might be expected that tiller length and tiller weight previously considered would show similarities but this was not exact as may be seen by comparing figs. 22 and 23. One example is parent 17 which consistently passed on to its progeny the ability to produce heavier tillers, but these were often shorter tillers than the progeny of parent 56.

Parent 82 was again extreme in its behaviour. Families in which 82 was a parent did not show an actual decline in average tiller length as had been found for tiller weight but the absence of an increase in length when all the other families were increasing led to its fall in combining ability. The other parents exhibited a constant increase in length and little variability following regeneration until Aug. and Sept. when the effect of the difference between parents in internode elongation was at a maximum. By Nov. when all families had elongated reproductive tillers this variability again declined.

The s.c.a. mean square was significant at several harvests but the effects were not constant and a cross such as 17 x 56 might be

Table 46.

Geometric mean for tiller length in each family (in cm.)

	Apr. 28	May 24	June 29	Aug. 10	Sept. 19	Nov. 7
17.43	14.8	15.8	26.9	46.8	47.9	61.7
52	14.5	13.5	20.0	23.4	38.0	66.1
56	9.8	12.0	27.5	45.7	54.0	77.6
63	10.5	15.1	21.9	36.3	40.7	58.9
80	14.1	20.0	24.5	45.7	51.3	46.8
82	13.8	15.8	17.8	39.8	58.9	63.1
92	12.0	19.5	19.5	38.0	38.9	44.7
93	14.8	17.8	20.4	33.9	38.9	58.9
43.52	14.8	14.1	17.0	33.9	38.0	57.5
56	12.9	17.0	20.9	47.9	51.3	49.0
63	9.3	14.1	22.9	30.2	32.4	39.8
80	11.5	14.8	28.8	40.7	45.7	45.7
82	9.5	8.5	13.8	31.6	22.4	61.7
92	16.6	8.5	20.9	20.4	31.6	34.7
93	14.1	14.8	19.5	28.2	33.9	52.5
52.56	14.1	15.5	24.5	46.8	35.5	61.7
63	12.6	12.9	24.0	33.9	25.1	45.7
80	10.0	12.9	19.1	39.8	38.0	51.3
82	7.6	12.0	18.6	26.3	33.9	61.7
92	13.8	7.9	18.2	26.3	23.4	41.7
93	13.5	17.0	20.0	27.5	21.9	38.0
56.63	10.0	17.0	25.1	37.2	41.7	63.1
80	10.5	18.2	27.5	43.7	49.0	67.6
82	12.6	12.6	19.5	28.8	50.1	61.7
92	15.8	18.2	22.4	34.7	45.7	42.7
93	14.1	17.8	22.4	38.9	45.7	49.0
63.80	14.1	18.6	20.0	32.4	39.8	56.2
82	11.5	12.9	11.0	23.4	26.9	38.0
92	10.0	17.0	18.6	15.8	26.9	37.2
93	11.5	15.8	18.2	26.9	24.0	34.7
80.82	10.0	6.6	18.2	33.9	25.7	41.7
92	15.1	12.0	19.5	26.3	31.6	51.3
93	12.0	15.1	21.4	30.9	29.5	46.8
82.92	15.1	15.1	13.5	26.3	32.4	52.5
93	11.0	15.8	16.2	26.3	26.3	39.8
92.93	9.3	13.2	11.0	13.8	17.0	43.7

Table 47.

Combining ability mean squares for tiller length at harvests of the second year (Med. diallel)

	D.F.	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7
g.c.a.	6	.0043	.0180xx	.0230xxx	.0190xxx	.0327xxx	.0122xxx
s.c.a.	14	.0079xxx	.0097x	.0055x	.0052xx	.0074xxx	.0047x
error	> 60	.0020	.0047	.0022	.0016	.0017	.0022

Table 48.

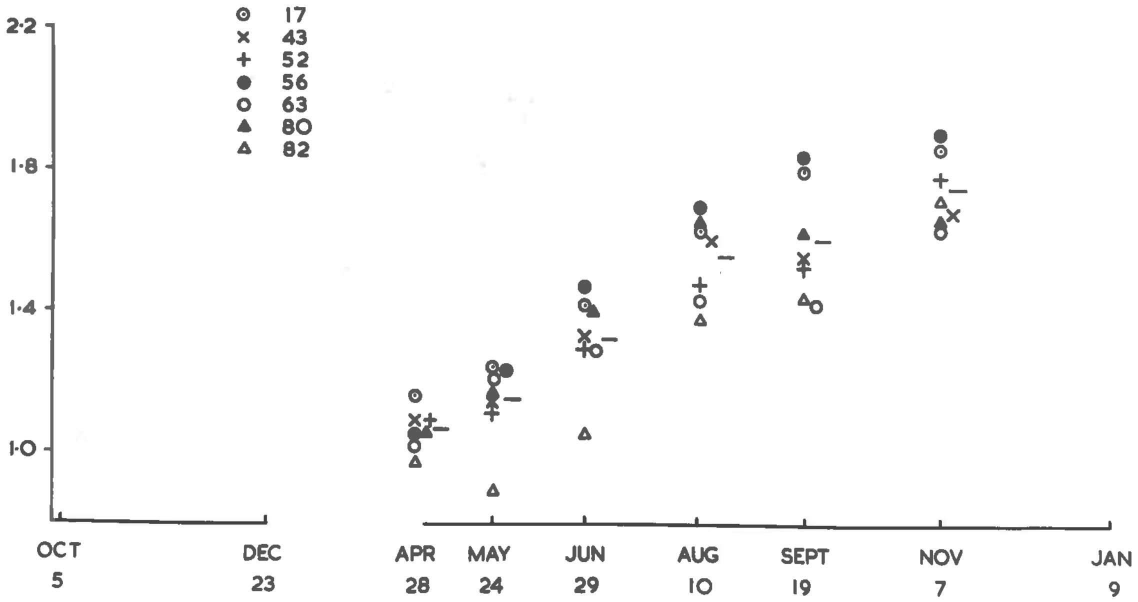
Estimates of the g.c.a. effects for tiller length in the Med. diallel (estimates are x 1000) and the mean μ

	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7
17	47	47	47	40	97	59
43	13	- 5	5	30	-21	-31
52	13	-17	-13	-40	-37	17
56	- 5	47	73	72	119	69
63	-19	39	-19	-60	-85	-57
80	- 3	15	43	46	11	-41
82	-47	-123	-133	-88	-81	-15
μ	1.066	1.143	1.320	1.553	1.600	1.741

Apr. 28 82 63 56 80 52 43 17
May 24 82 52 43 80 63 56 17
June 29 82 63 52 43 80 17 56

Aug. 10 82 63 52 43 17 80 56
Sep. 19 63 82 52 43 80 17 56
Nov. 7 63 80 43 82 52 17 56

Fig. 23. The combining ability values $\mu + 2\,gi$ for tiller length for Mediterranean parents plotted against harvest occasion. Assessment by Mediterranean diallel test.



2·2
1·8
1·4
1·0
⊙ 17
× 43
+ 52
● 56
○ 63
▲ 80
△ 82
OCT 5
DEC 23
APR 28
MAY 24
JUN 29
AUG 10
SEPT 19
NOV 7
JAN 9

significant at two harvests but not at the next. As in the other isolated instances of s.c.a. found in this study this variability could only be utilised under very precise and restricted circumstances.

Mean tiller lengths for the Mediterranean, Mediterranean x Northern European and Northern European families showed many clearly expressed differences (Table 49). They did not entirely conform to those previously found for tiller weight for in April the Northern European families had shorter tillers than the Mediterranean families but these had been found to be heavier. As the season progressed tiller length of the Mediterranean families rapidly increased and already by June exceeded both Mediterranean x Northern European and Northern European families. For this and the next few months the ranking in tiller length was Mediterranean, Mediterranean x Northern European and Northern European respectively. This ranking was most pronounced in Sept. and was only partially lost in Nov. with increase by Mediterranean x Northern European families as they became reproductive. The extent of the variation between the groups in Sept. is not obvious from the data in logarithmic form whereas in fact the swards of the Mediterranean family 17 x 56 for example were three times the height of the Northern European 92x93 swards.

For the winter months a greater variability was expressed by the Mediterranean parents in the topcross than had been found in the diallel. Table 50 contains the combining ability mean squares and table 51 and fig. 24 the g.c.a. effects. As the pure Northern European families had characteristically shorter tillers during the winter the greater variability in the topcross must have been due to differing

Table 49.

Values of the mean μ for tiller length of Med., Med. x N.E. and N.E. families

	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7
Med.	1.066	1.143	1.320	1.553	1.600	1.741
	xxx		x	xxx	xxx	xxx
Med. x N.E.	1.127 x	1.168	1.283 xxx	1.446 xxx	1.496 xxx	1.643 x
	xx		xxx	xxx	xxx	
N.E.	.970	1.120	1.040	1.140	1.230	1.640

Table 50.

Combining ability mean squares for tiller length at harvests of the second year (Med. x N.E. topcross)

	D.F.	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7
Between N.E. (g.c.a.)	1	.0035	.0266*	.0014	.0151**	.0021	.0012
Between Med. (g.c.a.)	6	.0051*	.0155**	.0064 *	.0162***	.0218***	.0057*
Interaction (s.c.a.)	6	.0034	.0103	.0007	.0044*	.0008	.0055*
Error	> 60	.0020	.0047	.0022	.0016	.0017	.0022

Table 51.

Estimates of the g.c.a. effects for tiller length in the Med. x N.E. topcross (estimates are x 1000) and the mean μ

	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7
17	- 2	102	17	109	94	67
43	58	-118	22	- 66	19	-13
52	8	-103	- 3	- 16	-141	-43
56	48	87	67	119	164	17
63	-97	47	-18	-131	-91	-88
80	3	- 38	27	9	-11	47
82	-17	22	-113	- 26	-31	17
92	16	- 43	-11	- 33	13	-10
93	-16	43	11	33	-13	10
μ	1.127	1.168	1.283	1.446	1.496	1.643

Apr. 28 63 82 17 80 52 56 43

May 24 43 52 80 82 63 56 17

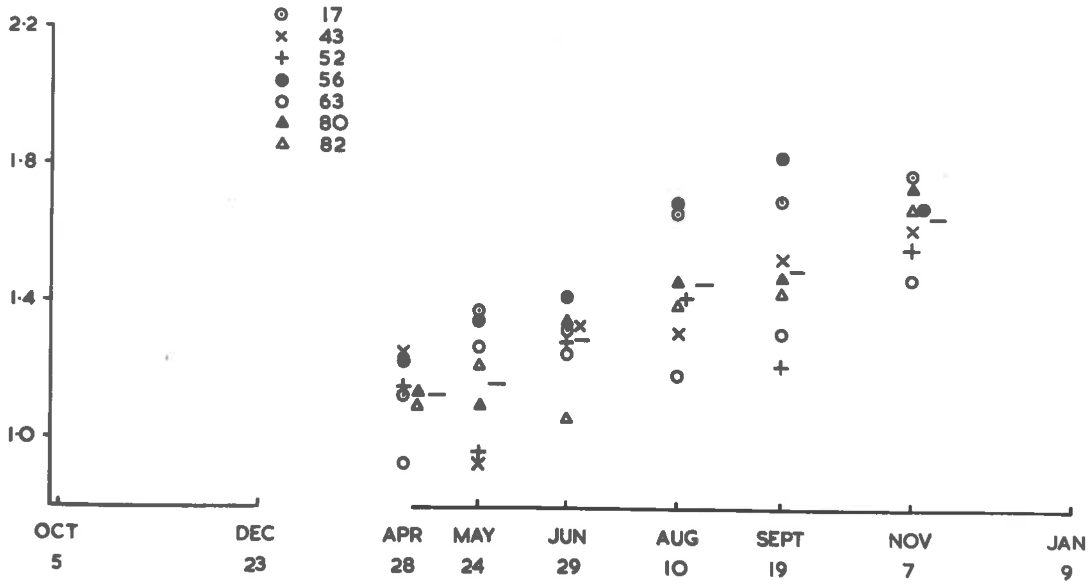
June 29 82 63 52 17 43 80 56

Aug. 10 63 43 82 52 80 17 56

Sep. 19 52 63 82 80 43 17 56

Nov. 7 63 52 43 82 56 80 17

Fig. 24. The combining ability values $\mu + 2\ gi$ for tiller length for Mediterranean parents when crossed to Northern European parents plotted against harvest occasion.


2·2
1·8
1·4
1·0
⊙ 17
× 43
+ 52
● 56
○ 63
▲ 80
△ 82
OCT 5
DEC 23
APR 28
MAY 24
JUN 29
AUG 10
SEPT 19
NOV 7
JAN 9

degrees of dominance when Mediterranean parents were combined with the Northern European parents.

A further interesting facit of the situation was that the diallel and topcross assessments were correlated in June and Sept. indicating that although the topcross variability was greater, it was with a similar ranking of the parents. At the midwinter Aug. harvest this correlation was not quite significant but whereas in other characters considered this was clearly due to the winter cessation of growth of 52 and 63 crosses with Northern European parents this was not conclusive for the present character.

A summary may be drawn of the above three sections relating to tiller development, namely the tiller number, tiller weight and tiller length sections.

The Mediterranean families in Apr., May and June underwent a period of rapid tillering to a maximum, the magnitude and timing of which was probably determined by competition, followed in Aug., Sept. and Nov. by a period when no new tillers were formed and there was a death of some of the existing tillers. Between Nov. and Jan. some new tillers were formed resulting from either or both the reduction in shading, following heading and drying off of the tops, or from the unseasonal rain in Nov. Differences in tiller weight and in tiller elongation were clearly evident as early as June but great variation was still present in Aug. and Sept.

The Mediterranean x Northern European families differed from the Mediterranean families in being slower in tillering in the first three months, in some families showing a mid winter cessation of tillering and in not reaching an overall maximum until Sept. At the break of the season they had a greater tiller weight and length than the Mediterranean families but were soon surpassed. They were later in developing reproductive tiller elongation but there was some overlap of the later Mediterranean families.

The Northern European families were much slower in developing new tillers from the beginning of the season, showed a pronounced winter cessation and did not reach a maximum until Sept. They mainly differed from the Mediterranean x Northern European families in being later; and internode elongation was not recorded until Nov. In terms of internode elongation they had only reached in Nov. the same stage that some of the Mediterranean families had reached by the end of June, four months earlier.

Survival

Of critical importance in the breeding of a perennial pasture grass is the question of survival, and in this environment this entails survival of the hot dry months, Nov. to Apr. In May 1960 a count was made of the plants surviving after the summer. As two samples had been taken from the experimental plots before the summer, data were not obtained on the whole plot, but on an intact group of plants bounded by guard rows. The group consisted of 30 plants in each plot so that with three replicates, a total count was made on 90 plants of each family. The results are given as a mean percentage in table 52.

Survival of families having both parents of Mediterranean origin was almost complete, averaging 97%. Families arising from crosses between Mediterranean and Northern European parents showed a lower survival

Table 52.

Percentage survival following the 1959/1960 summer

	17	43	52	56	63	80	82	92	93
17		99	97	100	97	98	99	90	95
43	100		100	99	95	99	99	94	67
52	99	100		100	94	97	90	82	86
56	100	99	100		100	99	92	93	97
63	99	90	96	98		99	83	92	76
80	96	95	98	99	100		91	97	89
82	100	95	94	90	86	93		90	94
92	92	85	69	92	86	97	85		57
93	94	80	85	98	87	84	95	61	

88% and between the two N.E. parents 59%. Although the Mediterranean x Northern European families were capable of responding to summer showers this had not markedly affected their survival.

It was considered unwarranted to carry out a combining ability analysis on the Mediterranean diallel because of the low variability, and analyses were restricted to the 14 Mediterranean x Northern European families and their reciprocals in the topcross. The replicated samples were converted to percentages, because of a few missing plants lost during establishment, and the analysis carried out on angular transformed data. The effects tested for in the analysis were reciprocal differences, differences between the Northern European parents and differences between the Mediterranean parents, none of which proved to be significant. Evidently the particular summer was not sufficiently severe to detect differences, if they occur, between Mediterranean parents for summer survival. Besides further evaluation of the hybrids in the present environment, a kmowledge of the extent to which Mediterranean x Northern European hybrids could be extended into dry environments needs to be obtained from tests in areas marginal for the survival of purely Mediterranean material.

The summer of 1959/1960 was not a particularly severe one for summer survival as several heavy showers were experienced. This almost certainly accounts for the higher survival of plants of purely Northern European origin than in a very dry summer when values of only 8% survival were recorded (Knight, 1960).

Combining ability for heading date

Each F_1 family was assessed for date of heading from samples of 20 and 10 plants in 1959 and 1960 respectively. The error was calculated by pooling the within family variability for all F_1 families including both the diallel and topcross.

With some of the families not all of the plants in the sample headed. In 1959 these families were - with the number in brackets of plants that headed - 63x92 and reciprocal (7, 6) 63x82 and reciprocal (2, 2) 82x93 and reciprocal (6, 5) 92x93 and reciprocal (8, 8) and in 1960, 63x92 and reciprocal (2,2) 63x93 and reciprocal (4, 4) and 92x93 and reciprocal (5, 5).

In table 53 the mean date of heading for all the families in the study are presented together. It is evident that for each of these families there was a large and consistent difference between years in the heading date. This is more likely to be a reflection of the age of the plants rather than a climatic difference between years, as it is a commonly observed phenomenon that perennial grasses head later in their seedling year than in subsequent years.

The combining ability mean squares for the Mediterranean diallel are presented in table 54. This includes analyses for the individual years and for the two years combined. When the years were combined there was evidence of significant interaction of g.c.a. and s.c.a. with years but too great an emphasis should not be placed on this in view of the very large years main effect. With main effects of this magnitude any slight departures from additivity are magnified. If these interactions

Table 53.

HEADING. 1959 and 1960 (Mean of 20 and 10 plants per family respectively)

	17	43	52	56	63	80	82	92	93
17		Nov. 4 Sep. 25	Oct. 27 Oct. 4	Oct. 14 Sep. 21	Nov. 3 Oct. 11	Oct. 24 Oct. 6	Oct. 24 Sep. 27	Nov. 1 Oct. 16	Nov. 10 Oct. 18
43	Oct. 19 Sep. 20		Oct. 18 Oct. 4	Oct. 11 Sep. 20	Oct. 31 Oct. 11	Oct. 20 Oct. 11	Oct. 14 Sep. 25	Nov. 10 Oct. 16	Nov. 11 Oct. 16
52	Oct. 27 Oct. 9	Oct. 23 Oct. 12		Oct. 17 Sep. 25	Nov. 14 Oct. 24	Nov. 7 Oct. 18	Oct. 23 Oct. 9	Nov. 24 Oct. 27	Nov. 24 Nov. 5
56	Oct. 14 Sep. 21	Oct. 9 Sep. 20	Oct. 21 Sep. 23		Oct. 21 Oct. 5	Oct. 17 Oct. 5	Oct. 7 Sep. 21	Oct. 20 Oct. 6	Oct. 20 Oct. 1
63	Nov. 2 Oct. 13	Nov. 7 Oct. 13	Nov. 14 Oct. 24	Oct. 20 Oct. 5		Nov. 7 Oct. 21	Nov. 9 Oct. 14	Nov. 20 Oct. 21	Dec. 3 Nov. 11
80	Nov. 1 Oct. 10	Oct. 22 Oct. 9	Nov. 6 Oct. 14	Oct. 18 Oct. 3	Nov. 3 Oct. 20		Nov. 1 Oct. 12	Nov. 19 Oct. 22	Nov. 20 Oct. 29
82	Oct. 21 Oct. 1	Oct. 16 Sep. 30	Oct. 27 Oct. 9	Oct. 13 Sep. 21	Nov. 6 Oct. 14	Nov. 2 Oct. 12		Nov. 5 Oct. 21	Nov. 18 Nov. 1
92	Nov. 4 Oct.12	Nov. 4 Oct. 16	Nov. 24 Oct. 28	Oct. 24 Oct. 9	Dec. 4 Nov. 10	Nov. 17 Oct. 27	Nov. 2 Oct. 21		Nov. 27 Nov. 10
93	Nov. 21 Oct. 19	Nov. 14 Oct. 15	Nov. 19 Nov. 1	Oct. 28 Oct. 7	Dec. 1 Nov. 12	Nov. 22 Nov. 1	Dec. 15 Oct. 24	Nov. 29 Nov. 10	

are used in the test of significance of the g.c.a. and s.c.a. main effects the former were highly significant but the later were not. Evidently in the individual years the s.c.a. effects were significant but these effects were not consistent over the two years.

The g.c.a. effects (table 55) are illustrated in Fig. 25 where it may be seen that the effects were large, consistent and distinct between parents. The s.c.a. and the reciprocal effects were of much less importance and provided only a fraction of the variability engendered by the g.c.a. effects.

The results from the topcross were very similar (table 56) in the individual years the s.c.a. and reciprocal mean squares were found to be significant, but when the years were combined, these were no longer significant against the s.c.a. x years and reciprocal years interactions. In contrast the g.c.a. was large and significant for the two years.

The g.c.a. effects (table 57) are also illustrated in Fig. 25 where it will be seen that the ranking of the Mediterranean parents by the topcross test was similar to that previously obtained from the purely Mediterranean diallel. This occurred despite the fact that the value of μ differed by as much as 20 days between the two tests as a result of using the different testers.

Data on the heading of the parents were obtained from clonal swards during 1957. The swards had been established that year and in this respect would be more comparable to the progeny values for 1959. The strong resemblance between the parents as clones and $\mu + 2gi$ is evident from Fig. 25 and Fig. 26.

Table 54.

The heading date analysis of variance for 1959, 1960 and the two years combined (Med. diallel).

	D.F.	M.S.	D.F.	M.S.
g.c.a.	6	560.4***	6	637.1***
s.c.a.	14	33.6***	14	11.2***
reciprocal	21	12.2**	21	5.0
error	> 250	3.3	>250	3.2

	D.F.	M.S. †
g.c.a.	6	1168.0
s.c.a.	14	20.1
reciprocal	21	12.3
Years	1	8340.1
g.c.a. x years	6	29.5
s.c.a. x years	14	24.7
recip. x years	21	4.9
error	> 250	3.3

† Significance discussed in text

Table 55.

General combining ability effects for heading date in 1959 and 1960 (Med. diallel)

	1959	1960
17	- 0.9	- 4.8
43	- 4.9	- 4.6
52	4.3	4.9
56	-12.3	-11.6
63	11.1	10.9
80	4.0	7.5
82	- 1.8	- 2.1
μ	55.5	35.5

1959   56 43 82 17   80 52 63

1960   56 17 43 82   52 80 63

Table 56.

The heading data analysis of variance for 1959, 1960 and the two years combined (Med. x N.E. topcross)

	1959		1960	
	D.F.	M.S.	D.F.	M.S.
N.E. parents g.c.a.	1	424.0***	1	142.0***
Med. parents g.c.a.	6	595.6***	6	443.5***
Interaction s.c.a.	6	104.1***	6	25.1***
Reciprocal	14	43.8***	14	20.7***
Error	> 250	3.3	>250	3.2

Years combined	D.F.	M.S.†
N.E. parents g.c.a.	1	528.4
Med. parents g.c.a.	6	1026.8
Interaction s.c.a.	6	32.3
Reciprocal	14	37.0
Years	1	7223.0
N.E. g.c.a. x years	1	38.0
Med. g.c.a. x years	6	12.3
s.c.a. x years	14	23.1
Recip. x years	14	27.5
Error	> 250	3.3

† Significance discussed in text.

Table 57.

General combining ability effects for heading date of the Med. parents in Med. x N.E. topcross

	1959	1960
17	- 5.7	- 6.2
43	- 4.7	- 6.7
52	8.6	8.3
56	-22.2	-16.7
63	15.3	14.3
80	5.3	5.0
82	3.3	2.0
92	- 3.9	- 2.3
93	3.9	2.3
μ	75.2	52.5

1959 56 <u>17 43</u> <u>82 80 52</u> 63

1960 56 <u>43 17</u> <u>82 80 52</u> 63

Fig. 25. The combining ability values $\mu + 2\ gi$ for heading for Mediterranean parents when assessed in the diallel and top cross test. There was a strong similarity of ranking of parents over tests and years. The y-axis is in days from Sept. 1.

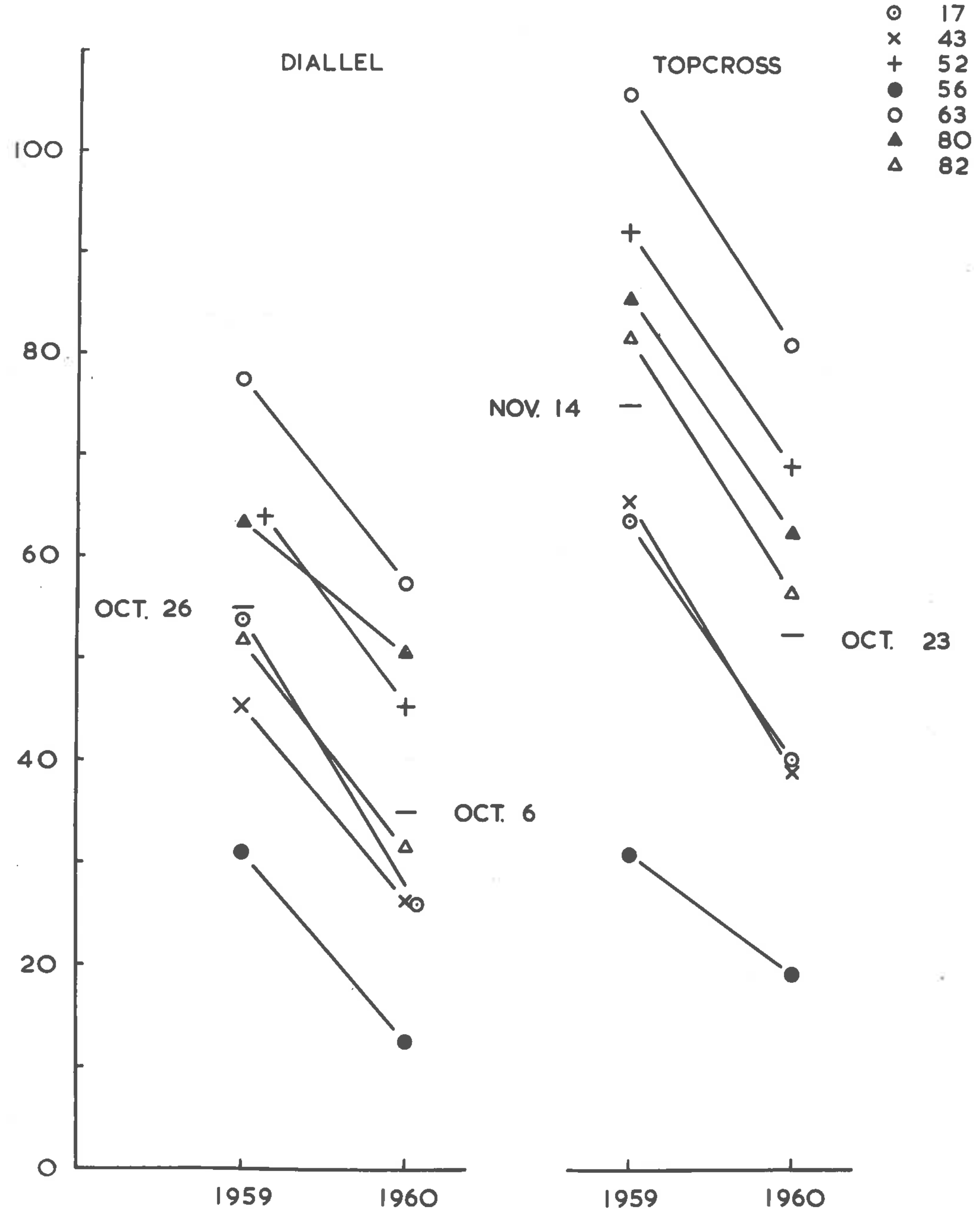
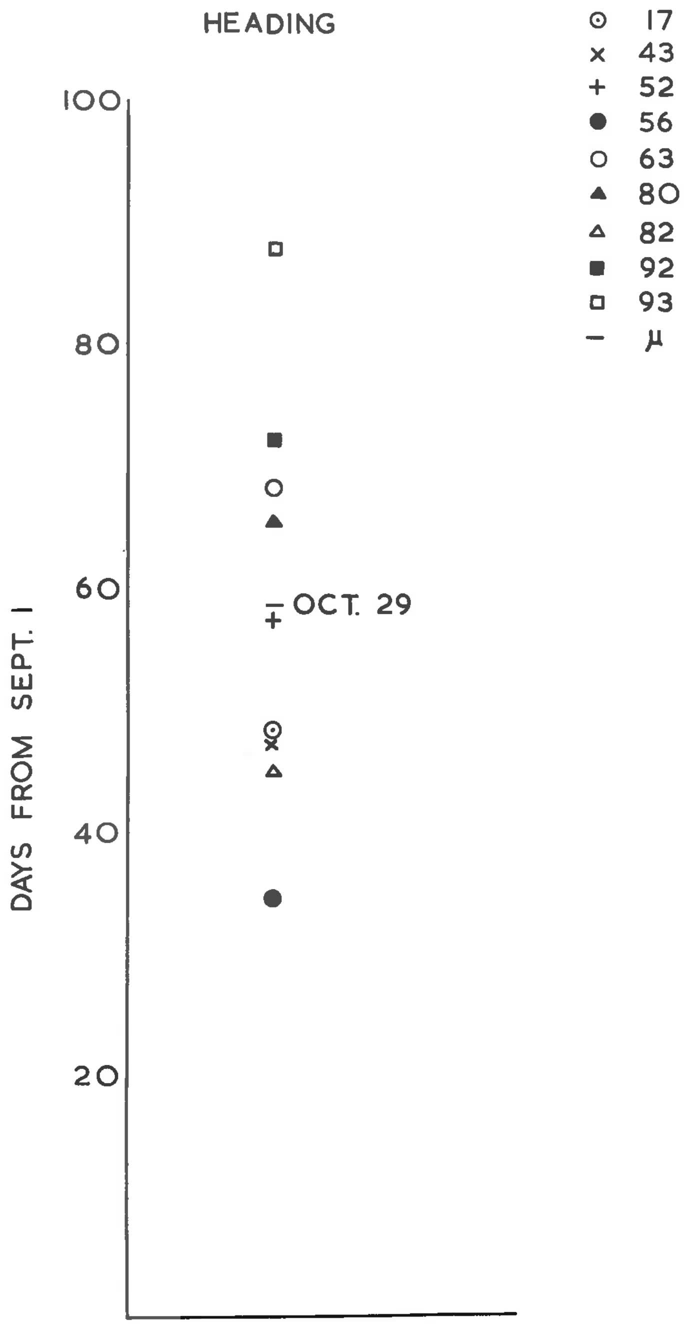

DIALLEL
TOPCROSS
⊙ 17
× 43
+ 52
● 56
○ 63
▲ 80
△ 82
100
80
60
40
20
0
OCT. 26
OCT. 6
NOV. 14
OCT. 23
1959
1960
1959
1960

Fig. 26. The heading date of the parents as clones.


HEADING
100
80
60
40
20
DAYS FROM SEPT. I
OCT. 29
⊙ 17
× 43
+ 52
● 56
○ 63
▲ 80
△ 82
■ 92
□ 93
— μ

The large g.c.a mean squares and effects are indicative of the variability available for breeding should the agronomic value of heading date be established. Considerable genetic advances would be possible before it became necessary to utilise the variability present in the s.c.a. or reciprocal effects. In the studies that have been published dealing with the inheritance of heading data or the related bloom-flowering date (see literature review) differences of the present magnitude were not obtained. The probable reason for this is that these other studies were carried out on indigenous races in which the variability has been reduced by natural selection, and not on material introduced from a wide range of environments as in the present study. Here the parents were artificially crossed after having been induced to flower simultaneously by subjecting them to a photoperiod and were not merely the result of mutual pollination in an isolation block. In the latter circumstance parents differing widely in heading-flowering time would not be crossed and differences between progeny families would not be as large. A second factor possibly giving rise to the increased variability was that the plants were being grown in a locality having a winter growing season. Under these conditions photoperiodic induction occurs in mid winter, halfway through the growing season, while heading begins in September five months from the beginning of the season and at a time of slowly increasing daylength. In the summer growing environments of Northern Europe and the United States, where many studies of heading have been made, photoperiodic induction occurs in the cold winter when little or no growth is possible. With the beginning of spring there is a rapid increase in daylength and temperature and the plants show stem elongation and heading soon after the beginning of the season. This contrast in the rapidity of the change of conditions favourable for heading may be responsible for the greater variability found in this Mediterranean type of environment in comparison with Northern European environments.

WITHIN FAMILY VARIABILITY

In the Introduction it was mentioned that crosses between locally adapted races might be analagous to F_1 hybrids between inbreds in producing a low within-family variability. This would be the situation if some degree of homozygosity had been attained as a result of adaptation to the local environment. A measure of within-family variability was obtained at each harvest with the calculation of the error. No comparable data were available for F_1 hybrids between inbreds but the parents as clonal swards (Knight 1960) were a good substitute. Within a clone there is no genetic variability, the variation is purely environmental and everything possible was done in the experiments to keep this to a minimum. In table 58 the within-family variability for topweight, stubble weight and tiller number is given for the F_1 families, and beneath them the within-clone variability, both being an error mean square per plant. The F_1 mean square was derived from 250-324 degrees of freedom and the clonal values from 85-117 degrees of freedom. Harvests were not taken on identical dates in the two experiments so that a staggered arrangement has been used in the table.

In the second year of the parents as clones the error was derived from the Mediterranean parents alone. So many plants had died in the Northern European swards as to preclude the taking of results. For the F_1s however in general the error was derived from all of the families. One time at which separate errors were calculated, because of differences, was the Apr. harvest when the top weight error for the purely Mediterranean families was 0.137 and for the Mediterranean x

Table 58.

The error mean square of top weight per plant for the F_1 families and the parents as clones

F_1 Within-family		Oct.5 .043		Dec.23 .067	Apr.28 .213	May 24 .122	June 29 .129		Aug.10 .168	Sep.19 .121	Nov. 7 .137	Jan. 9 .091
Parents Within-clone	Sep.12 .049		Nov. 7 .092	Dec.23 .085	Apr.11 .085	May 20 .156	June 12 .084	July 21 .134		Sep. 4 .082		Dec. 23 .104

The error mean square of stubble weight per plant for the F_1 families and the parents as clones

F_1 Within-family		Oct.5 .037		Dec.23 .043	Apr.28 .208	May 24 .121	June 29 .134		Aug.10 .175	Sep.19 .147	Nov. 7 .104	Jan. 9 .065
Parents Within-clone	Sep.12 .047		Nov. 7 .065	Dec.23 .036	Apr.11 .096	May 20 .124	June 12 .066	July 21 .106		Sep. 4 .081		Dec.23 .090

The error mean square of tiller number per plant for the F_1 families and the parents as clones

F_1 Within-family	Sep.11 .019	Oct.5 .024		Dec.23 .017	Apr.28 .106	May 24 .067	June 29 .083		Aug.10 .128	Sep.19 .079	Nov. 7 .071	Jan. 9 .023
Parents Within-clone	Sep.12 .033		Nov.7 .031	Dec.23 .023	Apr.11 .056	May 20 .110	June 12 .059	July 21 .054		Sep. 4 .059		Dec.23 .078

Northern European families 0.264. The former value is quite comparable to the 0.085 obtained for the parents-as-clones error. The latter high value may have arisen in these families because of their reduced dormancy and their attempts to grow before the main opening rains when there was a limited moisture supply. Environmental variability would increase under such circumstances. However, there is the more remote possibility that genetic segregation within these families was responsible for the inter plant differences at this time.

Apart from this one harvest there was good agreement between the hybrid family variability and the parents-as-clone variability. It may be concluded that the evaluation of the present material obtained by crossing locally adapted races was almost as good as comparing clonally propagated material. One could not generalise this result to all races as it will depend on the degree to which any race has evolved in relation to its local environment, and the dissimilarity of these environments. When it is desired to assess the relation of growth patterns to total yield, hybrids between sufficiently diverse ecotypes would enable precise experimentation.

CORRELATIONS BETWEEN G.C.A. EFFECTS

Genotypic correlations between characters may occur in F1 families from the pleiotropic action of genes or as a result of linkage developed in response to local adaptation. In the latter case a genotypic correlation is indicative of the simultaneous effects of natural selection on plant characters.

Correlations were calculated between the gi values obtained for the different characters, for example between tiller number and top weight at the Apr. 28 harvest. These correlations provide a measure of the association of characters within the restricted set of parents under consideration. They are therefore different from the genotypic correlations calculated for circumscribed populations, such as a named variety, under the assumptions of Model II (Griffing 1956b), and in which the parents are considered as a random sample of that population.

A correlation between gi effects is not free from confounding by an error component, but as a gi effect is derived from an average of an array of families this error component will be reduced according to the number of families in the array. This error effect is comparable to that obtained in a uniformity trial, where the only difference between groups is environmental, and the effect is reduced according to the number within the group. The confounding will not be important when the g.c.a. mean square of each character has been found to be significant with respect to its error.

A method of calculating genotypic correlations free of error within the set of parents would have been to carry out a multivariate analysis at the level of the individual plant, however this could not have been done for many of the characters. The reason being that when for instance dry weight during the winter was being correlated with heading date, these determinations of necessity were done on different plants as plants were destroyed in making the dry weight assessment. Because this type of difficulty would have been experienced for many of the correlations it was decided to calculate all correlations by the one method of association between g.c.a. effects.

A satisfactory interpretation of correlations may only be made when there are clear cut trends in the values and where reasonable biological explanations can be advanced in support of the associations. No attempt was therefore made to derive correlations between characters at widely separated harvests. Emphasis is also placed on deriving correlations with top weight, the most important character.

The order in which the correlations are presented is that in which they have been considered in the previous sections beginning with top weights and stubble weights.

CORRELATIONS BETWEEN STUBBLE AND TOP WEIGHT

Values of the correlations are given in tables 59 and 60. A significant positive correlation was obtained at a harvest when the parents were similarly ranked for the two characters under consideration. This was obtained for stubble and top weight at both the Apr. and May harvests of the Mediterranean families and evidently the tops and stubble of the families were growing proportionately at these times. However, this did not mean that a correlation would also be found between the stubble of the Apr. harvest and the top weight of the May harvest. The reason for this was exemplified by parent 56 whose gi values were the least of all parents for tops and stubble weight in Apr., but had risen to 4th and 5th highest respectively by May. It is then understandable that there was a correlation for tops and stubble within a harvest but a much reduced one between harvests.

The correlation between the Dec. 1959 stubble and the Apr. 1960 top weight in the Mediterranean diallel deserves comment. It had been observed that regeneration following the summer was from the previous seasons sterile tillers. The first signs of regrowth, were green leaves protruding from the otherwise brown dry tillers as a result of renewed activity by the apical buds. Because of this observation an attempt was made to see if rapid regeneration in Apr. could be attributed to some characteristic of these sterile tillers, the most logical being the stubble weight. The stubble of sterile tillers contains the apical bud, the leaf bases, which are well developed, and a short stem, and may have at the time of going into dormancy a fructosan content of 12% of the dry weight (Knight and Jennings, unpublished). The correlation between the sterile stubble weight and the Apr. top weight was r = .90** indicating that this character was closely associated with regenerative ability. The subject will be discussed again in relation to tiller number.

There is no obvious explanation for the only other correlation observed in this material, a negative association of Oct. stubble weight and Dec. top weight.

Different results were obtained for the Mediterranean x Northern European topcross (table 60). Firstly there was no association between regrowth in Apr. and the stubble weight of the previous season, either total or sterile stubble weight, and secondly that at each harvest until Aug. 10 there was a strong positive correlation between top and stubble weight. The first result was in accordance with the suggestion that these families, with their low dormancy and slight sporadic growth before the main break of the season are less affected by plant characters present at the end of the previous season. The second result, is quite understandable when it is realised that winter dormancy has equally affected top and stubble weights of some families. The lack of correlation between harvests does not alter this conclusion.

To summarise the results for the tops-stubble correlations, the Mediterranean familie's rate of regeneration was related to the previous seasons sterile stubble weight whereas the growth of Mediterranean x Northern European families at the main break of the season was independent of any attribute present at the end of the previous season. Growth of tops and stubble were independent in the Mediterranean material during the main part of the growing year but were closely related, because of winter dormancy, in the Mediterranean x Northern European material until mid Sept.

Table 59

Correlations between gi effects for stubble wt. and top wt. in Med. diallel

Stubble Wt. / Top Wt.	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
Oct. 5	- .69	- .85*							
Dec. 23		- .28	.84*						
Apr. 28			.92**	.63					
May 24				.79*	.15				
June 29					.02	- .49			
Aug. 10						- .60	- .74		
Sep. 19							.52	.68	
Nov. 7								.09	.11
Jan. 9									.21

Table 60

Correlations between gi effects for stubble wt. and top wt. (Med. x N.E. top cross)

Stubble Wt. / Top Wt.	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
Oct. 5	.87*	- .07							
Dec. 23		.02	.52						
Apr. 28			.81*	- .35					
May 24				.73	.14				
June 29					.86*	.08			
Aug. 10						.96***	.07		
Sep. 19							.28	- .31	
Nov. 7								- .07	- .54
Jan. 9									.34

CORRELATIONS BETWEEN ROOT AND TOP WEIGHTS

In the literature review it was suggested that when sward plants were mutually competing for light an excessively large stubble or root system may be a disadvantage as it would constitute a respiratory load, but that at other times, when moisture was limiting, a large root system might be an advantage. The two effects would result in negative and positive correlations respectively.

Neither effect was evident in the stubble weight correlations considered above, nor were they evident in the root weight correlations (tables 61 and 62). A high positive correlation was obtained in Dec. of the first year but there was no correlation at the corresponding time in the second year to support the suggestion.

The roots and stubble together constitute a respiratory load on the photosynthetic tops, and correlations were made for the roots and stubble combined and the tops. These correlations were no more conclusive; the only significant result for the Mediterranean families being a value of .83 at the May harvest and for the Mediterranean x Northern European families a value of -.83 at the Oct. harvest.

In this experiment therefore, there was no clear evidence that the size of the stubble or roots was affecting top growth in either of these suggested ways

The roots may also have played a part as storage organs for regeneration as they have been found to have a fructosan content similar to the stubble (Knight and Jennings, unpublished) but in the absence of Dec. root weight determination no evidence could be brought to bear on this suggestion. Their contribution to the top weight regeneration would not be as direct as that of the sterile stubble which represents the dormant bud from which regeneration occurs.

CORRELATIONS OF TILLER NUMBER WITH TOP WEIGHT

Significant correlations between tiller number and top weight were found at two periods in the growth phase of the Mediterranean families (table 63). One of these was when the reproductive phase differences between families were most pronounced, that was in Oct. of the first year and in Aug. and Sept. of the second. At these harvests those families with high top weights had very low tiller numbers. A similar negative correlation had been observed for the parents (Knight 1961) when the cessation of tillering was attributed to the increased mutual shading of plants as they began stem elongation.

The second period in which a significant correlation was obtained was at regeneration from dormancy (Apr.). High top weights were associated with high tiller numbers of the Dec. harvest, which was at the end of the previous growing season. An even more significant correlation of r = .998 was obtained with the sterile tiller numbers of the Dec. harvest. This is understandable, as already discussed, if the initial regrowth in Apr. arises from the renewed activity of the terminal buds of the sterile tillers; other buds would have been present in the leaf axils of the fertile tillers but being much smaller their contribution was less to the initial regeneration.

This picture was considerablymodified in the Mediterranean x Northern European families (table 64). Firstly at regeneration when the correlation between the number of sterile tillers in Dec. and yield

Correlation between gi effects for root wt. and top wt. in Med. diallel

Root Wt. Top Wt.	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
Oct. 5	.59	.91**							
Dec. 23		-	-						
Apr. 28			-	-					
May 24				.81*	.27				
June 29					.07	.19			
Aug. 10						-	-		
Sep. 19							.38	.58	
Nov. 7								.05	.14
Jan. 9									.36

Table 62

Correlations between gi effects for root wt. and top wt. in Med. x N.E. topcross

Root Wt. Top Wt.	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
Oct. 5	-.27	-.34							
Dec. 23		-	-						
Apr. 28			-	-					
May 24				-.84*	-.18				
June 29					-.30	-.64			
Aug. 10						-	-		
Sep. 19							.48	.13	
Nov. 7								.55	-.12
Jan. 9									-.44

Correlation between gi effects for tiller no. and top wt. in Med. diallel

Tiller No. Top Wt.	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
Sep. 11	-.72								
Oct. 5	-.78*	-.63							
Dec. 23		.54	.80*						
Apr. 28			.72	.01					
May 24				.01	-.33				
June 29					-.40	-.80*			
Aug. 10						-.86*	-.76		
Sep. 19							-.24	-.22	
Nov. 7								-.33	-.32
Jan. 9									-.20

Table 64

Correlations between gi effects for tiller no. and top wt. in Med. x N.E. topcross

Tiller No. Top wt.	Oct. 5	Dec. 23	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
Sep. 11	-.41								
Oct. 5	-.35	.47							
Dec. 23		.25	.79*						
Apr. 28			.96***	-.65					
May 24				-.10	.00				
June 29					.52	-.06			
Aug. 10						.40	-.04		
Sep. 19							-.19	-.09	
Nov. 7								.41	.26
Jan. 9									.64

in Apr. was not significant (r=.690). This may be accounted for by similar reasoning to that presented in the section on stubble weights. Tiller number in Apr. was however strongly correlated with its current top weight but in this instance whether high tiller numbers led to high top weights or vice versa is less clear than with the regeneration of the Med. families.

Later in the year there were no clear cut associations. Any correlation between tiller number and yield that might have occurred and been attributed to stem elongation was nullified through the tendency of some families to show winter dormancy at this time. Winter dormant families in fact had positive correlations with low top weights and low tiller numbers. At the next harvest Sept. 19 there was still not a significant negative correlation partly due to a carry over of the winter dormancy effect but also partly due to an anomalous result at this harvest for the top weight of one family (56 x 92) which led to a low g.c.a. effect for parent 56. Unforunately this top weight result was at a critical period and affects some of the other correlations within the topcross.

CORRELATIONS BETWEEN HEADING DATE AND TOP WEIGHT

Frequent reference has been made in the results to the change from the vegetative to the reproductive phase and the relation of this change to top weight. Three characters were assessed that might have been good indicaters of this change, namely date of heading, internode elongation as judged by tiller length and the tiller weight distribution. The first of these, heading date in relation to top weight is given in tables 65 and 66. These correlations were obtained by relating the 1959 and 1960 top weights to the 1959 and 1960 heading dates respectively, but as there were only minor differences in heading date in the two years the use of either years heading date in the correlations would have made little difference.

In the Mediterranean material none of the correlations was significant apart from the one on Apr. 28. With this exception yield and heading date were not uniformly related in this material and heading could not be used as a guide to seasonal productivity. At first sight there appears to be no reason why yield at regeneration in Apr. should have been related to heading date but the reason lies in the fact that both were related to a third character, the sterile component of the plants when they went summer dormant. The later heading families had a larger sterile component and as has been discussed, it was from this sterile component with its dormant terminal buds that regeneration in Apr. began.

In the Mediterranean x Northern European families there was no correlation of Apr. top weight with heading date.

In these families there was slightly more indication of a

Table 65.

CORRELATIONS BETWEEN GI EFFECTS FOR HEADING DATE AND TOP WT. IN MED. DIALLEL

Heading date	Top Wt.	Oct. 5	Dec. 23		Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
1959		- .52	- .23	1960	.98***	.55	.15	-.29	-.06	.03	.09

Table 66.

CORRELATION BETWEEN GI EFFECTS FOR HEADING DATE AND TOP WT. IN MED. x N.E. TOPCROSS

Heading date	Top Wt.	Oct. 5	Dec. 23		Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
1959		-.76*	-.09	1960	.03	-.12	-.20	-.53	-.25	-.63	-.48

relation between heading date and spring yields but it only just reached significance in Oct. of the first year.

CORRELATIONS OF TILLER LENGTH WITH TOP WEIGHTS

A very strong trend was evident in the correlations between tiller length and top weight in the Mediterranean families (table 67). At regeneration there was no association but as the season progressed so did the correlations reaching a maximum in Aug. and then declining again. Such a result is in accord with the suggestion that at the beginning of the season tiller length was of little importance but that it became a major factor determining yield during mid winter and early spring. The correlation between the late May tiller length and the June top weight indicates that as early as late May this factor became important. Towards the end of the season, when all families showed stem elongation, tiller length was no longer capable of differentiating families with high yields.

In the Mediterranean x Northern European families there were no significant correlations (table 68). The failure to detect in these families what was a dominant feature in the growth of the Mediterranean material was again due to dormancy in the midwinter in some families and to the anomalous result of the family 56 x 92 at the spring harvest of Sept. 19. Winter dormancy was largely manifest as low top weights and a reduced tiller number, whereas tiller length was affected to a much smaller degree. The low yields of the dormant families were not therefore invariably associated with smaller tiller lengths during the winter and no correlation was obtained.

CORRELATIONS OF TILLER WEIGHTS WITH TOP WEIGHTS

Little need be said about these correlations (tables 69 and 70) as they very closely reflect the results for tiller length. Tillers that had undergone stem elongation were long and had high weights so that their correlations with top weights were very similar.

In conclusion, both tiller length and tiller weight were closely related to the increase in yield that occurred at the change from the vegetative to the reproductive phase whereas heading date was not a good indication of this change. This was clearly exemplified by parent 80 which early showed stem elongation and a high yield but was comparatively late in the emergence of its heads.

A composite picture may now be drawn from the results, with attention concentrated on the second year as being more typical of a perennial grass. Heavy rains opened the season on Apr. 4, and the first harvest of regeneration from summer dormancy was taken on Apr. 28. In the Mediterranean families high top weights at this time were related to the development of the sterile component of the previous year, both the stubble and tiller number. As initial regeneration was from the renewed activity of the sterile tillers, a large number of sterile tillers at the end of one season led to a large number of growing tillers at the beginning of regeneration and a high top weight by Apr. 28. Variability in tiller weight does not appear to have been important at this time.

Following regeneration for a period in Apr. and May, the growth of tops and stubble were related, and families showing development of their tops showed development of their stubble, but tiller number was no longer related to yield. From late May until Sept. the differences in top weights were associated with the production of long tillers by families entering the reproductive phase. Either there was a change in the photosynthetic metabolism of the plants as they became reproductive and long tillers were merely a manifestation of this change, or else long tillers and tall swards enabled these families to partially overcome the effects of limiting factors present under conditions of competition. The onset of this tiller elongation differed greatly between the families but it was not well correlated with subsequent heading date. During this period and for the rest of the year, tiller number was unimportant in relation to yield, nor was there any evidence that root weight or root + stubble weight constituted a respiratory load reducing top growth.

At the end of the season all families had headed and the association of top weight with tiller length declined. High top weights were now associated with the degree of development of the fertile components of the plants.

The major difference in the establishment year was that the growth phases were later, resulting in a smaller fertile component at the end of the year. Characters correlated with the sterile component were of more importance in this than in the second year when the absolute size of the sterile component was the same but the fertile component had greatly expanded.

Table 67

Correlations between gi effects for tiller length and top weight in Med. diallel

Tiller length / Top Wt.	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
Apr. 28	-.25	.05					
May 24		.31	.97***				
June 29			.83*	.91**			
Aug. 10				.87*	.85*		
Sep. 19					.80*	.70	
Nov. 7						.47	.37

Table 68

Correlations between gi effects for tiller length and top weight in Med. x N.E. topcross

Tiller length / Top Wt.	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
Apr. 28	-.03	-.21					
May 24		.61	.44				
June 29			.58	.13			
Aug. 10				.57	.23		
Sep. 19					.31	.70	
Nov. 7						.14	.60

Table 69

Correlations between gi effects for tiller wt. and top wt. in Med. diallel

Tiller Wt. Top Wt.	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
Apr. 28	.21	.66					
May 24		.53	.47				
June 29			.75	.94**			
Aug. 10				.93**	.91**		
Sep. 19					.82*	.69	
Nov. 7						.66	.61

Table 70

Correlation between gi effects for tiller wt. and top wt. in Med. x N.E. topcross

Tiller Wt. Top Wt.	Apr. 28	May 24	June 29	Aug. 10	Sep. 19	Nov. 7	Jan. 9
Apr. 28	.15	.21					
May 24		.27	.05				
June 29			.44	-.03			
Aug. 10				.75	.37		
Sep. 19					-.09	.37	
Nov. 7						.53	-.11

DISCUSSION

Most of the specific breeding objectives of this study, such as determining if any parents showed high combining ability for top weight at all seasons of the year, and the relative performance of Mediterranean, Mediterranean x Northern European and Northern European families for seasonal growth, have been dealt with in the discussion following the top weight results. The other major finding, relevant to the breeding objectives, was that summer survival was virtually 100% in the Mediterranean families and 88% in the Mediterranean x Northern European families in an environment that led to only a 59% survival in the Northern European families.

Together these results indicate that the breeding programme could profitably be extended to other environments. One of which would be areas having a lower annual rainfall, no summer rain, and where the Mediterranean material would potentially be the most valuable. How far this extension could go before there was a serious fall in survival is not known. Secondly, to areas that have a higher summer incidence of rain, or a limited irrigation supply, and in these localities the summer growth of the Mediterranean x Northern European hybrids and their high survival might show to advantage. And lastly to areas that can be irrigated all the summer but have cold winters where the Mediterranean x Northern European hybrids might compare favourably with the existing Northern European strains, but in regard to winter growth. It is this winter growth potential of Mediterranean material that is engaging the attention of plant breeders in New Zealand and Britain (Barclay 1960, Borrill 1961).

The out-of-season summer growth of the Mediterranean x Northern European was very slight in the summers experienced, and no measure of it was obtained, but it was sufficient to lead to a higher yield of these families at the true break of the season. The out-of-season growth was interesting from the evolutionary point of view as it occurred at a time when the Mediterranean families were dormant and the Northern European families severely wilted. The hybrids apparently combined the drought resistance of the Mediterranean parents with the lack of dormancy of the Northern European parents. This is an example of luxuriance or pseudoheterosis (Dobzhansky, 1952) arising from the complementary action of two sets of genes. A similar situation was mentioned by Hagberg (1952) who attributed some forms of heterosis to a combination in the hybrids of the complementary growth rhythms of the two parents. Such luxuriance can be of great importance in breeding programmes. It can be a disadvantage to a genotype under conditions of natural selection but it can be an advantage to agriculture where it is possible to adjust the environment by irrigation and careful management.

A second major objective of this study was to follow variation in other plant characters that might be important attributes of pasture grasses. As introduction to this discussion brief mention needs to be made of current thought on the question of yield components and associated characters. Williams (1959) suggested that since some components such as fruit weight and number in tomatoes were multiplicative in giving yield, a hybrid may be intermediate between its parents for the individual components but following multiplication exceed either parent in yield. This may be illustrated by reference to table 71. Both he and Grafius (1960) argued that inheritance studies on the components would be of great value because the component expression was more basic, and therefore closer to primary gene action, whereas yield results from the interplay of many such components. This view was opposed by Moll et al.(1962) who considered that yield was probably limited by some biochemical process such as photosynthesis, which was more closely determined by the important primary gene action and that secondary gene systems may then partition the photosynthetic products between the components.

Against this background it is interesting to look at some of the results in the present study. In these it is suggested that when the plants were small at regeneration in April there was little competition between plants for light but as the season progressed and the plants grew larger so did their mutual competition. It has further been suggested (Knight, 1960) that when grass plants show stem elongation the affects of competition are less apparent so that there is a contrast between the vegetative and reproductive phases. The physiological reasons for this change are unknown but may be due to a better light or CO_2 distribution through the expanded profile, a change in shoot:root ratio, a change in the tissues being formed and hence

Table 71. Components of yield in two parents and their F_1

	Expression of component A	Expression of component B	Yield A x B
P_1	3	1	3
F_1	2	2	4
P_2	1	3	3

Table 72.

Components of yield and yield at three harvests

Apr. 28	Tiller no.		Tiller wt.		Top wt.	
Med.	1.469	**	$\bar{2}$.658	***	$\bar{1}$.975	*
Med. X N.E.	1.353	***	$\bar{2}$.910	*	.079	**
N.E.	.721	***	$\bar{2}$.803		$\bar{1}$.506	***
May 24						
Med.	1.660	***	2.845	*	.367	
Med. x N.E.	1.532	***	2.912		.330	**
N.E.	1.216	***	2.815		.034	**
Sept. 19						
Med.	1.540	***	1.510	***	1.006	
Med. x N.E.	1.675	*	1.386	**	.977	
N.E.	1.719		1.271		.873	

Table 73.

The significance of the g.c.a. mean squares for yield of top weight and its components, and the significance of the correlations with top weight (Med. families)

	Apr. 28	May 24	June.29	Aug.10	Sep.19	Nov.7	Jan.9
Top wt. g.c.a. mean square	**			*	***	***	***
Tiller no. " " "	***	***	***	***	***	***	***
Tiller wt. " " "	*		***	**	**	***	***
Correlation tiller no. top wt.				- *			
Correlation tiller wt. top wt.				**	*		

differences in respiratory load, or a change in photosynthetic products and their utilisation.

There were three harvests in the second year in which there were large differences in the tiller number and tiller weight components of yield and the results for these harvests are presented in Table 72. In April the results were similar to the hypothetical situation in table 71, differing only in that for the hybrid the tiller component was not intermediate but was similar to the higher parent. The hybrid showed hybrid vigour, the yield exceeding either parent population. At the next harvest the tiller weight variability was reduced but yield was still ranked in a similar manner to number. In Sept., however, although there were large differences in tiller number and tiller weight these compensated each other and the differences in yield were not significant. At other harvests there were no large differences in tiller number or tiller weight and yield did not differ between these groups except as a result of winter dormancy.

The data for variability within the populations complement these results. Variability in the Mediterranean families is presented as the significance of the g.c.a. mean squares for tiller number, tiller weight and yield (table 73). Also indicated are the occasions when the correlations between yield and its components were significant. Three situations are envisaged in these results. Firstly at regeneration when there was little competition between plants, no environmental factor was limiting growth, and genetic differences could be expressed in both components and in yield. Secondly as in May and June yield differences were not significant although the components continued to show large differences. Competition for some factor in the environment limited growth, and detectable variation in yield was lost. Although the components continued to vary this was in a manner that was compensating. It is similar to the situation visualised by Moll et al. (1962) where yield is limited by some fundamental process such as photosynthesis. Variation may occur in the components but only as a result of a different partitioning of the photosynthetic products. The third situation first evident in Aug. and Sept. occurred when the yields again showed differences but now attributable to stem elongation and hence the correlation with tiller weight. Stem elongation and the physiological changes associated with the reproductive phase reduced or circumvented the effects of competition within the swards and these families were able to show increased yields. Later all families became reproductive, but those with a high proportion of their plants with elongated fertile tillers were less subject to competition and were able to develop high yields. At these last harvests there was no correlation of yield with either tiller number or tiller weight and the important fertile portion could be made up of many small tillers or a few large tillers.

The significance of these conclusions is that no gains in yield would be made by breeding for the yield components tiller number and tiller weight if the plants were to be grown under conditions of severe competition, the only characters that would be important were the timing of stem elongation and proportion of the plants that became fertile. There was considerable scope for breeding for these characters judging by the variation found in this unselected sample of Mediterranean material. It is not considered that the failure to establish a stem elongation yield association in the Mediterranean x Northern European families invalidates these suggestions. In this material an additional factor in yield variation was winter dormancy but the failure to establish an association in Sept. is attributed to the sampling anomaly already mentioned.

The components of yield in April were not compensating but it is still very doubtful that they were the determinants of yield. Although the April values in fig. 72 were similar to those in fig. 71 the explanation suggested for the hybrid vigour of the Mediterranean x Northern European families was in the observed out-of-season growth rather than in a favourable combination of components.

The conclusion that yield reflects the primary process limited by the environment and that its components vary only in a compensatory manner refers to the immediate yield components. Components of components may show variation that is not compensating as was found for instance in tiller number in which parent 17 had both low sterile and fertile numbers.

Cooper and Edwards (1961) have also concluded, from somewhat different reasoning, that yield components in pasture grasses were not profitable factors on which to select. They arrived at this conclusion from a study of plants that where in the seedling stage and not competing, , but went on to suggest that selection for components was not likely to increase yield in mature competitive swards. If photosynthesis is the primary process in production then the argument against selection of components is more applicable in pasture plants than in most other crop plants as the total photosynthetic organ of the grass plant is harvested to constitute the economic yield. Selection of components of this organ could not increase photosynthesis or yield. Possibly in other species where economic yield is only a small portion of the plant, such as a fruit, then the relation to photosynthesis may not be so complete and conceivably selection of the components may influence yield.

In view of the striking association of stem elongation with seasonal yield obtained in the present study if might be wondered why stem elongation has not been emphasised as a means of increasing productivity in those countries which have long been concerned with pasture grass breeding. Most of these countries are in the Northern temperate regions where plants are dormant during the winter, when daylength is very short and temperatures low, and where growth in the spring begins under increasing daylengths and rising temperatures. All pasture species within two months or less from regrowth have completed the process of stem elongation and have headed (Thomson, 1959). Although there is some variability under these conditions, and early and late varieties are designated, this variation is nowhere near as large as occurred here, where genotypes within one species differed by four months in their beginning of stem elongation. In Adelaide regrowth begins at the change from a hot dry period to a cooler wet period with shortening daylength. Evidently these latter conditions were not so severe as to restrict some genotypes from exhibiting stem elongation in

May and June, while others did not until Sept. Wide variation may occur between these genotypes in their countries of origin, but as pointed out by Heslop Harrison (1959) variation between ecotypes may increase greatly when introduced to new environments particularly for characters such as the reproductive phase, determined by natural photoperiod and temperature. The increase in variation is due to an interaction between the new environment and small genetic or developmental differences present within and between ecotypes. In the grasses, examples of increased variation in exotic material attributable to genetic differences have been found in *Bouteloua* (Olmsted, 1944) and *Lolium* (Cooper 1954).

One other character found to be associated with top weight was the stubble of the sterile tillers, which affected the regrowth from summer dormancy. It is logical to suggest from our knowledge of the fructosan content of the stubble that initial regrowth was from reserves. Added to this the plants when summer dormant, had all their leaves and stems brown and seared with no photosynthetic area exposed. A greater assurance would be gained of the importance of stubble weight as an attribute, if it were known for how long the regrowth was dependent on reserves and when it was replaced in function by current photosynthesis. Difficulties in answering this type of question have been discussed by May and Davidson (1958). It is possible that reserves are important when the photosynthetic area is small, a situation occurring in the present experiment only at regeneration from dormancy. In spite of this it might have been anticipated that any advantage in regrowth and hence leaf area, initially conferred by reserves, would be subsequently accentuated, but this did not occur the advantage was transient soon to be replaced in importance by stem elongation. With so short term an effect on yield there must be doubt as to whether selection for this character would be worthwhile.

Of the other characters considered none was so highly correlated with top weight as to warrant selection although a knowledge of their variation, particularly the variation in heading date is necessary for breeding purposes. The techniques used to overcome this variation in the parents and bring about simultaneous flowering and pollination were sufficiently successful in terms of seed production to be used in the continuation of the breeding programmes of topcrossing and crossing between strains that have been proposed.

The present results were obtained under one system of management but it is possible to speculate on what the results would be if the grass swards were defoliated paying particular attention to effects on stem elongation and its relation to yield. During stem elongation the terminal buds rise progressively above ground. Defoliation may therefore remove these buds depending on the stage of stem elongation and level above ground of the defoliation. Once the buds are removed the tillers are incapable of regenerating new terminal buds and further development of that bud ceases. In vegetative tillers the terminal buds are so close to the ground that they are seldom removed by defoliation and regrowth may occur by further activity of these buds. When, therefore, a defoliation is carried out both the yield and subsequent regrowth will be dependent on whether or not the plant has reached, and how far it has advanced, into the reproductive phase. A very high yield but poor chances of regrowth, may be anticipated from a plant in the reproductive phase and vice versa from plants that have not yet reached this phase. This situation has been clearly demonstrated in *Phleum* (Davies, 1956). Under defoliation therefore, each family will show a peak yield at a certain time of the year coinciding with its stem elongation. There is then no reason why the suggested breeding plans will not have picked out genotypes with high seasonal yields under defoliation coinciding with their stem elongation, but a discrepancy may arise in the spring when some of the early elongating genotypes may have had all their fertile tiller buds removed by defoliation so that their yields will be less than suggested by cumulative growth in undefoliated swards. This may not be important to the breeding objectives as the emphasis in the selection of the families was placed on the autumn and winter periods when the grazing animals are most short of feed under the existing varieties and managements.

Following early work on the chemical composition of grasses (Fagan and Jones, 1924) it was thought that stemmy material was of low nutritive value but more recent work on digestibility of grasses including cocksfoot indicates that this view was not correct (Minson *et al*. 1960). No marked decline in digestibility occurs until after head emergence, and under a grazing routine the number of heads that actually emerge may be very small. Selection for high yield, occurring as a result of stem elongation, should not therefore lead to a forage in any way inferior in terms of quality, and quality should not be a major problem in the proposed breeding programme.

SUMMARY

1. As part of a breeding programme on cocksfoot (*Dactylis glomerata* L.) investigating the merits of Northern European material and recently introduced Mediterranean material, an assessment was made of the combining ability of seven parents of Mediterranean origin and two of Northern European origin on a basis of their progeny performance after crossing in all combinations. Because of the known differences in seasonal growth of the parents, the F_1 families were not analysed together, but considered as a diallel of Mediterranean families and a topcross of Mediterranean x Northern European families.

Broad comparisons were made between the purely Mediterranean, Mediterranean x Northern European and purely Northern European groups of families. It was known, from previous experimentation, that in the winter rainfall growing season (Apr. to Nov.) of South Australia purely Northern European material might show a low survival while purely Mediterranean material might have an excessively pronounced summer dormancy. Information on the Mediterranean x Northern European hybrids for these characteristics was therefore needed, but also on their autumn and winter growth, for in this environment it is at these seasons of the year that pasture growth is limiting to an increase in animal production.

2. The F_1 seed was obtained by a special technique of emasculation and controlled pollination.

3. The main assessment of the progenies was in terms of seasonal top growth measured by sampling from undefoliated swards at nine harvests

over two years. Other characters assessed were stubble weights, root weights, tiller numbers, tiller weights, tiller lengths, heading dates and summer survival.

4. Differences in seasonal top growth were found between the Mediterranean, Mediterranean x Northern European and Northern European groups of families at the beginning of the growing season (early autumn) and again in mid-winter. In the early autumn the average yield of the Mediterranean x Northern European group was higher than either of the other two groups, a result tentatively attributed to the combination in these hybrids of drought resistance from the Mediterranean parents and lack of summer dormancy of the Northern European parents. This combination enabled slight growth to occur from intermittent rain before the main break of the season giving an early advantage to these families. Before the main break, the purely Mediterranean families were summer dormant and the Northern European families severely wilted.

In mid winter the Mediterranean group exceeded the other two groups on average as it did not show the winter dormancy apparent in the Northern European families and in some conbinations of Mediterranean x Northern European families.

Differences were found within the groups on the basis of the diallel and topcross tests. For the Mediterranean families, analysed in the diallel, significant differences in general combining ability were found in the early autumn and during mid winter and spring. In the topcross of Mediterranean x Northern European parents no significant differences between Mediterranean parents were found in the autumn but they did occur during midwinter through winter dormancy of some combinations, and in the spring. There were few differences between the Northern European parents in the topcross, and these were not constant.

In both the diallel and topcross no one parent excelled in combining ability for yield at all seasons of the year, rather the situation was that one parent excelled at one time, another parent at another.

The general combining ability assessments of the Mediterranean parents by the diallel tests and by the topcross test did not agree. One of the occasions when the disagreement was clearly expressed was midwinter, when two Mediterranean parents showed winter dormancy in their combinations with Northern European parents but none with Mediterranean parents. Disagreement between assessments did not occur for all characters analysed, being small for tiller number and negligible for heading date.

5. Significant variation in general combining ability was found for the other characters at many of the harvests.

For stubble weights, parents differed from the top weights in having uniformly high or low general combining ability and not showing wide fluctuations with the season of the year. Differences between parents were most marked at the beginning of regrowth and at the reproductive phase at the end of the season but with an additional midwinter period for the Mediterranean x Northern European topcross when the same families, already noted, were winter dormant.

For root weights parents also tended to be uniform in general combining ability, but a parent high for combining ability for stubble weight was not necessarily high for root weights. The Mediterranean x Northern European group of families consistently had a greater development of their roots and stubble than the Mediterranean families and were little different from the Northern European families.

The picture for number of tillers was completely different from the other characters considered as numbers for all families rose to a maximum value in the middle of the growing season and then declined, however the date of occurrence of this maximum and its value was not the same for all families. A second small rise was recorded in the spring between the penultimate and last harvest of the year. There was wide variability for tiller number and parents tended to be uniform over harvests in their general combining ability but the expression of this was considerably modified through the differences in timing of the maxima.

Two major factors were detectable in the results for tiller weights firstly that there were inherent differences between families in the weight of their vegetative tillers and secondly the increase in weight that occurred when the tillers elongated in the reproductive phase. Histograms of tiller weights, from the time this occurred, gave a bimodal distribution comprising light tillers that remained vegetative and heavier reproductive tillers. Between the earliest and the latest families there was a difference of four months in the time at which reproductive tillers were first apparent so that this was a major factor determining tiller weight differences. As a result early parents had a high combining ability for most of the growing season.

An identical picture was obtained for tiller length as the reproductive tillers, with elongated internodes, gave high values for tiller lengths.

Clear cut results were obtained for heading dates. A large difference shown by all families between the two years was attributed to age of the plants from establishment. The two Northern European parents were later heading than the Mediterranean parents and this was reflected in the topcross families on average being later than the Mediterranean families. Despite this difference and the differences between years in mean heading dates, the diallel and topcross assessments gave almost identical rankings of the parents for general combining ability. Reasons were suggested for the far greater range in heading date of nearly 60 days, found in this study, than in similar studies in northern temperate environments.

Summer survival by the Mediterranean families was virtually complete and therefore no analysis of the small differences was attempted. In the Mediterranean x Northern European topcross where the average survival was 88% an analysis was performed but without detecting significant differences. The survival of the purely Northern European families was 59%. The particular summer experienced was slightly better than average for summer survival if this is determined by summer rainfall.

6. The specific combining ability was found to be significant on several harvest occasions for the different characters but there was very little constancy between harvests of the effects and it would be difficult to utilise this variability in a breeding programme with the

material under test. For all harvests and characters the specific combining ability was rarely as important as the general combining ability.

7. Genotypic correlations were calculated from the general combining ability effects to determine the association between top weight yields and other characters. It was concluded that the differences in regenerative ability between the Mediterranean families at the beginning of a new season was related to the sterile component present at the end of the previous season. The relationship was with both the sterile tiller number and sterile stubble, from which regeneration began. There is a possibility that the roots were also concerned, but this could not be rigorously tested.

During the mid winter period, the high yield of some of the Mediterranean families was associated with the early development of reproductive tillers. It was concluded that changes in metabolism of the plants, or changes in the profile of the swards, that occurred when plants entered the reproductive phase, gave rise to these high yields during a vitally important period of the year. There was wide variability in the date of development of reproductive tillers, even though the parent had not been chosen to show this variation. It should be possible to breed or select genotypes even earlier in the date at which they begin stem elongation.

Later in the spring high yields were found in genotypes in which a large proportion of the tillers had become reproductive.

For the Mediterranean x Northern European families the differences in yield in mid winter were related to the occurrence of winter dormancy but in the spring yields were again related to the proportion of the tillers that had become reproductive.

None of the other characters were found to be associated with differences in top weights.

8. The discussion was devoted to a consideration of possible breeding programmes with Mediterranean material and with Mediterranean x Northern European hybrids, emphasising extension to new environments, to the importance of selection of components to increase yields and to a consideration of how applicable the results would be under other managements. Mention was also made of the question of quality which should not be a problem during the stem elongation phase of the winter but which might be important at maturity in the summer.

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APPENDIX I .

The geometric mean in gm. of sterile and fertile components of top weight at harvests of the reproductive phase.

	Dec. 23, 1959		Nov. 7, 1960		Jan. 9, 1961	
	Ster.	Fert.	Ster.	Fert.	Ster.	Fert.
17.43	.92	2.93	1.35	15.78	.97	15.07
52	2.16	5.81	1.96	19.41	1.27	14.83
56	.78	4.72	.61	21.28	1.01	15.03
63	2.65	4.46	3.22	20.99	2.03	22.54
80	2.43	7.10	1.85	18.92	1.69	21.68
82	2.73	5.40	1.69	19.82	1.52	12.19
92	3.34	1.91	2.10	16.94	1.40	8.05
93	3.08	1.63	4.84	13.27	3.76	9.14
43.52	1.35	4.40	3.56	10.12	1.60	3.56
56	1.04	4.07	1.23	15.70	1.17	12.47
63	2.17	1.93	3.99	7.87	4.09	3.72
80	1.86	4.61	1.16	12.05	2.19	10.42
82	1.46	3.52	1.13	7.45	1.50	5.27
92	3.03	2.25	5.33	23.17	2.87	10.81
93	2.33	1.90	4.14	14.29	4.42	10.02
52.56	.97	3.52	1.67	25.59	1.50	16.03
63	1.75	1.29	3.88	9.00	3.03	12.13
80	2.31	6.68	2.82	18.11	1.53	16.48
82	1.57	2.81	3.22	11.07	4.09	9.93
92	2.64	2.04	7.46	4.66	2.01	6.65
93	3.27	3.15	3.59	7.45	3.70	4.66
56.63	1.51	3.24	2.12	15.35	2.67	11.35
80	1.87	8.61	1.69	23.99	1.52	18.00
82	.94	4.51	1.82	13.55	2.18	12.36
92	2.56	3.48	1.14	10.57	4.22	15.74
93	2.52	3.85	2.76	19.10	2.94	21.48
63.80	3.07	2.17	4.63	24.43	2.42	19.50
82	1.64	.66	2.58	7.40	3.21	7.38
92	5.68	1.14	11.61	5.26	8.15	9.51
93	3.66	.30	8.77	3.59	4.24	5.87
80.82	2.07	3.78	3.37	12.16	2.59	17.06
92	4.01	4.02	9.84	10.28	4.01	18.89
93	3.48	5.42	6.10	15.10	5.42	18.41
82.92	4.46	2.65	4.70	17.54	5.18	14.49
93	3.34	1.24	2.52	4.55	4.22	16.33
92.93	6.01	1.06	7.74	4.20	1.11	1.93

APPENDIX II.

The geometric mean in gm. of sterile and fertile components of stubble weight at harvests of the reproductive phase.

	Dec. 23 1959		Nov. 7 1960		Jan. 9 1961	
	Ster.	Fert.	Ster.	Fert.	Ster.	Fert.
17.43	.68	.95	.52	3.79	0.37	3.32
52	1.26	1.96	1.03	5.32	0.60	6.00
56	.37	1.41	.19	3.92	0.48	4.06
63	2.07	1.94	1.79	6.24	0.93	7.10
80	.93	1.54	.49	2.42	0.44	3.72
82	1.54	1.95	.54	5.40	1.04	4.41
92	2.15	.92	.41	5.52	0.73	3.37
93	2.56	.55	2.05	3.74	1.65	3.36
43.52	1.09	1.45	1.85	2.59	0.85	2.54
56	.62	1.12	.39	3.05	0.47	3.66
63	2.24	.90	2.62	2.45	3.12	1.81
80	1.21	1.39	.41	1.95	0.82	2.25
82	1.36	1.15	.57	1.97	0.79	2.35
92	2.53	.86	2.29	5.32	1.61	3.86
93	2.02	.79	2.60	4.40	2.23	4.84
52.56	.65	1.40	.87	6.00	0.65	4.98
63	2.15	.62	2.37	3.06	1.95	4.98
80	1.17	1.58	.66	3.56	0.48	3.16
82	1.65	1.14	2.19	4.41	2.79	4.76
92	2.52	1.07	4.55	2.42	1.71	3.55
93	2.85	1.12	1.71	2.92	2.17	2.03
56.63	1.49	1.38	1.25	4.50	1.26	4.19
80	.78	1.40	.45	3.30	0.60	3.56
82	.72	1.15	.93	3.01	1.42	4.25
92	1.81	1.27	.79	3.05	3.53	5.15
93	2.26	1.16	1.31	4.90	2.00	6.61
63.80	2.30	.78	1.29	3.28	1.12	3.11
82	2.35	.33	1.66	2.92	2.24	5.07
92	5.73	.79	8.77	3.10	5.08	5.47
93	4.72	.40	5.43	1.37	2.61	2.95
80.82	1.57	1.06	1.38	2.86	0.86	4.37
92	2.41	1.08	3.13	2.21	1.66	4.62
93	2.33	1.17	1.93	3.01	1.45	4.11
82.92	3.94	1.03	2.35	5.35	3.00	6.47
93	3.83	.47	1.43	1.33	2.45	6.59
92.93	5.18	.47	4.17	1.81	1.13	1.61

APPENDIX III.

The geometric mean number of sterile and fertile tillers at harvests of the reproductive phase

	Dec. 23 1959		Nov. 7 1960		Jan. 9 1961	
	Ster.	Fert.	Ster.	Fert	Ster.	Fert.
17.43	13.9	5.6	4.2	11.2	9.4	13.7
.52	16.7	6.7	7.2	11.0	9.8	12.2
.56	10.6	6.5	3.9	11.2	8.4	12.9
.63	29.3	7.9	11.8	13.8	11.8	19.5
.80	19.1	8.5	5.4	12.8	11.3	17.6
.82	22.9	8.2	8.4	11.7	12.9	12.0
.92	20.7	3.6	5.2	9.3	8.6	8.1
.93	26.1	2.3	13.9	8.5	14.1	8.0
43.52	21.5	12.4	27.4	13.4	22.8	10.9
.56	20.0	9.2	10.1	14.8	12.3	18.1
.63	56.6	7.4	30.6	12.1	42.2	9.7
.80	34.4	13.1	24.2	22.1	25.8	25.0
.82	25.5	9.8	16.4	12.1	19.9	18.6
.92	43.4	6.3	32.8	19.8	30.7	8.9
.93	35.9	6.4	23.7	18.3	40.1	24.1
52.56	14.9	8.4	9.9	18.5	15.6	19.1
.63	51.1	5.8	22.2	14.0	30.5	16.7
.80	25.4	12.5	11.5	21.6	12.1	25.2
.82	33.3	7.4	18.4	16.1	31.0	19.5
.92	31.7	7.1	22.7	6.9	15.2	10.4
.93	30.8	5.2	15.1	7.4	20.2	7.4
56.63	33.9	7.7	13.3	15.8	18.6	18.4
.80	23.7	12.8	8.2	22.6	16.3	27.8
.82	19.3	8.3	12.8	13.4	27.1	19.0
.92	24.8	7.6	7.6	9.1	29.8	19.7
.93	25.0	6.0	10.9	13.6	16.6	19.1
63.80	46.9	6.0	24.8	25.6	23.1	32.8
.82	63.5	3.9	17.1	13.1	26.6	15.8
.92	65.2	3.4	38.3	7.0	30.6	14.5
.93	42.0	1.2	19.2	3.4	20.0	3.7
80.82	40.2	10.2	18.5	18.5	20.3	19.6
.92	34.0	9.4	26.6	12.9	32.1	24.3
.93	37.4	7.7	29.9	17.8	31.3	26.9
82.92	34.9	6.3	14.1	17.1	29.3	20.6
.93	40.9	2.5	13.9	3.9	20.9	14.6
92.93	33.0	2.1	19.5	3.6	3.1	1.4

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