STUDIES IN METHODS FOR THE ASSESSMENT OF PROGENIES IN HERBAGE GRASSES

by

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SUMMARY of CONTENTS

SECTION 1

General Introduction

SECTION 1.1 INTRODUCTION

The forage grasses in common use in Great Britain and other temperate countries are in general more or less obligate outbreeders and the breeding programmes developed for their improvement depend on selection based on the assessment of combining ability of potential parent lines or clones. This means that the breeding value of a line or a clone is assessed on the basis of the performance of its progeny rather than on its intrinsic agricultural merit and the actual plant material which is subjected to agronomic testing is not necessarily that upon which selection is practised; part, therefore, of the problem of devising suitable breeding techniques for outbreeders lies in finding appropriate methods of testing progenies. These methods should ideally correspond to the agricultural practice for the crop concerned in the region for which the eventual variety is intended; at the same time they should be economical in their use of resources per progeny since, especially in the early stages of a breeding programme it is desirable to test a very large amount of material. In many cases it may be better to sacrifice some degree of precision in the interest of handling large numbers of progenies. Later in the breeding programme when the number of potential parents has been reduced a larger proportion of resources may be allocated to each progeny.

The practical problems raised by the above requirements are particularly acute in the herbage grasses which are normally grown in a sward and almost always in mixture with other grasses or with legumes. The management of small sward progeny trials is complicated by the difficulty of obtaining uniform stands due to variable seed quality and to chance variations in establishment which may have disproportionately large effects in small plots, leading to inflation of the error variance and the failure to detect "real" differences between treatments. In addition sward plots require large quantities of seed for a given area.

The problem of devising methods for progeny testing trials of grasses then becomes one of finding some combination of plot size and plant density which reflects sward performance with sufficient accuracy without the attendant disadvantages of sward trials.

Assuming that it is possible to find such a combination, there remain the problems of relating pure-stand performance to performance in mixtures, mixtures not only with other species or varieties but also with other progenies in the same breeding programme.

The work to be described, falls, therefore, into three distinct parts which form the matter of the three next sections.

Section 2 deals with the relative performance of some Italian ryegrass populations, grown over a range of densities.

One of these is a sward density and is the standard against which the other densities are judged. The remaining densities were chosen as being likely to give a reasonable reflection of sward performance while being comparatively easy to manage and economical of space and seed.

Section 3 examines the effect of varying plot size and shape on the efficiency of trials carried out at one of the densities investigated in Section 2.

Section 4 describes the behaviour of a group of grass cultivars, grown alone and in two-component mixtures with each other, in an attempt to examine the relationship between pure stand performance and performance in mixtures.

SECTION 2

THE CHOICE OF A SUITABLE NON-SWARD DENSITY FOR ASSESSING SWARD PERFORMANCE

SECTION 2.1 INTRODUCTION

Ideally the density chosen for grass variety trials should be one that gives results in conformity with those from sward trials and which uses as little seed as possible per progeny.

It is also desirable that the density should be one which permits the identification of single plants, so that in a selection programme, progeny plots can also be used for selection purposes.

Most of the early breeding work with forage grasses was based on the assessment of plants grown at relatively wide spacings where neighbouring plants might be expected to affect each other little, if at all. Spaced plant trials are easy to conduct and are of value for the preliminary assessment of potential breeding material particularly with regard to such characters as flowering time habit of growth and disease susceptibility. However, within any one group of plants all of the same general type as regards flowering time and habit of growth there may be expected to exist fairly large differences in sward yielding ability. Sward tests are themselves notoriously difficult to conduct and in addition require relatively large quantities of seed

SECTION 2.2 LITERATURE

The early work on the breeding of herbage grasses depended essentially on the selection of parent plants based on their behaviour as widely spaced individual plants. Comprehensive accounts are given by Stapledon (1930, 1931) and by Jenkins (1930, 1931, 1951, 1955). These authors emphasised the value of widely spaced plants for the assessment of leafiness, vigour, habit of growth, disease reaction and winter hardiness. Even in the early stages, however, the importance of considering performance under conditions closer to those of agriculture was obviously realised.

Stapledon (1931) reported on the relationship between some spaced plant characters and sward behaviour, stating, for example, that plants having a high proportion of barren tillers compared to fertile tillers tended to produce persistent and leafy tiller swards. Spaced plant trials retain their importance, particularly for the preliminary assessment of general plant type e.g. pasture as opposed to hay type, erect versus prostrate, and for the other characters mentioned above. Spaced plant assessment is also important in "strain" identity trials (Gregor 1956, Thomson, 1961).

Many authors have reported on the behaviour of herbage varieties grown at various densities compared to their behaviour under sward conditions. Ahlgren, Smith and Nielson (1945) working with Poa pratensis reported that there was little relationship between yields of selections grown in spaced-planted rows and in mass seedings. Kramer (1947) found a similar situation when comparing the yields of individual plants and yields in mowing plots and remarked that yield, in spaced plantings, depends largely on height and basal diameter, characters which have little effect on yield in solid stands. Proudfoot (1957), however, comparing the yields of five cultivars of perennial ryegrass, while agreeing that the order of spaced plant performance differed from that of the swards, found that the discrepancy tended to disappear when single plant production was related to the actual area occupied by the individual plant.

Murphy (1952) examined yield correlation between broadcast swards, drilled rows and widely spaced plants for a range of differently derived progenies in cocksfoot, smooth bromegrass and red fescue. He reported simple correlation coefficients ranging from -.63 to +.89 for the comparison between drilled and broadcast polycross progenies and from -.93 to +.95 for that between spaced and broadcast polycross progenies.

Torrie (1956), in reviewing the findings of a number of workers with outbreeding forage grasses, pointed out that while spaced plantings are, in general, satisfactory for the evaluation of characters of high heritability, a density more akin to that of the agricultural sward is required for the assessment of yielding ability, a character showing large genotype-environment interactions.

Nissen (1961) reported finding low correlations between hay yields in Timothy grown as spaced plants and in swards. Green and Eyles (1960), while finding that the order of yields in perennial ryegrass varieties was reversed in spaced plantings compared to swards also found that either density was suitable for assessing the order in which varieties attained their maximum rate of growth in the spring.

Miles (1961) emphasised the importance of sward testing in the assessment of herbage cultivars and Scheijgrond and Vos (1961) in a paper delivered on the same occasion emphasised the suitability of spaced plant testing for many characters, including seasonality of production, but once again found that for yield assessment the sward was required.

Knight (1961) examined the behaviour of nine Cocksfoot clones grown under spaced plant conditions and in tiller swards. He found, in general, very low correlations between spaced plant and sward performance and further, that tillering ability in the spaced plants was not associated with dry matter production under sward conditions. This latter finding conflicts with the belief of some earlier workers that tillering ability of spaced plants was a useful guide to sward performance.

Heinrichs, Lawrence and Morley (1962) found, in <u>Agropyron intermedium</u>, the almost customary low association between spaced plant and sward yields and in fact, in the first year (presumably the seeding year) found a negative correlation between the two. These authors claim however that in a creeping grass such as <u>Agropyron</u>, "creep" and height assessments made on spaced plants were a good indication of sward performance.

The almost overwhelming impression created by the literature is that, while spaced plant assessment is necessary for the evaluation of many economically important characters, it is of little value for the assessment of yielding ability, which must be carried out under conditions closer to those of the sward. There has been relatively little work on the value of densities intermediate between that of the spaced plant (that is with about two feet between neighbouring plants) and of the sward. Lazenby and Rogers, however, in a series of papers have reported on the behaviour of cultivars mainly of perennial ryegrass grown over a logarithmic range of densities ranging from the sward up to 27 inches between plants. In an early paper (1960) these authors make the point that spaced plants are probably valuable in the early stages of a breeding programme when differences are likely to be large and morphological characters of importance. They also point out that the highest sward yields are likely to be restricted to varieties with a very large leaf area index when grown as spaced plants. In subsequent papers Lazenby and Rogers (1962, 1964, 1965a, 1965b, 1965c) examined the relationship between yield per plant and plant density and found this to be effectively log. linear over the range of densities studied, although the 24 inch spacing tended to yield less than would be expected on a log. linear basis. They found a close association between tiller number and total yield but the relationship was much poorer at individual harvests. In an experiment with four cultivars of perennial ryegrass, Lazenby and Rogers (1964), found that the three lowest densities (that is, sward, three and nine inch square plantings) gave the same relative order of performance, whereas plants spaced at 27 inches apart sometimes showed the reverse order of performance and that only the comparisons between this spacing and the other three gave significant density X variety interactions. In two later papers (Lazenby and Rogers, 1965a, 1965b) these authors examined the effect of applied nitrogen on spaced plants and on swards of Lolium perenne and found significant genotype X nitrogen and genotype X density interactions in each of the first two harvest years. The general conclusion of Lazenby and Rogers is that plant densities corresponding to a between plant interval of up to nine inches are suitable for assessing sward yielding ability, that such densities are easier to manage than the sward itself and that the lower of the suitable densities (6-9 inch spacing) permit the identification of individual plants and might be useful for selection purposes under conditions approximating to those of the sward.

SECTION 2.3 MATERIALS and METHODS

The material for this study consisted of seven cultivars of Italian ryegrass and seven two-component mixtures. Six of the mixtures contained equal proportions of the two components but because of shortage of seed of one of the varieties, the seventh mixture contained 58.5% of one component and 41.5% of the other. In calculating the weight of seed of each variety in a mixture allowance was made for differences in 1,000-seed weight, and percentage germination and purity. Details of the cultivars and mixtures used are given in Table 2.3.1.

Four different densities were chosen for study. These were -

(1) Broadcast sward

(2) Sown rows with three inches (7.6 cms) between rows in one yard square plots (i.e. each plot consisted of 12 rows each 1 yard (2.74 m) long)

(3) Three inch square planting in one yard square plots

(4) Six inch (15.2 cms) square planting in two yard square plots.

The numbers per plot in density treatments (3) and (4) were the same i.e. 144.

The trial was laid out as a split plot of four replications, having densities as the main treatments and varieties as sub-treatments. (In the account of this portion of the work the term "variety" is used when reference is intended to any one of the fourteen sub-treatments irrespective of whether it is in fact a pure variety or a mixture the two latter terms being used when necessary to distinguish between the two types of population.)

The position of the main treatments within the replications was not completely at randon; this course was adopted to facilitate harvesting. The non-random positioning of the density treatments, while it might be expected partially to invalidate the overall comparisons between densities, would not adversely affect the overall variety comparisons nor, more importantly, the estimates of density X variety interaction or the correlations between variety yields at different densities.

The trial plan is shown in Fig. 2.3.1. The whole trial was sown between 25th and 29th May, 1961. The three inch sown rows were sown with the aid of a yard square shallow box with parallel slits at three inch intervals in the bottom through which the seed was sown. The seed intended to provide plants for the three and six inch spaced plantings was broadcast in the centre of the appropriate plots, on 30th June. As soon as these plants were large enough to handle they were lifted and planted in the plot at the spacing required. Dates of sowing and planting are given in Table 2.3.2.

During 1961 the plots were kept mown but no yield data were taken. Four harvests were taken in 1962 as detailed in Table 2.3.3. The whole trial area received 6 cwt/acre CCF 3 immediately before sowing, and six hundredweight of CCF 1 after each cut. Harvesting was carried out with an "Allen" autoscythe, the end rows of the sown rows and the edge plants in the spaced plant plots having first been cut with sheep shears. The actual areas harvested are shown in Table 2.3.4.

SECTION 2.4 RESULTS

The yields for each cut and for the sum of all four cuts are given in Table 2.4.1, and summarised analyses of variance in Table 2.4.2. The most notable feature of the analyses are the low and mostly sub-normal variance ratios for the density X variety interaction. The F value for this item is significant at $P = .05$ for the third cut only. In Table 2.4.3 the sums of squares for each of the six comparisons of two densities are given and also the percentage contributions of each density to the total sum of squares. The only significant value is that for the interaction between the three inch sown rows and the three inch square planting in cut three.

A possibly more realistic way of comparing the behaviour of varieties at different densities is to examine the correlations between the yields for each pair of densities.

The simple correlation coefficients, calculated over all fourteen varieties, are given in Table 2.4.4 and for the pure varieties and mixtures separately in Table 2.4.5. The same data are shown graphically in Figs. 2.4.1 to 2.4.5. The most important values are those for the comparisons of each of the non-sward densities with the sward. In Table 2.4.4 all the values for the first and fourth cuts and for the sum of all cuts are significant at the 5% level; the values for the second and third cuts are less satisfactory.

Turning now to Table 2.4.5 there is immediately apparent a contrast between the correlations obtained using the pure variety yields and those based on the mixture yields. Considering, for the moment, only the pure varieties, most of the coefficients are reasonably high, approaching or exceeding + 0.7. The main exceptions occur for the sward VS six inch, sward VS three inch and to a lesser degree in sward VS three inch rows comparisons for the third cut. The low values in these instances are difficult to account for, especially in view of the rather higher values for comparisons between other pairs of densities. Inspection of Figs. 2.4.3 (a) (b) and (c) suggests that this is largely due to variety five giving disproportionately high yields under sward conditions but again, it is difficult to see why this should be so. There is some indication that in this cut variety five tends to perform relatively better as plant density increases since the effect noted is also present to a lesser extent in the next lowest density, the three inch sown rows.

In general, the correlations show a high degree of agreement between the performance of pure varieties at sward and non-sward densities. This is certainly true for the total yields. While the agreement is not quite so good for individual cuts, it is, with the exceptions noted above, quite satisfactory. The effect of varying density on the relative performance of mixtures is, however, more marked and it would seem likely that densities lower than that of the sward are of limited use as guides to sward performance of mixtures of varieties.

Quite apart from the degree of agreement which any non-sward density may show with the sward, its usefulness will also depend on its ability to detect differences between varieties. This problem is dealt with more fully in the later sections of this work but for comparative purposes the error variances per plot and the coefficients of variations are given in Table 2.4.6. On the basis of the plot sizes actually used all the coefficients of variation for total yield are satisfactory, and the same applies to many of those for individual harvests. There is a tendency for the six inch spacing to be less good than other densities. Table 2.4.6 also gives error variances and coefficients of variation on a per square yard basis for three different assumed values of "b", the index of soil heterogeneity. (The interpretation of the magnitude of b is more fully discussed in a later section, but briefly it can take any value between 0 and minus 1, the"higher" values, i.e. nearer to -1, indicating a lower degree of correlation between adjacent areas of ground. The higher the correlation the less is the advantage to be gained from increasing plot size.)

On the basis of the magnitude of the coefficient of variation per square yard, density treatments (2) and (3) are clearly superior, these being the density treatments grown in the smallest plots; as the value of b falls, this superiority decreases and, with an assumed value for b of 0.2, the relative sensitivities of the density treatments are much as they were in the original plot sizes.

SECTION 2.5 EASE OF MANAGEMENT OF DIFFERENT DENSITIES

It had been hoped to make some objective assessment of the time taken in the harvesting of the different density plots. This proved difficult to achieve in practice (some critical data were obtained for the six inch spacing in a later trial and are presented in a later section). Notwithstanding this difficulty, it was possible to make some assessment of the relative ease of management and rate of harvesting of the different densities. The main objection to any of the non-sward plots lay in the time required to cut out the discard rows around each plot; This operation could, however, be accomplished on the day preceding actual harvest and did not interfere with harvesting itself. The six inch spaced plots, as might be expected, proved the easiest to manage, there being no difficulty in distinguishing individual plants and hence the limits of any one plot. The three inch spacing was rather less satisfactory from this point of view. More time was required to locate plot boundaries and minor errors were fairly frequent; much the same was true of the three inch sown rows with the additional complication that it was not always easy to be sure of harvesting a constant length of row. In spite of these difficulties, the low coefficients of variation for the three inch rows suggest that they were, in fact, handled with a satisfactory degree of precision.

Once the cutting out of plot borders was completed, the three non-sward densities were more or less equally easy to handle. The six inch spaced plots, being larger, took a little longer to cut than the others and because of limited capacity of the balance available, two weighings per plot were sometimes required, necessitating two subsequent tare adjustments for the containers plus adherent soil. (In a later experiment a larger capacity balance was available with tare adjustment and this probably largely accounts for the better results obtained - see Section 3 of this report.) The sward plots, mainly because of their larger size, took longer to harvest and to weigh.

SECTION 2.6 QUALITY OF ASSESSMENT OF SWARD PERFORMANCE FROM NON-SWARD PERFORMANCE

The sward density is inconvenient for progeny testing purposes in a breeding programme and to a lesser extent in the carrying out of trials of cultivars. It is, nevertheless, true that performance at sward density is what determines the value of a progeny or cultivar. However convenient certain non-sward techniques may be, they are of no use unless they permit the ranking of varieties in the same or nearly the same order as that resulting from a sward test. It is not to be expected that the yields from a non-sward density will be the same, nor in exactly the same ranking order, as that from the sward density but the agreement might well be sufficiently good for most practical purposes, more especially if the non-sward technique permits the testing of a larger number of varieties and requires less seed of each variety.

The most obvious general guide to the degree of correspondence between sward and non-sward performance is the correlation coefficient, the magnitude of which, of itself, gives a fairly good indication of the value of any particular non-sward technique. However, it is possible to use the correlation coefficient to arrive at a more precise estimate of the efficiency of assessment.

The problem of estimating the efficiency of selection or assessment is, of course, a general one and has been discussed by Keuls and Sieben (1955) in connection with the genetic efficiency of selection based on observed (i.e. phenotypic) performance. Gilbert (1961) has discussed the possible value of, for example, selection based on seedling characters, pointing out that even quite low correlations between seedling and adult characters can give a useful gain in the efficiency of selection compared to a random discard i.e. $r = 0$ (which is the only alternative when a large body of material has to be reduced to a more manageable size).

For the purposes of further discussion it is convenient to consider two measures of performance the 'true' performance (in the present case the sward performance) and "test" performance (non-sward). The value of the correlation coefficient between them is estimated from comparative trials such as that described earlier in this section.

If the varieties are assessed on the basis of their test performance as being either "good" or "bad" (i.e. in the upper fraction p_t or in the lower fraction $1-p_t$) then the population can be regarded as falling into four sections as in Table 2.6.1.

TABLE 2.6.1

		true performance		
		bad	good	
test performance	good	(A) wrongly assessed as good	(B) correctly assessed as good	p_t
	bad	(C) correctly assessed as bad	(D) wrongly assessed as bad	$1-p_t$
		$1-p_T$	p_T	1

p_t = "Superior" fraction of population on basis of test performance.

p_T = "Superior" fraction of population on basis of 'true' performance.

p_t may or may not be equal to p_T (in the sense that the fraction actually selected on the basis of test performance may be equal to, larger, or smaller than the fraction p_T in which the experimenter is actually interested).

The problem of measuring the efficiency of assessment now becomes one of estimating the value of B in Table 2.6.1.

If the magnitude of r is known, then this can be done by reference to the tables published originally by Everitt (1910, 1912) and extended by Lee (1927). The values of p_t and p_T must be converted to the corresponding values for the normal probability integral which is most easily done from a table of probits such as that in Fisher and Yates (1953). The values of p_t and p_T expressed in terms of the normal probability integral are called h and k by Lee; since her tables of tetrachoric volumes are symmetrical about the leading diagonal it does not matter which is which. The value read from the tables gives the value of B as a proportion of the original population; for practical purposes it is usually more convenient to express it as a fraction or percentage of the selected (i.e. assessed as best) fraction p_t. The percentage derived is, in words, the percentage of the superior test varieties which are also "truly superior". For some purposes it may be more useful to present the value of B as a proportion of the p_T fraction of the population since in the early stages of a multistage selection programme it might be desired to retain that fraction of the population which would maximise the chances of retaining all the material falling into some fraction p_T where $p_T < p_t$.

The value of B as a proportion of p_t or p_T gives two measures of efficiency of assessment one of which, B/p_t, is usually taken as the measure of efficiency or quality of selection; the other, B/p_T, is not normally used but seems of some importance because it measures the average efficiency of "retention" of varieties, progenies or plants.

Table 2.6.2 gives for various values of p_t and p_T the efficiency of selection ($^B/p_t$) for values of r from + 0.5 to + 0.95. Since $p_t = p_T$ the efficiency of selection is the same as that of retention.

Table 2.6.3 gives similar information for various values of $p_t \neq p_T$. In this table the estimates of efficiency of selection $^B/p_t$ are given first and those of efficiency of retention $^B/p_T$ second and are enclosed in brackets.

Parts of Tables 2.6.2 and 2.6.3 overlap with those of Keuls and Sieben and of Gilbert but these authors do not consider values of p_t or p_T less than 20%.

The information in Table 2.6.2 is shown graphically in Fig. 2.6.1.

Table 2.6.2 shows that a high correlation between true and test performance is particularly desirable if the selected test fraction (p_t) is to be small. With a lenient selection of 50% an increase in the value of the correlation coefficient from .50 to .95 improves the quality of the selected fraction 1.34 times (90/67) for $p_t = p_T$, whereas if only 0.5% of the best test varieties are taken the quality improves 6.5 times (65/10) for the same increase in the value of r.

The actual quality of a selection would tend to be rather higher than the figures in the tables indicate. The method adopted only classifies varieties as good or bad. Those 'good' varieties wrongly rejected as bad would, in fact, tend to be the poorest of the 'good' varieties and similarly those 'bad' varieties wrongly retained would tend to be the best of the 'bad' varieties.

Considering now the values of the correlation actually found for sward and non-sward densities it is obvious that so far as total yield goes any of the non-sward densities investigated would be adequate for purposes of varietal or progeny assessment of pure-stands. The correlation for the sward VS three inch rows and sward VS six inch are both over 0.9 and that for the three inch spacing is nearly 0.9. Taking for practical purposes a value of r = + 0.9, a 1% selection would consist of 55% of varieties in the top 1% on the basis of true performance and would consist entirely of varieties included in the truly best 10%.

The correlations for individual harvests are lower than those for the total (sum of four cuts) this is probably largely due to a genuinely lower correlation but possibly in part to too low a degree of replication; conversely, the higher values for the total harvest, may be due to the fact that the summation of successive cuts on the same plots will have an effect comparable to that of increased replication. Excluding the lower values for r at the third harvest a value of r of +0.7 seems reasonable for sward v non-sward. On this basis and otherwise using the example above, a 1% selection consists of 27% of the truly best 1% of varieties and 79% of the best 10%. Considering the figures for "efficiency of retention" a 50% selection contains all the best 1% of varieties and 95% of the best 10%, it would seem that a non-sward technique having a correlation of 0.7 with the sward is adequate for early testing in a breeding programme.

The low values of r recorded for the third harvest suggest that some caution is required in accepting non-sward techniques as adequate substitutes for sward testing, at least for single harvests. In general, however, the evidence is that the non-sward densities described are suitable for assessing relative sward performance of varieties of Italian ryegrass. There was little difference between the three non-sward densities as far as their correlation with the sward was concerned. The three inch sown rows were slightly better than the six inch or three inch square plantings. The two latter densities differed hardly at all. On grounds of convenience the six inch spacing was much better than the others and further work concerning optimum plot size for this density is reported in Section 3.

The correlations recorded for the mixtures are rather lower than those for pure varieties. It is not obvious why this should be so except in the general sense that one would expect any difference there might be, to be in this direction. It is difficult to imagine any important environmental differences between the mature sward and, say, the mature three inch spacing and it is most likely that the difference in behaviour of mixed swards and mixed non-swards is due to factors operating at the seedling stage when there might be selective elimination of one component of a mixture in the sward which would not occur under non-sward conditions.

SECTION 2.7 CONCLUSIONS AND SUMMARY OF SECTION 2

2.7.1. Conclusions:

The absence of density x variety interactions for yield indicate that any of the densities tested is suitable for the assessment of sward yielding ability.

A more sensitive measure, that of the correlation between sward and non-sward yields, confirms this conclusion and permits the estimation of the quality of selections based on non-sward yields compared to those based on sward yields. Since the correlations between the yields of varietal mixtures grown at different densities were rather lower than those for pure-stands it is considered that non-sward densities are less suitable for assessing the sward yielding potential of mixtures.

All three non-sward densities were about as good for comparing the sward yielding ability of pure-stands but because of its greater ease of management the six inch square planting is considered to be better than either the three inch sown rows or the three inch square planting. The latter two densities however gave rather higher correlations when the yields of mixtures were concerned.

2.7.2. Summary:

An experiment was conducted to compare the relative performance of fourteen populations of Italian ryegrass at sward and three non-sward densities. The non-sward densities were three inch sown rows, six inch square planting and three inch square planting. Seven of the populations were commercial cultivars and seven were 50:50 mixtures of two cultivars.

There were no significant density X variety interactions in comparisons between the yields at sward and non-sward densities. At one harvest there was a significant interaction of this kind in the comparison between yields at three inch square planting and in three inch sown rows.

The correlation coefficients between sward and non-sward yields were about + 0.9 for the total yield of pure varieties and above + 0.7 for three of the four single cuts. At the remaining cut the correlations were rather low at about + 0.3.

The correlations for mixture yields followed the same general trend but were not so high as those for pure varieties.

The sward was the most difficult of the four densities to manage, followed by the three inch rows, the three inch planting and the six inch planting.

It is concluded that the non-sward densities are all suitable for the assessment of the sward yielding ability

of pure-stands of Italian ryegrass varieties and that of the three tested the six inch spacing is best solely on grounds of ease of management and the fact that it permits identification of single plants. Non-sward densities do not on the whole seem likely to be suitable for the assessment of the mixtures of varieties.

TABLE 2.3.1 Pure Varieties and mixtures used to assess the effect of density on relative performance

pure varieties		mixtures	
1.	Hinderupgaard	8.	EF 486 + S22
2.	Danish EF 486	9.	EF 486 + Hinderupgaard
3.	Roskilde	10.	EF 486 + Melle
4.	S22	11.	S22 + Roskilde
5.	Irish Commercial	12.	S22 + Hinderupgaard
6.	Combi	13.	S22 + Melle
7.	Melle	14.	S22 + Combi.

TABLE 2.3.2 Dates of sowing and planting in 1961 for density trial.

Density	Rep. 1		Rep. 2		Rep. 3		Rep. 4	
	Sown	Planted	Sown	Planted	Sown	Planted	Sown	Planted
Sward and 3" sown rows	25 May	-	26 May	-	29 May	-	29 May	-
6" and 3" planting	25 May	30 June	26 May	6 July	29 May	12 July	29 May	14 July

TABLE 2.3.3 Dates of harvest in 1962 for density trial.

	Replication				
	1	2	3	4	Mean Date
Cut 1	14 May	15 May	25 May	29 May	20 May
Cut 2	3 July	3 July	10 July	10 July	6 July
Cut 3	28 Aug.	29 Aug.	4 Sept.	5 Sept.	1 Sept.
Cut 4	24 Oct.	2 Nov.	9 Nov.	15 Nov.	3 Nov.

TABLE 2.3.4 Plot areas and areas actually harvested for density trial.

Main (= density) Treatment	Dimensions of plot Length x Breadth. ft.	Area sq. ft.	Dimensions of harvested area. ft.	Harvested area. sq. ft.
Sward	16.6 x 6	99	15 (approx.) x 4	60 (approx.)
3" sown rows	3 x 3	9	2.5 x 2.5	6.25
6" square planting	6 x 6	36	5 x 5	25
3" square planting	3 x 3	9	2.5 x 2.5	6.25

TABLE 2.4.1 Dry matter yields of populations in densuty trial. Lbs/acre

Variety	Cut 1 20 May	2 2 July	3 1 Sep	4 3 Nov	TOTAL
10 EF 486 + Melle	3,150	2,833	4,384	1,521	11,888
7 Melle	3,067	2,903	4,263	1,621	11,854
11 S22 + Roskilde	3,346	2,745	4,174	1,353	11,618
3 Roskilde	3,274	2,626	4,261	1,441	11,602
2 EF 486	3,224	2,734	4,193	1,432	11,583
6 Combi	3,099	2,673	4,286	1,429	11,487
13 S22 + Melle	2,939	2,654	4,313	1,578	11,484
8 EF 486 + S22	3,126	2,744	4,278	1,286	11,434
9 EF 486 + Hinder.	3,269	2,656	4,184	1,313	11,422
1 Hinderupgaard	3,296	2,583	4,176	1,210	11,265
5 Irish	2,972	2,702	4,146	1,287	11,107
12 S22 + Hinder	3,062	2,552	4,131	1,324	11,069
14 S22 + Combi	2,909	2,636	3,974	1,312	10,831
4 S22	2,763	2,474	4,013	1,261	10,511

<u>TABLE 2.4.2</u> Summarised analyses of variance for density trial.

HARVEST		1	2	3	4	
Densities	3	7.60**	13.92**	4.93*	0.53	13.22**
Error	9					
Varieties	13	6.55**	3.38**	3.94**	14.04**	12.01**
Varieties x Densities	39	0.86	0.55	1.51	0.88	1.15 NS
Error	156					
Plot mean lbs/acre		3107	2680	4196	1383	11349

TABLE 2.4.3. Interaction sums of squares for each comparison of two densities and percentage contribution of each pair of densities to the total interaction sum of squares

	CUT 1			CUT 2			CUT 3		
	3" rows	6" sp	3" sp	3" rows	6" sp	3" sp	3" rows	6" sp	3" sp
Swd	3430 (14.6)	2693 (11.5)	3799 (16.2)	2702 (21.6)	3479 (27.8)	2749 (21.9)	7711 (20.7)	3535 (9.5)	4728 (12.7)
3" rows		5032 (21.4)	4459 (19.0)		1352 (10.8)	1228 (9.8)		5478 (14.7)	9862** (26.4)
6" space			4142 (17.7)			1020 (8.1)			5988 (16.1)

	CUT 4			TOTAL		
	3" rows	6" sp	3" sp	3" rows	6" sp	3" sp
Swd	1184 (19.8)	850 (14.2)	932 (15.6)	18975 (20.5)	9037 (9.8)	11168 (12.1)
3" rows	657 (11.0)	1579 (26.4)			16675 (18.0)	25584 (26.6)
6" space		790 (13.2)				12067 (13.0)

TABLE 2.4.4 Simple correlation coefficients (r) between all pairs of densities at each harvest.

		Density		
Density	Cut	3" rows	6"	3"
Sward	1	+ .73**	+ .64*	+ .62*
	2	+ .47	+ .34	+ .38
	3	+ .30	+ .31	+ .36
	4	+ .75**	+ .80**	+ .82**
	T	+ .76**	+ .74**	+ .62*
3" rows	1		+ .59*	+ .70**
	2		+ .74**	+ .72**
	3		+ .55*	+ .21
	4		+ .87**	+ .71**
	T		+ .81**	+ .67**
6"	1			+ .57*
	2			+ .78**
	3			+ .15
	4			+ .85**
	T			+ .72**

TABLE 2.4.5 As table 2.4.4. but showing pure varieties and mixtures (bracketed figures) separately.

Density

Density	Cut	3" rows	6"	3"
	1	+ .85* (+ .62)	+ .78 (+ .49)	+ .74 (+ .53)
	2	+ .78 (+ .41)	+ .76* (+ .07)	+ .71 (+ .21)
Sward	3	+ .65 (+ .35	+ .32 (- .01)	+ .35 (+ .52)
	4	+ .89** (+ .64)	+ .91** (+ .71)	+ .90** (+ .76*)
	T	+ .96** (+ .58)	+ .93** (+ .47)	+ .87* (+ .65)
	1		+ .65 (+ .53)	+ .69 (+ .64)
	2		+ .81* (+ .61)	+ .69 (+ .82*)
3" rows	3		+ .72 (+ .73)	+ .65 (- .02)
	4		+ .95** (+ .72)	+ .85* (+ .69)
	T		+ .91** (+ .73)	+ .82* (+ .51)
	1			+ .76* (+ .40)
	2			+ .85* (+ .66)
6"	3			+ .80* (- .12)
	4			+ .93** (+ .95**)
	T			+ .94** (+ .52)

TABLE 2.4.6 Error variances and coefficients of variation for density trial.

	Density	Mean yield lbs/acre	per plot		per Sq. Yd. b = 1		b = 0.7		b = 0.2	
			V_e	CV%	V_e	CV%	V_e	CV%	V_e	CV%
Cut 1	Sward	282	163	4.5	1084	11.7	615	8.8	238	5.5
	3" rows	309	251	5.1	173	4.3	222	4.8	226	4.9
	6"	323	137	3.6	382	6.0	280	5.2	168	4.0
	3"	329	146	3.7	101	3.0	129	3.5	132	3.5
Cut 2	Sward	297	127	3.8	849	9.8	479	7.4	186	4.6
	3" rows	247	163	5.2	112	4.3	144	4.9	147	4.9
	6"	233	204	6.1	568	10.2	417	8.8	250	6.8
	3"	288	163	4.4	112	3.7	144	4.2	147	4.2
Cut 3	Sward	406	117	2.7	782	6.9	442	5.2	171	3.2
	3" rows	442	194	3.1	134	2.6	172	3.0	175	3.0
	6"	436	201	3.3	538	5.4	411	4.7	247	3.6
	3"	447	121	2.5	83	2.0	107	2.3	109	2.3
Cut 4	Sward	137	37	4.5	244	11.3	140	8.6	54	5.3
	3" rows	135	47	5.1	32	4.2	42	4.8	42	4.8
	6"	140	56	5.4	155	8.8	114	7.6	69	5.9
	3"	142	36	4.2	25	3.5	32	4.0	33	4.4
TOTAL	Sward	1122	414	1.8	2760	4.7	1562	3.5	605	2.2
	3" rows	1087	582	2.2	402	1.8	515	2.1	525	2.1
	6"	1138	602	2.2	1673	3.6	1231	3.1	738	2.4
	3"	1206	466	1.8	322	1.5	413	1.7	421	1.7

TABLE 2.6.2 Quality of Selection % "truly" superior varieties included in a given percentage of varieties selected on basis of test performance (when $p_t = p_T$)

	$p_t = p_T$ %								
r	50	40	30	25	20	10	5	1	0.5
.50	67	60	52	48	44	33	25	13	10
.60	70	65	58	54	50	39	31	19	15
.70	75	69	63	60	57	47	39	27	23
.80	80	75	70	68	65	56	50	38	34
.90	86	83	79	77	75	69	64	55	51
.95	90	88	86	84	83	78	75	67	65

e.g. if sward and non-sward yields have a correlation of + .80 and 10% of the total number of varieties is selected on the basis of superior non-sward (test) yields; then on average 56% of that 10% will be varieties also falling into the top 10% for sward (true) yields.

TABLE 2.6.3 Quality of Selection % "truly" superior varieties included in a given percentage of varieties selected on basis of test performance, for various values of p_t and p_T

p_t

r = + 0.50		50	25	10	1
	50	67(67)	76(38)	84(17)	94(2)
	25	38(76)	48(48)	60(24)	74(3)
p_T	10	17(84)	24(60)	33(33)	52(5)
	1	2(94)	3(74)	5(52)	13(13)

r = + 0.70		50	25	10	1
	50	75(75)	87(44)	95(19)	100(2)
	25	44(87)	60(60)	76(31)	93(4)
p_T	10	19(95)	31(76)	47(47)	79(8)
	1	2(100)	4(93)	8(79)	27(27)

r = + 0.90		50	25	10	1
	50	86(86)	98(49)	100(20)	100(2)
	25	49(98)	77(77)	95(38)	100(4)
p_T	10	20(100)	38(95)	69(69)	100(10)
	1	2(100)	4(100)	10(100)	55(55)

r = + 0.95		50	25	10	1
	50	90(90)	100(50)	100(20)	100(2)
	25	50(100)	84(84)	99(40)	100(4)
p_T	10	20(100)	40(99)	78(78)	100(10)
	1	2(100)	4(100)	10(100)	67(67)

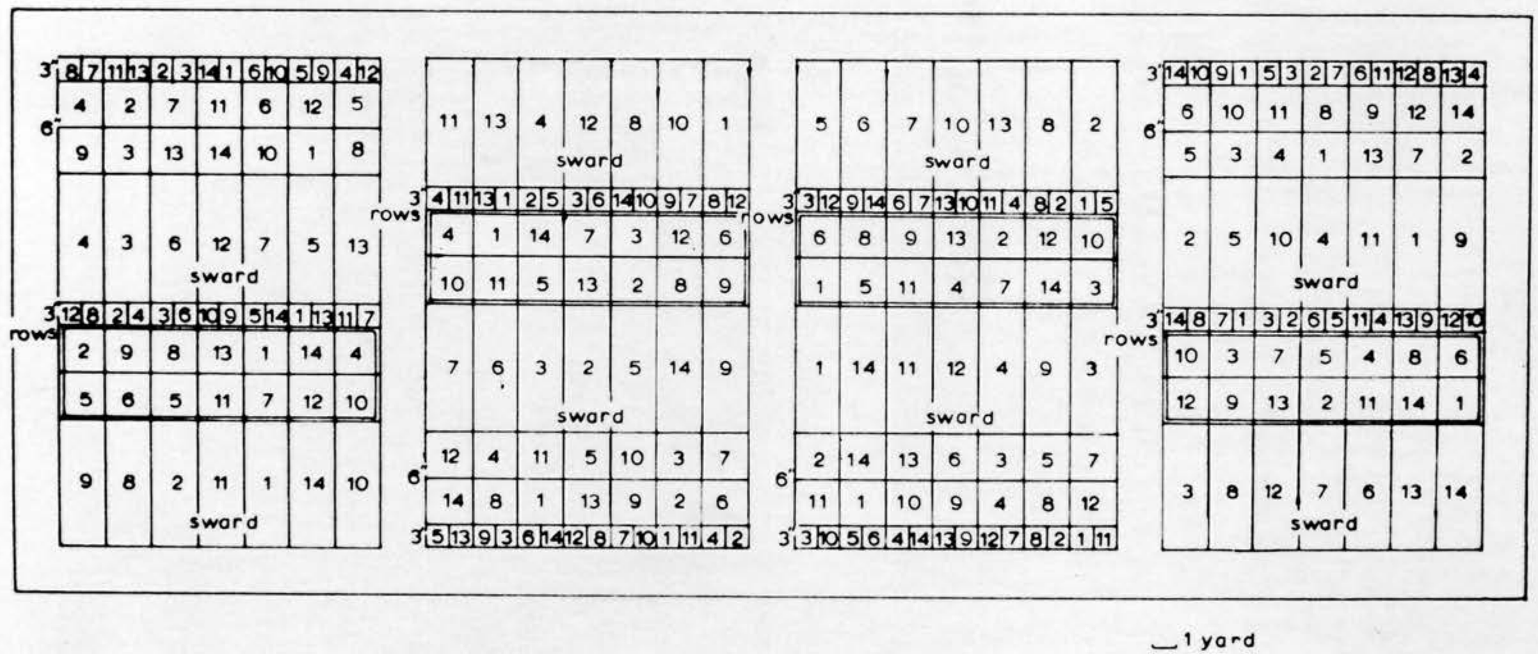


FIGURE 2.3.1 Plan of trial layout used for density trial

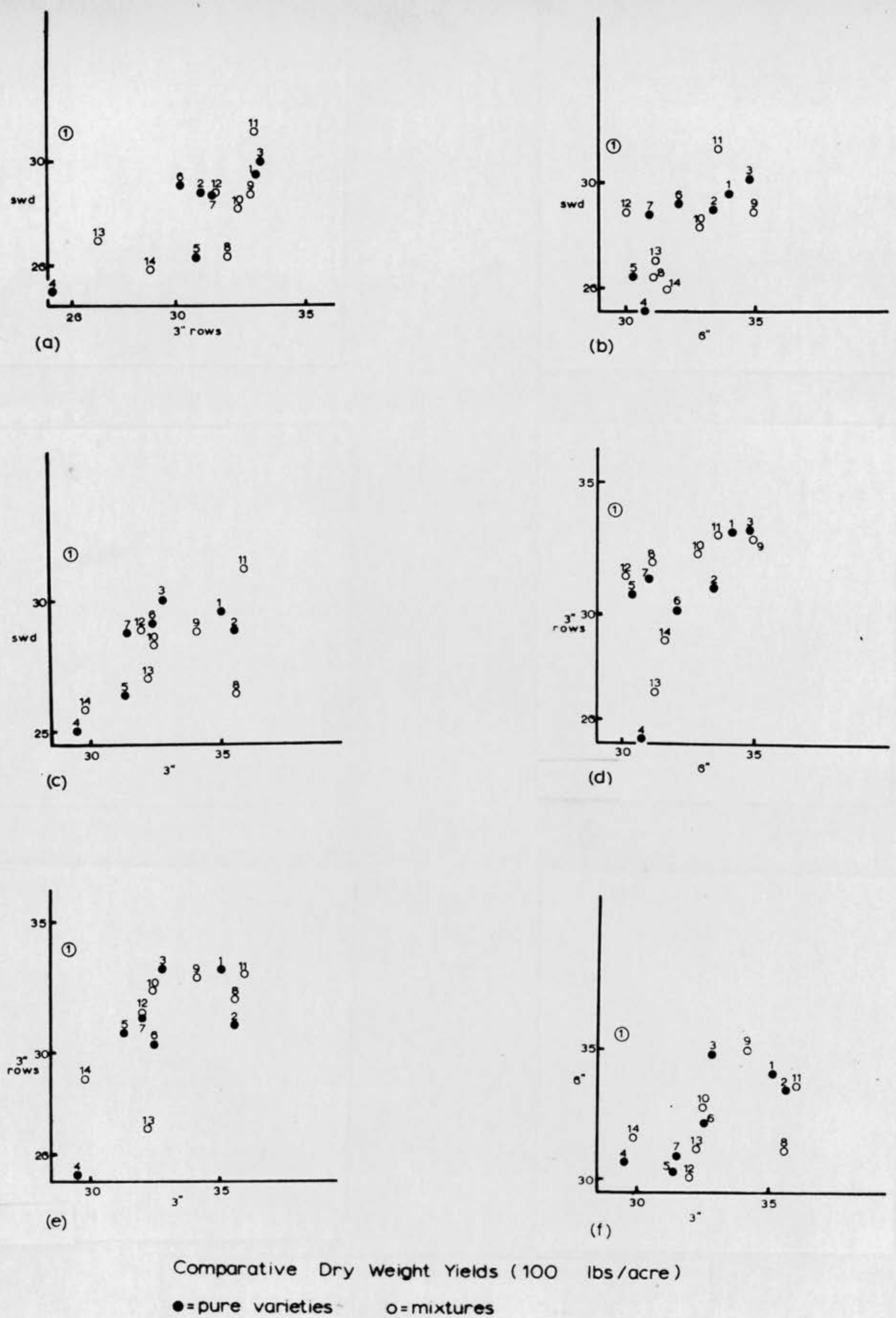
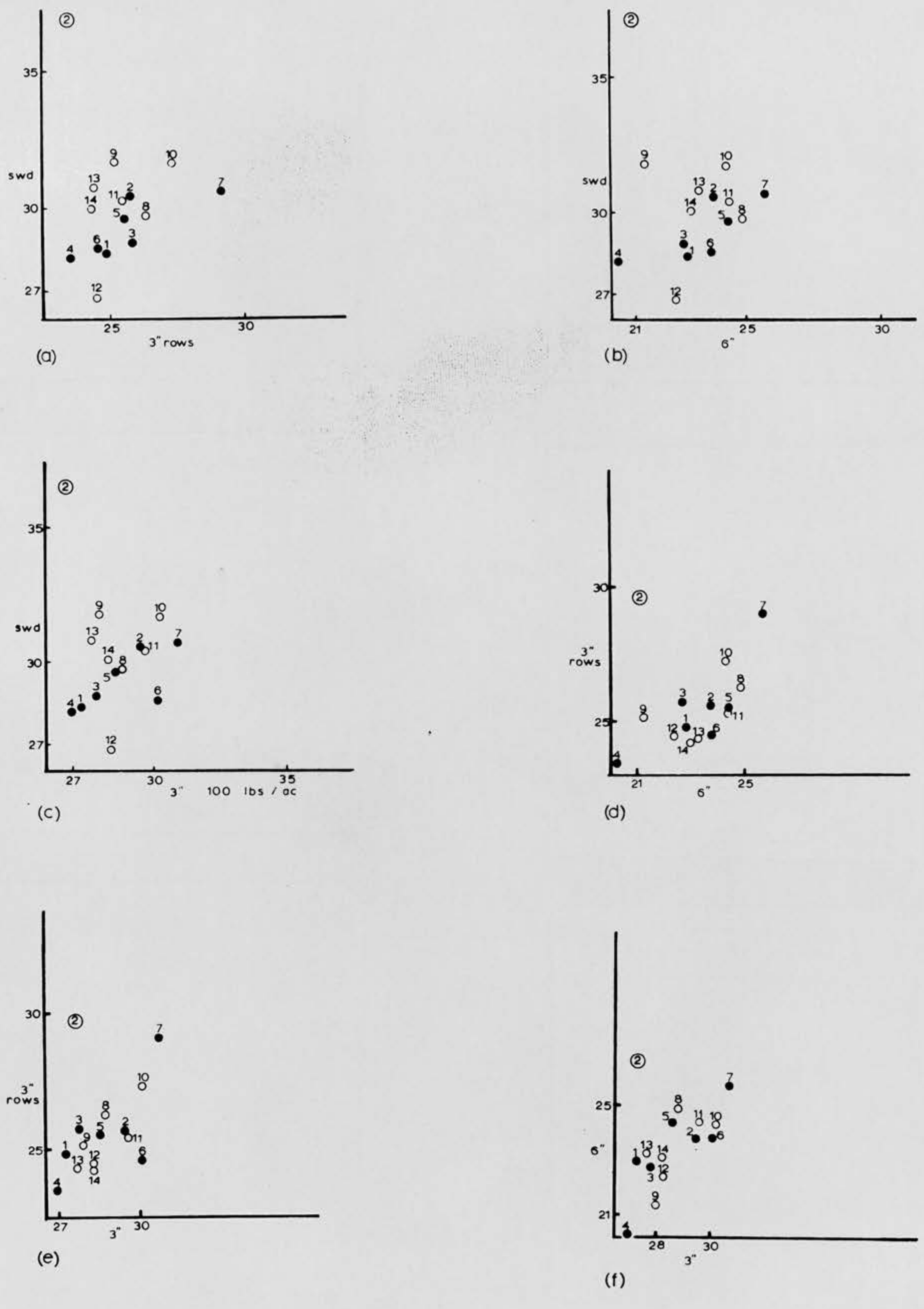


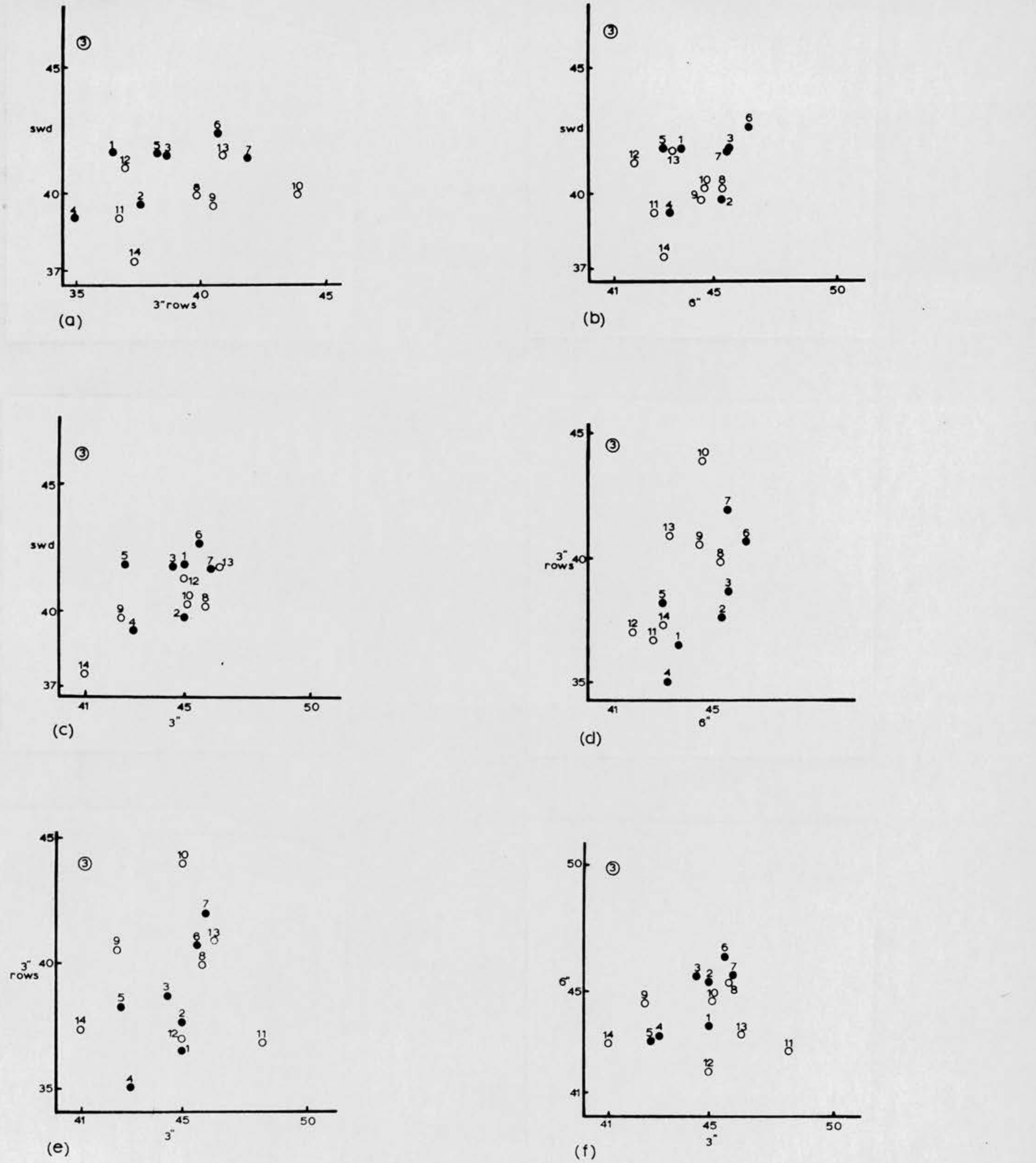
FIGURE 2.4.1 Relationship between yields at the different densities. Data for first harvest.



Comparative Dry Weight Yields (100 lbs/acre)

● = pure varieties   o = mixtures

FIGURE 2.4.2 Relationship between yields at the different densities. Data for second harvest



Comparative Dry Weight Yields (100 lbs/acre)

● = pure varieties   o = mixtures

FIGURE 2.4.3 Relationship between yields at the different densities. Data for third harvest.

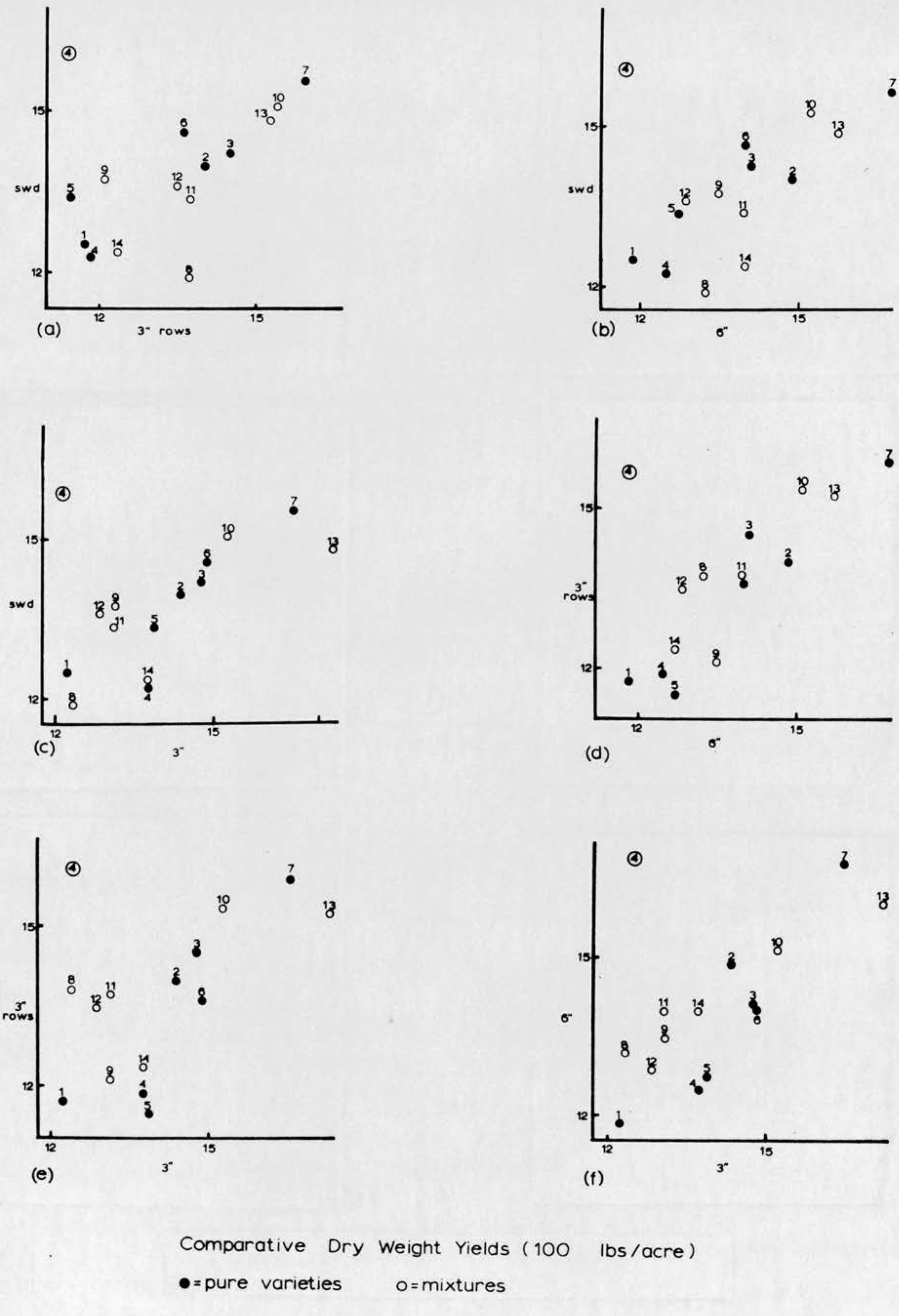
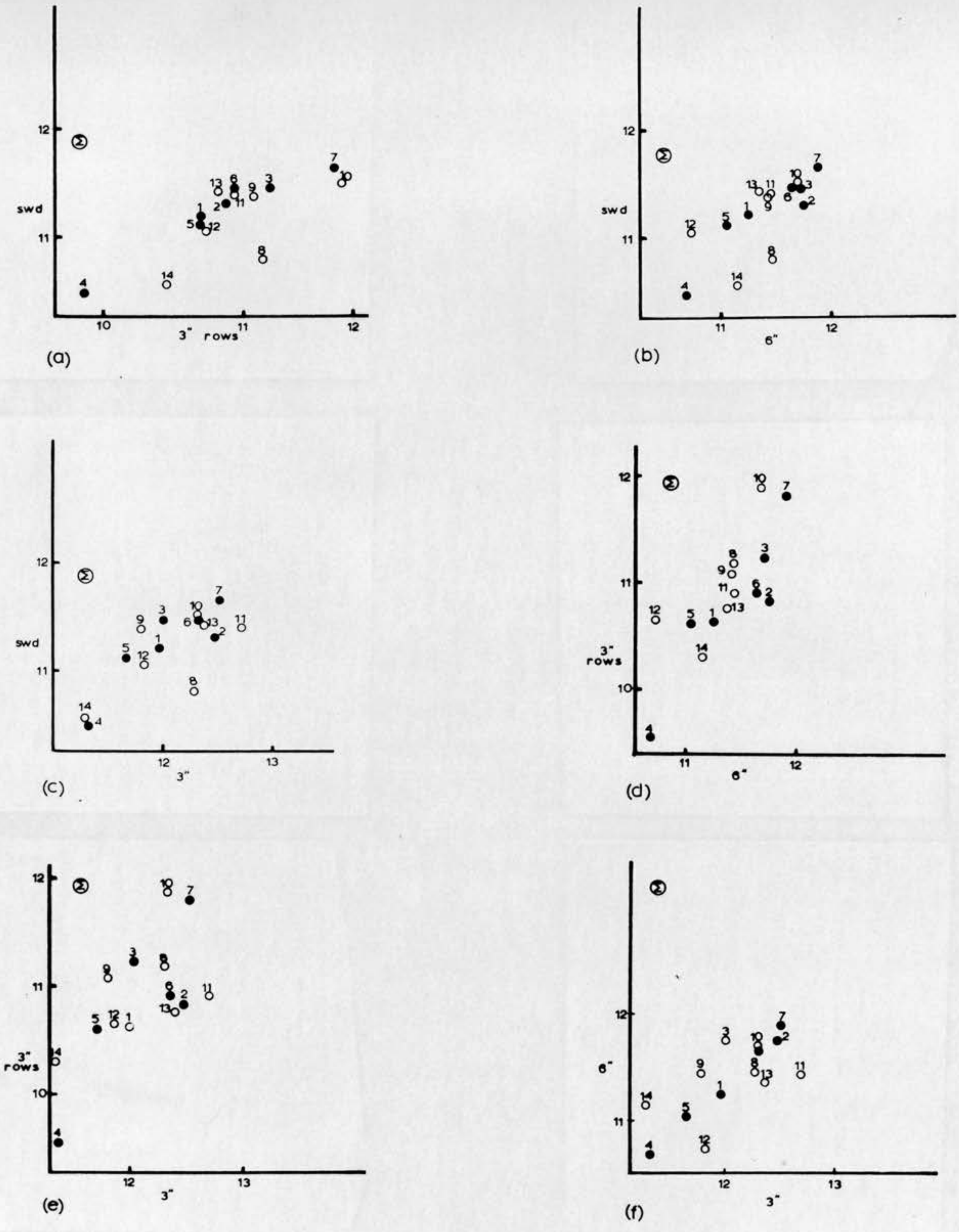


FIGURE 2.4.4 Relationship between yields at the different densities. Data for fourth harvest.



Comparative Dry Weight Yields (1000 lbs/acre)

● = pure varieties   o = mixtures

FIGURE 2.4.5 Relationship between yields at the different densities. Data for total yield (sum of four harvests).

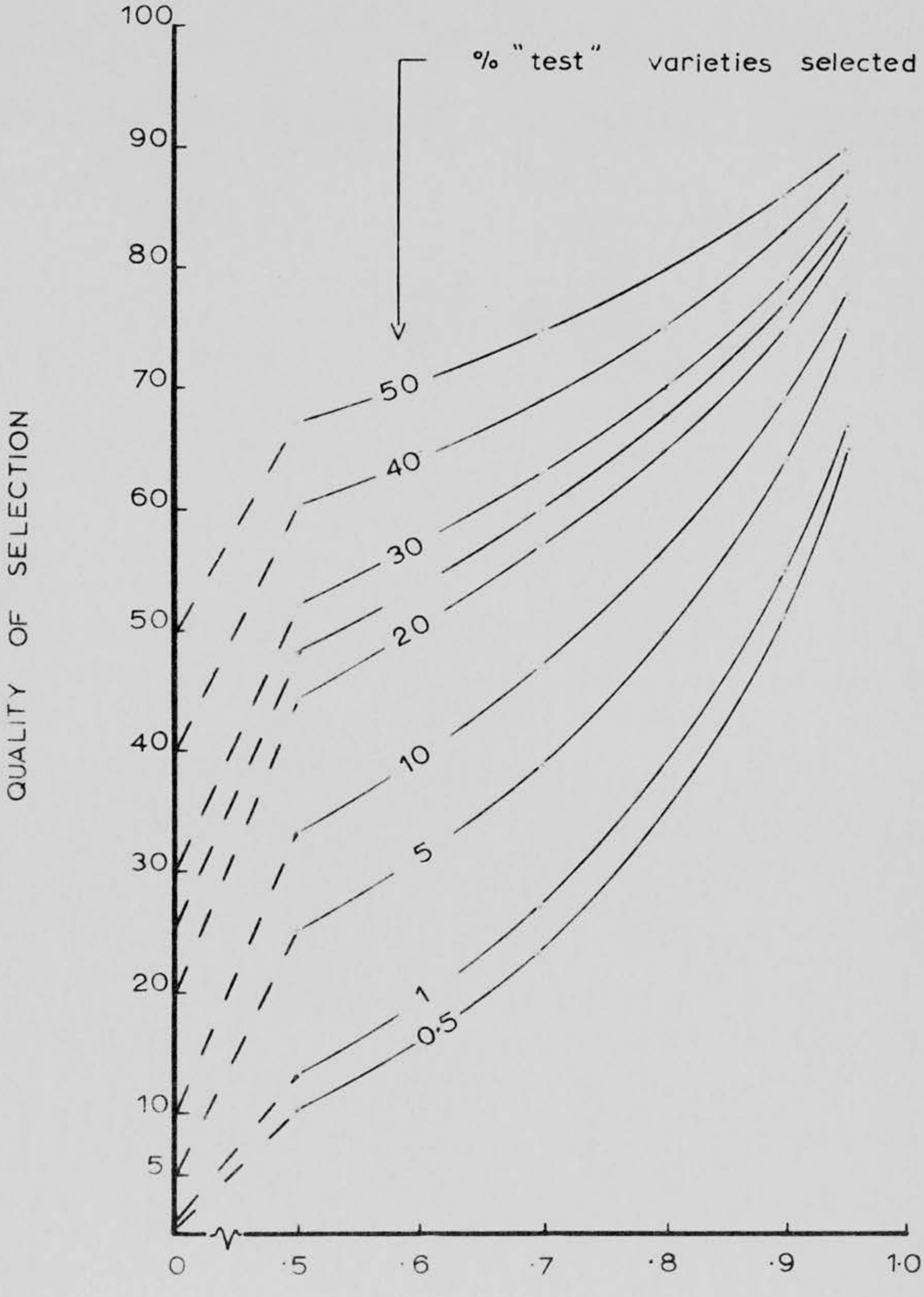


FIGURE 2.6.1 "Quality" of selection = percent of truly superior varieties in a given selection (as percent of the original population) of superior "test" varieties.

SECTION 3

CONVENIENT PLOT SIZE AND NUMBER OF REPLICATIONS FOR ASSESSING PROGENIES IN A GRASS BREEDING PROGRAMME

SECTION 3.1 INTRODUCTION

Evidence presented in Section 1 suggests that non-sward densities are capable of giving sufficiently accurate measures of sward performance in Italian ryegrass. In the interests of economy of seed and research resources it is desirable to keep plot size and amount of replication as low as is compatible with the required degree of precision.

For the reasons given at the end of Section 1, it was decided to concentrate attention on the six inch spacing, the main argument in favour of this density, compared to the others, being its ease of handling. A possible disadvantage is that the smallest plots considered (1 yard x 1 yard) contained only 36 plants and any increase in precision due to the larger plot sizes could be due, partly, of course, to increased plot size as such, but also in part to an increase in the number of plants within the plot.

To be able to detect the differences of the magnitude with which the plant breeder is often concerned (of about 7% of the mean), without excessive replication requires great accuracy in the management and harvesting of plots. In ordinary variety trials a coefficient of variation of around 12% (where CV = $\left\{\frac{\text{SE one observation x 100}}{\text{mean all observations}}\right\}$) is quite usual. To detect a seven per cent difference at the five per cent significance level in eighty per cent of cases, requires about 45 replications. Even with a coefficient of variation of seven per cent, sixteen replications are necessary. To bring the degree of replication to a manageable size the coefficient of variation needs to be reduced to about 3.5% when four replications would meet the above conditions.

SECTION 3.2 LITERATURE

The problem of devising the most efficient size and shape of plot is, of course, one that occurs with all crops and there are many papers discussing this matter.

The question of plot shape was investigated by Christidis (1939) who advocated the use of long, narrow plots as a means of reducing soil heterogeneity. Justesen (1932) pointed out that this is due to local differences being partitioned so that they become distributed over different plots.

Smith (1938) in summarising previous work on the effect of varying plot size pointed out that there was no method then available of determining, from experimental results, the best size of plot for any particular purpose. Smith devised an index of soil heterogeneity based on uniformity trial data which has been widely used by subsequent workers. Smith also presented a formula for estimating optimum plot size based on his index of soil heterogeneity and the ratio of those costs which were proportionate to plot size and those that were fixed regardless of plot size. Smith's work is further discussed under Material and Methods.

Patterson and Ross (1963) have stated that in many cases, the effect of varying plot size on variance can be expressed by the relationship that variance per plot is roughly proportional to $\sqrt[4]{n}$ where n is the number of basic units per plot.

Hatheway (1961) pointed out that in many fields of experimentation convenience is more important than cost and draws attention to the formula of Cochran and Cox (1950) which gives plot sizes and degrees of replication necessary to detect a given percentage difference. Hatheway presents a more convenient method of obtaining the same information when estimates of Smith's index of soil variability are available. Hallauer (1964) has presented some data obtained from trials with corn and used Hatheway's method for estimating convenient plot size and degree of replication.

Robinson, Rigney and Harvey (1948) working with peanuts calculated the optimum plot size for a given degree of precision and stated that when the proportion of cost per treatment due to total area used was relatively low (20%), a range of from two to ten basic units (each of 12½ foot single rows) per plot, gave very similar results, but that as the cost due to area increased the smaller plot sizes became more efficient.

Nonnecke (1958, 1959) and Nonnecke and Smillie (1963) in a series of papers have reported on the most efficient plot and block size and shape for a range of vegetable crops; they found in general that long, narrow blocks were more efficient than square or short wide ones, but that the optimum plot shape varied with the particular shape of block.

F.L. Smith (1958) working with beans found that, in attempting to reduce least significant differences to 200 lbs per acre, six replications were necessary and that this number of replications was adequate even with plot sizes as small as 100 square feet. Using only four replications much larger plots (900 square feet) did not give the required degree of precision.

A number of authors have pointed out the possibility of estimating soil heterogeneity from ordinary trial data, such as those obtained from lattice trials, where it is possible to amalgamate groups of adjacent plots to simulate larger ones. The largest plot possible corresponds to a replication.

Koch and Rigney (1951) were the first to use trial data in this way and both they and Hatheway and Williams (1958) pointed out that the simple weighting of variances of different sizes of plots by their respective degrees of freedom was not adequate and the latter authors state that this objection applied with equal force to uniformity trial data. Hatheway and Williams present a scheme for weighting the sums of squares and products which define Smith's regression coefficient to give an estimate of minimum variance.

Among recent papers describing the effect of plot size and shape on variability are those of Dutta and Heath (1960), who found that in tea, a large reduction in error was brought about by an increase in plot size of from nine to 36 bushes but that a further doubling in plot size only reduced error by another one per cent. These authors found that long, narrow plots were more effective than square ones in reducing error. Wiedemann and Leininger (1963), however, found that plot shape had little effect on variance in safflower yield trials. The coefficients of variation in this material were rather high, 24.5% for plots of one unit size (5 foot row) falling to ten per cent for a plot of 66 units. Wiedemann and Leininger also found some abnormally low estimates of 'b' in their data and attributed this to the occurrence of excessively high yields in one portion of their trial area. Removal of the portion of the data from this area increased the estimate of 'b' from -0.1 to -0.43.

Lessman and Atkins (1963) found in grain sorghum a reduction of the coefficient of variation of from nine per cent in plots of one unit (5 foot single row = 20 plants) to three per cent in plots of 40 units, their average estimate of 'b' was -0.59.

Weber and Horner (1957) in soybeans found average coefficients of variation for yield ranging from 10.5% for plots of sixteen square feet to 7.5% for plots four times that size. Long, narrow plots were superior to short, wide ones. Certain chemical characters were much less variable than yield. Brim and Mason (1959) also working with soybean, found a similar rate of reduction in CV although their basic plot size and CV were both about 1.5 times those of Weber and Horner. In tobacco, Crews, Jones and Mason (1963) found a reduction in CV of from 4.4 to 3.2 per cent when plot size was increased from 15 to 40 plants. Estimates of 'b' in this material ranged from -0.47 to -0.92 with a grand mean of -0.62.

Generalised computer programmes for the analysis of uniformity trial data has been published by Nonnecke (1963) and by Yates, Vernon and Nelson (1964). The material in the latter study was hybrid maize and the authors state that inter plot competition makes the use of very small plots undesirable especially where variety differences are large.

SECTION 3.3 MATERIALS and METHODS

3.3.1 Description of the uniformity trials

The material consisted of two cultivars of Italian Rygrass, S22 and Irish commercial. These were chosen to represent cultivars of rather sharply contrasted genetic background, S22 being based on a relatively small number of parent plants selected for certain characteristics (Jenkin 1955) while Irish is in effect a commercial land race. Both cultivars were sown in seed boxes at one inch (2.54 cm.) spacing on 27th-28th April, 1964. The plants were planted in the field in two separate trials between 3rd and 5th June. The plants were spaced six inches (15.24 cm.) apart. Each trial measured sixteen yards by eight yards (1 yard = 0.914 metres) and each trial was surrounded by a two yard wide discard planted at the same density as the trial itself; there was a further two yard wide discard in which seed was sown broadcast. At each harvest, each trial was cut as one yard square plots so that each trial contained 128 separate plots. In 1964 the plants were cut individually with sheep shears although fresh weights were recorded as plot totals. In 1965 the plots were cut with an "Allen" autoscythe using 1 yard long strips of hardboard to separate adjacent plots. Fresh weights were recorded to the nearest five gm. and from each plot a sub-sample of approximately 150 gm. was taken for dry matter determination. The statistical analyses were performed on dry yields estimated from the fresh weight and dry matter percentage. Each trial was cut twice in 1964 and three times in 1965. Dates of harvest are given in Table 3.3.1.

Table 3.3.1

Dates of Harvest

	1964		1965		
	1	2	1	2	3
S22	12 Aug.	13 Oct.	17 June	10 Aug.	20 Oct.
IRISH	20-21 Aug.	19-20 Oct.	24-25 June	12 Aug.	22 Oct.

Each trial received approximately three cwt per acre (377 kilo per hectare) of CCF 1 after each cut. This was applied in weighed quantities to each square yard plot (31.50 gms per square yard).

There are two possible approaches in considering the effects of plot size and shape. One is to examine the coefficients of variation for different combinations of plot size and shape (and also block size and shape). The other is to examine the regression of log variance on plot size.

3.3.2 Statistical methods. Estimation of the coefficient of variation (= CV = C)

The coefficient of variation is defined by the formula

$C = 100S \,/\, \bar{x}$ where S is the standard deviation (i.e. $\sqrt{\text{error mean square}}$

for a particular plot and block size and shape and x is the mean yield of all the plots used in determining S. The uniformity trials described here were analysed as randomized blocks on the assumption that each trial consisted of sixteen dummy varieties. This permits seventeen different randomized block analyses. The plot and block sizes and shapes are shown in Table 3.3.2 and are illustrated in Fig. 3.3.2.

In Table 3.3.2 plot sizes and dimensions are given in terms of the original 1 yard square units; blocks are given in terms of plots. The term "size" is used to indicate area; the term "dimensions" refers to lengths of side. Dimensions are given in terms of columns by rows.

The statistical analyses were carried out by the computer unit in the Statistical Department at Rothamsted Experimental Station. The computer print-out gave the total sums of squares and those for blocks and error and also the mean squares and mean squares per unit. In 1965 the computer programme also calculated the coefficient of variation itself.

3.3.3 Statistical methods. Regression analysis. Estimation of index of soil heterogeneity ('b')

In this, as in other uniformity trials, plots of successively larger size were constructed by combining adjacent units. Since the yields from adjacent areas of ground tend to be correlated, this gives rise to rather larger estimates of the variances of plot means than would otherwise be found. Smith (1938) devised an empirical rule which measures the degree of correlation between adjacent plots and hence provides an index of soil heterogeneity.

Smith found the variance per unit area plots of area x units was given approximately by the equation

$$V_{\bar{x}} = V_1 x^b$$

where b is an index of soil variability. If this equation is expressed in logarithmic form

$$\text{Log } V_{\bar{x}} = \text{Log } V_1 - b \log x$$

'b' can be estimated as the linear regression coefficient of $\log V_{\bar{x}}$ on $\log X$ The value of 'b' can be obtained by visual fitting after the points have been plotted on logarithmic graph paper or by least squares estimation. 'b' normally varies from 0 to -1; values less than -1 are possible but are difficult to interpret. A value of 0 for 'b' indicates complete correlation between adjacent plots, while a value of -1 indicates a complete lack of correlation. If 'b' = 0, which is, in practice, virtually impossible, there is no point, statistically speaking, in increasing plot size or in having more than one replication; when 'b' = -1 the effect of increasing plot size is the same as that of increasing replication.

Koch and Rigney (1951) pointed out that the type of data provided by a uniformity trial could be simulated by data from certain commonly used field trial layouts such as Latin squares, lattices and split plot experiments. Koch and Rigney mentioned that while Smith had advocated simple weighting by degrees of freedom when determining the variance of the different sizes of plot, this was not strictly correct for simulated uniformity trials based on data in which treatment effects were present. Hatheway and Williams (1958) stated that the same objections apply to uniformity trial data and devised a weighting system based on the inverse information matrix for log variance and log plot size which provided an unbiased estimate of 'b'.

In the present study, simulated split plot layouts were super-imposed on the trials, using as the largest plot, one consisting of eight basic units. For each set of data there are eight split-plot analyses possible according to the particular combination of plot shapes used. The eight possible combinations are shown in Fig. 3.3.2(a) For each set of data this provides eight estimates of the soil heterogeneity index.

The variances required for the calculation of 'b' are the total mean squares from the relevant analyses of variance divided by X^2 where X is plot size in basic units. The division by X^2 is necessary to bring the variances to a unit area basis.

The values of 'b' were estimated graphically. A number of possible layouts were analysed by the Hatheway and Williams method, but, in each case, tested, the difference between unweighted least squares estimate and that of Hatheway and Williams was very small, particularly when compared with the difference between estimates of 'b' based on the same data and plot sizes but using different plot shapes.

3.3.4 Estimation of convenient plot size and number of replications

Smith (loc.cit.) gives the formula

$$X = bK_1 / (1-b)K_2$$

for estimating the optimum plot size, where K_1 is that part of the total cost which is proportional to the number of plots per treatment and K_2 is that part proportional to the total area per treatment.

Hatheway (1961) pointed out that in fact most agronomists are more concerned with convenience than with cost; they require to know the minimum plot size and number of replications which will detect a difference of a specified size, irrespective of cost. When, as in the present case, uniformity trial data are available, this information can be obtained from the coefficients of variation for the different sized plots from the formula of Cochran and Cox (1950):-

$$R = 2C^2 (t_1 + t_2)^2 / d^2$$

where

- R = the number of replications required to detect a true difference of d units
- d = the true difference between two treatments, (as a per cent of the mean)
- C = CV = true standard error per plot as a per cent of the mean
- t_1 = the significant value of t in test of significance
- t_2 = the value of t corresponding to 2 (P-1), where P is the probability of obtaining a significant result.

As Cochran and Cox point out, the use of this equation is a little tricky, since the values of t_1 and t_2 depend on the numbers of degrees of freedom available for estimating error in the analysis of variance.

Hatheway substituted in Cochran and Cox's equation and obtained the expression:-

$$d^2 = 2(t_1 + t_2)^2 C_1^2 / Rx^b$$

where:-

C_1 is the coefficient of variation for plots of unit size and x is the number of basic units per plot.

Hallauer (1964) presents graphs of d plotted against plot size, for various combinations of C_1, number of replications and 'b'. It is, in fact, simpler to plot these graphs on double logarithmic paper when they become linear. Moreover, since C_1^2 appears in the numerator of Hallauer's equation, the effect on d of varying C_1 is simply proportional and all the necessary information for any one value of 'b' can be derived from one set of curves on one graph which can conveniently be drawn for a value of C_1 of one per cent. Four such graphs, for values of 'b' of - 0.3; - 0.5; - 0.7 and - 0.9 are presented in Fig. 3.3.3. On these graphs, the difference detected by any particular combination of plot size and number of replications when the coefficient of variation is C_2 is :-

$$d_{C_1} \times C_2 / C_1$$

SECTION 3.4 RESULTS

When discussing the yields of herbage grasses, it is usual to consider separately, total yield (i.e. the total yield during one year or the overall total of two or more years) and seasonal distribution of yield within any one season. In terms of the present work this means that attention must be paid to the effect of varying plot size and shape on the precision of the estimates of yield both for total yield and for yield at single harvests. In Italian ryegrass seasonal distribution of yield is less important than in some other forage grasses; since Italian ryegrass is used very largely for hay and silage, its importance for grazing is less than that of the perennial grasses. In this section the data for total yields are considered first and in rather more detail than the data for single harvests.

3.4.1 Results. Total yields. Coefficients of variation

There are three 'total yields' for each cultivar, the yields for each of the years 1964 and 1965 (the sum of two and three single cuts respectively) and the sum of the two years yields.

The coefficients of variation for the annual and overall total yields for each combination of plot and block size and shape are shown in Table 3.4.1 for S22 and in Table 3.4.2 for Irish. These tables also give the number of replications required to detect a true difference of seven per cent of the mean at the five per cent level in eighty per cent of trials and the area of ground required for this number of replications. The values for the number of replications were calculated from the formula given by Cochran and Cox (1950):-

$$R \geq 2(CV / d)^2 \, (t_1 + t_2)^2$$

where

- d = the true difference it is desired to detect
- t_1 = the significant value of t in the test of significance
- t_2 = the value of t in the table of t corresponding to 2(1-P) where P is the probability of obtaining a significant result

12.36

The value of $2(t_1 + t_2)^2$ was taken as $2\ (1.6449 + 0.8416)^2 =$ [redacted] which is appropriate when infinite degrees of freedom are available for estimation of the residual mean square; for practical purposes this applies when the error degrees of freedom exceed thirty.

Tables 3.4.3 and 3.4.4 show, for S22 and Irish respectively the average coefficients of variation for each plot size irrespective of plot shape.

In general, increasing the size of plot results in a decrease in the size of the coefficient of variation. In terms of the area of ground required to attain a given degree of precision, however, the smaller plot sizes are always more efficient than the larger, the smaller plot more than compensating for the extra replication required. The advantage of small plots is reduced progressively as the area allocated to guards is increased. Tables 3.4.3 and 3.4.4 also show the areas required per treatment for the required number of replications. With only one guard row, the smallest plot size is still without exception the most efficient, but in many cases the advantage of single unit plots over those of two units is so slight that two unit plots might well be preferred. When the situation with two guard rows per plot is considered, the differences in required area between one and two unit plots are quite negligable and sometimes favour the two unit plot.

Because the trials were rectangular in shape, rather than square, the effects of plot shape and block shape are largely confounded. When direct comparison is possible there seems a tendency for the "shorter" block shapes (i.e. those having smaller numbers of "columns") to give the lower coefficients of variation. This effect is not consistent however, the data for the 1965 harvests and for all harvests for Irish Italian ryegrass showing the reverse tendency.

The effects of plot shape are subject to the same difficulty of interpretation as are those of block shape. Again, when direct comparisons are possible, the longer (i.e."more columns") plots seem to have the lower coefficients of variation although once again the effects are not quite consistent.

The combined effects of varying plot and block shape are quite marked. The most extreme example is that for the eight unit plots in the 1965 data for S22 (Table 3.4.1). Here an ill chosen combination of plot and block shapes results in an increase of CV from 4.04 per cent for long, narrow plots in short, wide blocks to 7.95 per cent for short, wide plots in long, narrow blocks. This involves a four-fold increase in number of replications, from four to sixteen, or perhaps, more realistically, the failure of a trial of a given size, to detect differences which it could, in fact, have detected quite readily with a different shape of plot and block. Other, similar comparisons, while less spectacular are quite sufficiently striking to confirm the importance of correct choice of plot and block shape.

The evidence for the superiority of long plots and short blocks in this set of data is not quite consistent. The 1965 data for Irish ryegrass (Table 3.4.2) show an opposite trend, although the 1964 and the data for the sum of all five cuts do conform to the general rule.

The two varieties show a difference in behaviour in 1965 so far as the pattern of variation of the coefficient of variation is concerned. While for any one plot size, the lowest values of the coefficient are comparable, the effect of varying plot shape is much more marked in S22. This point is more clearly illustrated in the discussion of the index of soil heterogeneity in Section 3.4.3.

Section 3.4.2 Results. Single harvests. Coefficient of variation

The coefficients of variation of each plot and block size and shape at each harvest are shown in Table 3.4.5 for S22 and in Table 3.4.6 for Irish. As would be expected the general features of these tables are similar to those of Tables 3.4.1 and 3.4.2 for total yields; the larger plot sizes having the lower coefficients of variation. In S22, however, the third harvest in 1965 is somewhat anomalous. Here an eightfold increase in plot size has produced virtually no reduction in the CV and in the case of the 'short' plot 'long' block combination has rather tended to increase it. The effect of changing plot and block shape is very marked at some harvests but the direction of the effect is not consistent from one harvest to another and in one case not even from variety to variety at the same harvest. Both these points can be illustrated from the 1965 data. In both S22 (Table 3.4.5) and Irish (Table 3.4.6) the first and third cuts have relatively low values of the coefficient of variation for the combination of 'long' plots ('more columns') with 'short' blocks. The effect is especially noticeable at the first cut in S22, where in both the four and eight unit plots the highest value of the CV is about twice that of the lowest (corresponding to a fourfold increase in the degree of replication required to attain the same degree of precision). The data for the second cut show a contrast in behaviour of the two varieties, S22 again having the lower values of the CV for long plots in short blocks whereas in Irish this combination of plot and block shape has a CV nearly twice as large as that for the short plots in long blocks.

The average coefficients of variation for each harvest separately are shown in Table 3.4.7. This table also gives the number of replications required on the same basis as that for total yields and the area required per treatment without guard rows and with one guard row per plot.

The general features of Table 3.4.7 are the same as those of Tables 3.4.3 and 3.4.4. The coefficients of variation for single harvests tend to be higher than those for total yields; this is to be expected, since summation of the yields from several separate harvests will have an effect comparable with that of increasing plot size. As before, the coefficients decrease in size as plot size increases, a marked exception being the third harvest for S22 in 1965, in which the values for plots of one and eight units are virtually the same, 12.63 and 12.59 respectively.

Section 3.4.3 Results. Regression analysis. Estination of the index of soil heterogeneity ((b')

The effect of increasing plot size on the variance is shown in Figs. 3.4.1 for total yields and in Figs. 3.4.2 and 3.4.3 for yields at single harvests of S22 and Irish respectively.

The estimates of 'b' derived from the graphs in these figures are presented in Table 3.4.8.

It is clear that the estimates of 'b' based on data from the different cultivars do not differ to any extent, except possibly at the final cut in 1965 when the data for S22 give a rather lower value of 'b' (indicating a greater correlation between neighbouring plots), than do the data for Irish. The low value of 'b' in this case, is, of course consistent with the negligible decrease in coefficient of variation with increasing plot size at this harvest.

Although, with the above exception, the estimates of 'b' for any one harvest are similar for the two cultivars, there are marked differences between the estimates of 'b' at different harvests. The most noteworthy feature is the high values for 'b' in the first harvest in both cultivars in 1965; .81 for S22 and .83 for Irish. In both cases, the shape of plot used for any given size of plot, affects the estimate of 'b'. In general, at this harvest, increasing plot size by lengthening the plots produced a more rapid reduction in variance than widening them; the assemblage of plots 1-6-12-16 giving lower estimates of 'b' than the assemblage 1-4-8-14. This again is consistent with the change in coefficient of variation. The more rapid fall in 'b' for long plots applies to both cultivars, but the effect is more marked with S22 than with Irish. For S22 the maximum and minimum estimates of 'b' (estimated by eye fitting of the regression line) are 1.24 and .48. In Irish they vary only from .69 to .93. It

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should be pointed out that this effect is not necessarily a varietal one since the two varieties were on separate though neighbouring areas. It is in fact more likely that the ground on which S22 was grown or possibly differences in management were the main cause of the greater range of variation in 'b' in S22 than in Irish.

Section 3.4.4 Results. Estimation of convenient plot size and number of replications from the value of 'b'

Using the available estimate of CV for basic plot size and for 'b' it is possible to calculate the appropriate combinations of plot size and number of replications using Hallauer's (1964) formula. As already shown, different estimates of 'b', based on the same data, but using different plot shapes may vary widely, but when uniformity trial data are not available, some estimate of 'b' together with the coefficient of variation of plots of the size currently in use may be the only method of estimating optimum plot size and replication number.

For the present data, an average estimate of 'b' of between - 0.5 and - 0.7 for the sum of harvests in any one year or for the sum of all five harvests, seems reasonable. For single harvests the estimates are much less consistent and may go as high as - 0.8.

It is now possible to make an estimate of suitable combinations of plot size and number of replications to detect a difference of specified size, using the graphs of Fig. 3.3.3.

An overall average estimate of the coefficient of variation for the sum of one or two years harvests, for plots of one square yard, is about eight per cent. (The actual value is 8.06%). It is required to find the suitable combinations of plot size and number of replications to detect a true difference of seven per cent of the mean. The graphs are drawn for a coefficient of variation of one per cent. A seven per cent difference when the CV is eight per cent is equivalent to a difference of $7/8$ = .875% when the CV is one per cent. Using the graph for 'b' = - 0.7 suitable combinations may be read off. They are in terms of plot size by number of replications: four by eight, six by six, and, by extending the range of the graph slightly, ten by four. A similar process, using the graph for 'b' = - 0.5, gives combinations of six by eight and ten by six.

These estimates are of the same order as those in Tables 3.4.1 and 3.4.2 which were derived from the values of the coefficient of variation for plots of different sizes.

The larger (nearer to - 1.0) the estimate of 'b', the more marked is the effect of increasing plot size, (if 'b' is equal to - 1 the effect of increasing plot size is the same as that of the corresponding increase in replication). In a general way the larger estimates of 'b' in the present data are associated with the higher values of CV for the basic plot size. This is, on the whole, to be expected and the implication is that a low CV is not likely to be further reduced by increase of plot size and any further increase in precision must come about by increased replication. With the higher values of CV, greater precision can probably be attained by increasing plot size. It should be emphasised that this is by no means an invariable rule, merely a tendency apparent in the present data and one which is likely to occur more, rather than less frequently. Since small plots tend to be less convenient to manage than larger ones and more wasteful in terms of guard rows, larger plots, with or without increased replication, may be the better method of increasing precision when the basic coefficient of variation is relatively high.

SECTION 3.5 SOME OBSERVATIONS ON EASE OF MANAGEMENT OF THE TRIALS

The harvesting of any one trial fell into two distinct stages. The first of these was the cutting out of discard plots around the whole trial. This operation took three men about two and a half hours and was carried out on the day before the second stage, the harvesting operation itself.

The actual harvesting was usually performed by a squad of four men, three cutting the plots and carrying the cut material to the balance and one weighing and sub-sampling for dry matter determination. For practical purposes, the average time taken to cut and weigh one plot may be taken as two minutes; the actual figure was 1.85 minutes. On this basis a trial consisting of 240 one yard square plots could be harvested in an eight hour day. Larger plots would take longer but the increase would not be proportional to plot size. The greater part of the time required to harvest one plot was spent in demarcating it from surrounding plots. This would take very little longer for plots of, say, two square yards than for those of one square yard. It is unlikely that it would take more than two and a half minutes to harvest a two square yard plot, say 190 plots per day.

The main difficulty in handling this number of plots is due to the limitations of drying space. In the early stages of a testing programme, when the number of 'lines' to be assessed would be large, it would probably be satisfactory to use fresh rather than dry weights. The consequences of less than perfect correlation between fresh and dry yields can be assessed from Tables 2.6.2 : 2.6.3. The present trials, being based on one cultivar each, do not give any indication of the correlation between fresh and dry yields, but the data from the density trial, reported in Section 2 gave the following values:-

Cut 1	0.82
Cut 2	0.84
Cut 3	0.02
Cut 4	0.98
Total	0.67

With the exception of cut three, it is obvious that fresh yield gave a reasonable measure of dry yield. Cut three was made under rather unfavourable wet conditions and is also the one with the smallest range of variation of dry weights, nevertheless, the complete absence of correlation is difficult to account for. The low value in cut three also of course explains the relatively low correlation between total fresh and dry yields. The average value for the other three cuts is 0.88.

SECTION 3.6 DISCUSSION

In preceding portions of this section the precision of trials based on certain plot sizes and number of replications has been discussed. The criterion of suitability taken has been the ability of a certain layout to detect differences of a specified size with a reasonable degree of assurance. This approach is obviously relevant to the type of decisions which have to be made in the course of the testing of new varieties, where the usual procedure is to compare the new material with some accepted standard variety.

The plant breeder's problem is often of rather a different nature. At the beginning of a breeding programme, it is quite likely that none of the material will be as good as varieties in current use; but in any case the plant breeder has of necessity to reject part of his material at each stage in a selection programme. Once the decision has been taken to retain a given proportion of the available material the difference between the worst of the 'lines' retained and the best of those rejected is of academic interest and the important question becomes: How good on average is the selected fraction compared to what it might have been if it had been selected on the basis of its true genetic worth?

The question to which the breeder requires an answer, is, How efficient is his selection process? that is, If he retains a certain proportion of his material on the basis (say) of the results of a yield trial, how much of this material would, on average, have been retained if its true yielding ability were actually known? and How good is the remainder of the selected material? This question is formally identical with that posed in Section 2 when considering the suitability of non-sward densities for assessing sward performance and it can be answered in a similar manner. Tables 2.6.2 and 2.6.3 can be used as can those of Keuls and Sieben (1955). To use the tables some reasonable assumptions need to be made about the likely relationship between the magnitude of the genetic and environmental standard deviations. Estimates of the latter have already been made, i.e. the coefficients of variation in Tables 3.4.1; 3.4.2; 3.4.5; and 3.4.6. The individual breeder may quite likely have some idea of the probable genetic variation of his material before carrying out any trials even if all he can do is to make a reasonably accurate guess of the range between best and worse, he can forecast with some degree of certainty the probable standard deviation. (Tippet 1925, Pearson 1932, Snedecor 1956). As soon as trial results are available the relationship between genetic and environmental variation is known for that particular set of trials.

To use Tables 2.6.2 and 2.6.3 it is necessary to find the correlation between the genetic and observed standard deviations, we may consider

$$\sigma_o^2 = \sigma_g^2 + \sigma_e^2/r$$

where r is the number of replications.

Then

$$p_{g.o} = \sigma_g / \sigma_o = \sigma_g / \sqrt{\sigma_g^2 + \sigma_e^2}$$

The value of $p_{g.o}$ may be increased indefinitely by increasing the number of replications:-

$$p_r^2 = rp_1^2 / (r-1)p_1^2 + 1$$

where p_1 is the value of $p_{g.o}$ for one replication. The values of the coefficients of variation in Tables 3.4.1/2/5/6 enable us to make some reasonable guesses at the quality of selections made on the basis of data from trials of specified sizes.

Let us set up an example in which 150 'lines' are to be tested in a yield trial and we guess that the likely difference between the highest and lowest yielding is about twelve per cent of the mean; also that the best we can hope for so far as the precision of our trial goes, is a coefficient of variation of four per cent and that the CV may be as high as nine per cent. From the range assumed we estimate the genetic standard deviation to be about 2.25% of the mean (table 2.2.2 in Snedecor 1956). Then for a basic CV of four the correlation between genetic and observed values of yield will be:-

$$p_{g.o} = 2.25 / \sqrt{2.25^2 + 4.00^2} = 0.49$$

say 0.5

The use of four replications increases this value to .7559, say 0.75

$$p_4 = \sqrt{4 \times 0.5^2 / 3 \times 0.5^2 + 1} = 0.76$$

say 0.75

A similar calculation for a coefficient of nine per cent gives values of .24 and .45 respectively.

A smaller number of 'lines' to be tested will tend to increase the correlation since the standard deviation as a proportion of the range increases as the number of observations decreases also the efficiency of the range as an estimator of the standard deviation increases.

The efficiency of selection based on data from the model trials described above is shown in ~~Tables~~ Table 3.5.1. The unbracketed numbers in each case show the proportion of the selected fraction which is genetically superior. For example: when the correlation between genetic and observed values is 0.75 and ten per cent of the original population is selected on the basis of observed performance, then, on average the composition of the selected 'lines' will be as follows:-

96.9% of them will be from the genetically best	50%
81.1	25%
51.2	10%
32.1	5%
8.5	1%

The bracketed numbers in the tables show the efficiency of retention of 'lines', that is the proportion of material of a specified degree of genetic superiority originally present, which is retained in a given selection.

Using the same value for $p_{g.o}$ and intensity of selection as before, we find that a ten per cent selection, based on observed values, retains, on average:-

19.38% of the genetically best 50% of the original 'lines'

32.44	25%
51.2	10%
64.2	5%
85.	1%

Inspection of the figures for efficiency of retention indicates a considerable wastage of potentially valuable material under severe selection and it seems better to practise relatively lenient selection at the earlier stages so as to retain as much as possible of the very best material for further testing. Since the material retained will be assessed over two or more seasons, the correlation between genetic and observed values will increase and this correlation will be further improved by the increase in genetic standard deviation consequent on the reduction in numbers of 'lines' under test.

SECTION 3.7 SUMMARY AND CONCLUSIONS

Two uniformity trials were carried out, one with S22 Italian ryegrass and the other with Irish Italian. The plants in each trial were spaced six inches apart and the trials harvested in one yard square basic units. The results of these trials are described and discussed from three points of view:-

1) The relationship between plot and block size and shape, and the coefficient of variation, and the effect this has on the choice of convenient plot sizes and number of replications to detect a specified difference at a specified level of probability.

2) The estimation of the index of soil heterogeneity ('b') and the effect that different plot and block shapes have on this estimate. The use of the index to make estimates of the size of trial necessary to achieve a given degree of precision.

3) The estimation of likely values of the correlation between genetic and observed values for yield and the effect of various values of the correlation on the quality of selection based on observed values.

The effect of plot shape on the values for the coefficient of variation was very marked but, with this proviso, it is concluded that, to detect with reasonable certainty a difference of seven per cent of the mean, it is necessary to use between ten and twelve replications of two square yard plots or eight replications of plots of four square yards. Larger differences can be detected by fewer replications, the number of replications necessary varying inversely as the square of the difference to be detected.

Consideration of the effects of the correlation between genetic and observed values indicates that a satisfactory quality of selection may be achieved with four replications of two yard square plots, particularly if relatively lenient selection is practised in the early stages of a breeding programme.

TABLE 3.3.2 Key to plot and block sizes and shapes

Plot Size	Anova Type	Plot Dimensions	Block Dimensions	No. of Blocks
1	1	1 X 1	4 X 4	8
	2		2 X 8	
	3		8 X 2	
2	4	2 X 1	4 X 4	4
	5		2 X 8	
	6	1 X 2	8 X 2	
	7		4 X 4	
4	8	4 X 1	2 X 8	2
	9		4 X 4	
	10	2 X 2	4 X 4	
	11		8 X 2	
	12	1 X 4	8 X 2	
	13		16 X 1	
8	14	8 X 1	2 X 8	1
	15	4 X 2	4 X 4	
	16	2 X 4	8 X 2	
	17	1 X 8	16 X 1	

TABLE 3.4.1 S22. Coefficients of variation for plots and blocks of different shapes and sizes for total harvests.

BLOCK SIZE IN TERMS OF PLOTS (COLS X ROWS)

PLOT SIZE IN BASIC UNITS

1964

	CV				NO REPS				AREA PER TREAT			
	2X8	4X4	8X2	16X1	2X8	4X4	8X2	16X1	2X8	4X4	8X2	16X1
1X1	6.08	5.90	5.82		10	9	9		10	9	9	
2X1	4.74	4.98			6	7			12	14		
1X2		4.78	5.01			6	7			12	14	
4X1	3.98	4.70			4	6			16	24		
2X2		4.06	4.76			4	6			16	24	
1X4			4.60	5.22			5	7		20	20	28
8X1	3.87				4				32			
4X2		3.93				4				32		
2X4			4.36				5				40	
1X8				4.33				5				40

1965

	CV				NO REPS				AREA PER TREAT			
	2X8	4X4	8X2	16X1	2X8	4X4	8X2	16X1	2X8	4X4	8X2	16X1
1X1	11.20	10.60	10.23		25	25	25					
2X1	6.35	7.41			10	14			20	28		
1X2		8.22	9.06			7	21			34	42	
4X1	5.40	5.90			8	9			32	36		
2X2		5.88	6.36			9	10			36	40	
1X4			8.32	8.66			18	19			72	76
8X1	4.04				4				32			
4X2		5.09				7				56		
2X4			5.77				9				72	
1X8				7.95				16				128

1964 + 1965

	CV				NO REPS				AREA PER TREAT			
	2X8	4X4	8X2	16X1	2X8	4X4	8X2	16X1	2X8	4X4	8X2	16X1
1X1	8.45	8.12	7.87		18	17	16		18	17	16	
2X1	5.01	5.63			7	8			14	16		
1X2		6.41	6.91			11	12			22	24	
4X1	4.10	4.76			4	6			16	24		
2X2		4.50	5.22			5	7			20	28	
1X4			6.38	6.82			11	12			44	48
8X1	3.65				4				32			
4X2		4.24				5				40		
2X4			4.75				6				48	
1X8				6.19				10				80

TABLE 3.4.2 IRISH. Coefficients of variation for plots and blocks of different shapes and sizes for total harvests.

BLOCK SIZE IN TERMS OF PLOTS (COLS X ROWS)

PLOT SIZE IN BASIC UNITS	CV 2X8	CV 4X4	CV 8X2	CV 16X1	NO REPS 2X8	NO REPS 4X4	NO REPS 8X2	NO REPS 16X1	AREA PER TREAT 2X8	AREA PER TREAT 4X4	AREA PER TREAT 8X2	AREA PER TREAT 16X1
1964												
1X1	7.23	6.70	7.01		13	12	13		13	12	13	
2X1	5.42	6.25			8	10			16	20		
1X2		5.29	6.15			7	10			14	20	
4X1	4.44	5.30			5	7			20	28		
2X2		5.26	6.00			7	9			28	36	
1X4			5.26	6.00			7	9			28	36
8X1	3.75				4				32			
4X2		4.84				6				48		
2X4			5.40				8				64	
1X8				5.51				8				64
1965												
1X1	9.71	9.43	10.07		24	23	25		24	23		
2X1	7.48	6.80			14	12			28	24		
1X2		7.99	7.35			16	14			32	28	
4X1	6.32	5.14			10	7			40	28		
2X2		6.12	4.92			16	6			40	24	
1X4			6.62	5.56			11	8			44	32
8X1	5.09				7				56			
4X2		4.95				7				56		
2X4			5.40				8				64	
1X8				4.38				5				40
1964 + 1965												
1X1	7.02	6.61	7.06		13	12	13		13	12	13	
2X1	5.09	5.01			7	7			14	14		
1X2		5.74	5.66			9	8			18	16	
4X1	4.64	4.08			6	4			24	16		
2X2		4.48	3.92			5	4			20	16	
1X4			5.00	4.50			7	5			28	20
8X1	3.48				3				24			
4X2		3.90				4				32		
2X4			4.04				4				32	
1X8				3.65				4				32

TABLE 3.4.3 S22 Mean coefficients of variation for all plots of size shown. Number of replications required to detect 7 % difference = R. Area required per treatment = A with one guard row = A_1 two guard rows = A_2

		Plot size	CV	R	A	A_1	A_2
S 22	1964	1	5.93	9	9	16.0	25.0
		2	4.88	6	12	18.7	26.6
		4	4.55	6	24	33.6	44.6
		8	4.12	5	40	53.2	67.2
	1965	1	10.68	29	29	51.6	80.6
		2	7.76	16	32	49.9	71.0
		4	6.75	12	48	67.2	89.3
		8	5.71	9	72	95.8	121.0
	1964	1	8.15	17	17	30.3	47.3
	+	2	5.99	10	20	31.2	44.4
	1965	4	5.30	8	32	44.8	59.5
		8	4.71	6	48	63.8	80.6

TABLE 3.4.4 IRISH. Mean coefficients of variation for all plots of size shown. Number of replications required to detect 7 % difference at 5 % / 80 % = R

Area required per treatment = A. With one guard row = A_1 two guard rows = A_2

		Plot size	CV	R	A	A_1	A_2
IRISH	1964	1	6.98	13	13	23.1	36.1
		2	5.78	9	18	28.1	40.0
		4	5.38	8	32	44.8	59.5
		8	4.88	6	48	63,8	80.6
	1965	1	9.74	24	24	42.7	66.7
		2	7.41	14	28	43.7	62.2
		4	5.78	9	36	50.4	67.0
		8	4.96	7	56	74.5	94.1
	1964	1	6.90	12	12	21.4	33.4
	+	2	5.38	8	16	25.0	35.5
	1965	4	4.44	5	20	28.0	37.2
		8	3.77	4	32	42.6	53.8

TABLE 3.4.5 S22. Coefficients variation for each plot and block size and shape for single harvests.

BLOCK SIZE IN TERMS OF PLOTS (COLS X ROWS)

PLOT SIZE IN BASIC UNITS

1965 Cut 1

	2X8	4X4	8X2	16X1
1X1	17.16	16.95	16.49	
2X1	10.46	10.70		
1X2		12.87	13.07	
4X1	6.32	6.96		
2X2		6.92	7.34	
1X4			11.86	12.12
8X1	5.88			
4X2		4.69		
2X4			6.48	
1X8				10.80

1964 Cut 1

	2X8	4X4	8X2	16X1
1X1	6.71	6.72	6.64	
2X1	5.30	5.60		
1X2		5.80	6.05	
4X1	4.56	5.18		
2X2		5.18	5.74	
1X4			5.34	5.88
8X1	4.41			
4X2		4.81		
2X4			4.98	
1X8				4.67

1965 Cut 2

	2X8	4X4	8X2	16X1
1X1	11.44	10.97	11.24	
2X1	7.89	8.53		
1X2		9.12	9.67	
4X1	7.54	7.80		
2X2		8.02	8.26	
1X4			8.38	8.62
8X1	5.51			
4X2		7.32		
2X4			6.90	
1X8				7.30

1964 Cut 2

	2X8	4X4	8X2	16X1
1X1	10.12	9.66	9.61	
2X1	8.48	8.65		
1X2		5.77	6.02	
4X1	7.54	7.96		
2X2		4.94	5.56	
1X4			5.52	6.08
8X1	6.62			
4X2		4.33		
2X4			5.20	
1X8				5.09

1965 Cut 3

	2X8	4X4	8X2	16X1
1X1	14.43	12.36	11.15	
2X1	10.65	12.85		
1X2		10.42	12.67	
4X1	10.96	13.68		
2X2		11.58	14.18	
1X4		11.86		14.42
8X1	10.49			
4X2		12.44		
2X4			13.63	
1X8				13.82

TABLE 3.4.6 IRISH. Coefficients variation for each plot and block size and shape for single harvests.

BLOCK SIZE IN TERMS OF PLOTS (COLS X ROWS)

PLOT SIZE IN BASIC UNITS

1965 Cut 1

	2X8	4X4	8X2	16X1
1X1	13.47	13.29	13.56	
2X1	9.59	9.18		
1X2		10.76	10.39	
4X1	7.26	6.74		
2X2		6.98	6.44	
1X4			8.82	8.38
8X1	5.74			
4X2		5.23		
2X4			6.05	
1X8				6.25

1965 Cut 1

	2X8	4X4	8X2	16X1
1X1	9.78	8.81	8.41	
2X1	7.58	8.10		
1X2		7.49	8.03	
4X1	6.34	6.80		
2X2		7.28	7.66	
1X4			8.00	8.36
8X1	5.12			
4X2		6.45		
2X4			7.78	
1X8				7.41

1965 Cut 2

	2X8	4X4	8X2	16X1
1X1	15.07	15.79	17.43	
2X1	14.42	12.19		
1X2		13.55	11.13	
4X1	12.00	9.26		
2X2		11.52	8.64	
1X4			10.78	7.02
8X1	10.77			
4X2		10.21		
2X4			9.56	
1X8				5.83

1965 Cut 2

	2X8	4X4	8X2	16X1
1X1	8.07	8.30	9.35	
2X1	7.76	6.59		
1X2		7.82	6.66	
4X1	6.58	5.74		
2X2		6.70	6.10	
1X4			6.36	5.48
8X1	6.25			
4X2		6.42		
2X4			5.85	
1X8				3.85

1965 Cut 3

	2X8	4X4	8X2	16X1
1X1	10.32	9.56	9.63	
2X1	6.74	7.96		
1X2		7.44	8.55	
4X1	6.40	7.36		
2X2		6.76	7.68	
1X4			7.00	7.88
8X1	4.98			
4X2		6.84		
2X4			6.59	
1X8				6.99

TABLE 3.4.7 Mean coefficients of variation for the different plot sizes (calculated over all possible block shapes). R = number of replicates required to detect true difference of 7% of the mean at the 5% level in 80% of cases. A = area required in basic units for R replications without guard rows. Bracketed numbers show area required allowing one guard row around each plot. P = plot size in basic units.

1964		CUT 1			CUT 2		
	P	CV	R	A	CV	R	A
S 22	1	6.68	12	12(21)	9.79	24	24(43)
	2	5.69	8	16(25)	7.23	13	26(40)
	4	5.32	8	32(45)	6.28	10	40(57)
	8	4.72	6	48(64)	5.31	8	64(85)
IRISH	1	8.99	21	21(37)	8.56	19	19(34)
	2	7.80	16	32(50)	7.21	13	26(40)
	4	7.42	14	56(79)	6.21	10	40(57)
	8	6.69	12	96(127)	5.59	8	64(85)

TABLE 3.4.7 (cont).

1965		CUT 1			CUT 2			CUT 3		
	P	CV	R	A	CV	R	A	CV	R	A
S 22	1	16.84	25	-	11.21	25	-	12.63	25	-
	2	11.78	25	-	8.80	20	40(62)	11.65	25	-
	4	8.60	19	76(108)	8.12	17	68(96)	12.81	25	-
	8	6.96	12	96(127)	6.76	12	96(127)	12.59	25	-
IRISH	1	13.43	25	-	16.08	25	-	9.83	24	24(43)
	2	9.98	25	50(78)	12.82	25	-	7.67	15	30(47)
	4	7.45	14	56(79)	9.99	25	100(142)	7.19	13	52(74)
	8	5.82	9	72(95)	9.09	21	168(223)	6.35	10	80(106)

TABLE 3.4.8 Values of 'b', the index of soil heterogeneity values shown are the mean for all possible plot and block shapes. Numbers in brackets show extreme values. The negative sign has been ommitted in the bracketed numbers.

1964	CUT 1	S22	-0.46 (.39-.53)	IRISH	-0.42 (.31-.66)
	CUT 2		-0.63 (.41-.90)		-0.51 (.41-.69)
1965	CUT 1		-0.81 (.48-1.24)		-0.83 (.69-.93)
	CUT 2		-0.56 (.51-.74)		-0.60 (.48-.61)
	CUT 3		-0.27 (.20-.39)		-0.52 (.47-.71)
1964 TOTAL			-0.47 (.42-.54)		-0.43 (.32-.70)
1965 TOTAL			-0.62 (.34-.99)		-0.68 (.61-.82)
1964 + 1965			-0.57 (.33-.84)		-0.62 (.57-.72)

TABLE 3.5.1 Efficiencies of selection and retention for different selection intensities for correlation coefficients between genetic and observed values ($\rho_{g.o}$) of .75 (upper portion of table) and .45 (lower)

% of original number of 'lines' selected on basis of observed values

% genetically superior 'lines' present in original population	50	25	10
50	77(77)	90(45)	97(19)
25	45(90)	64(64)	81(32)
10	19(97)	32(81)	51(51)
5	10(99)	18(89)	32(64)
1	2.0(100)	3.9(97)	8.5(85)
50	65(65)	73(37)	81(16)
25	37(73)	45(45)	55(22)
10	16(81)	22(55)	30(30)
5	8.5(83)	12(61)	17(35)
1	1.8(91)	2.9(72)	4.7(47)

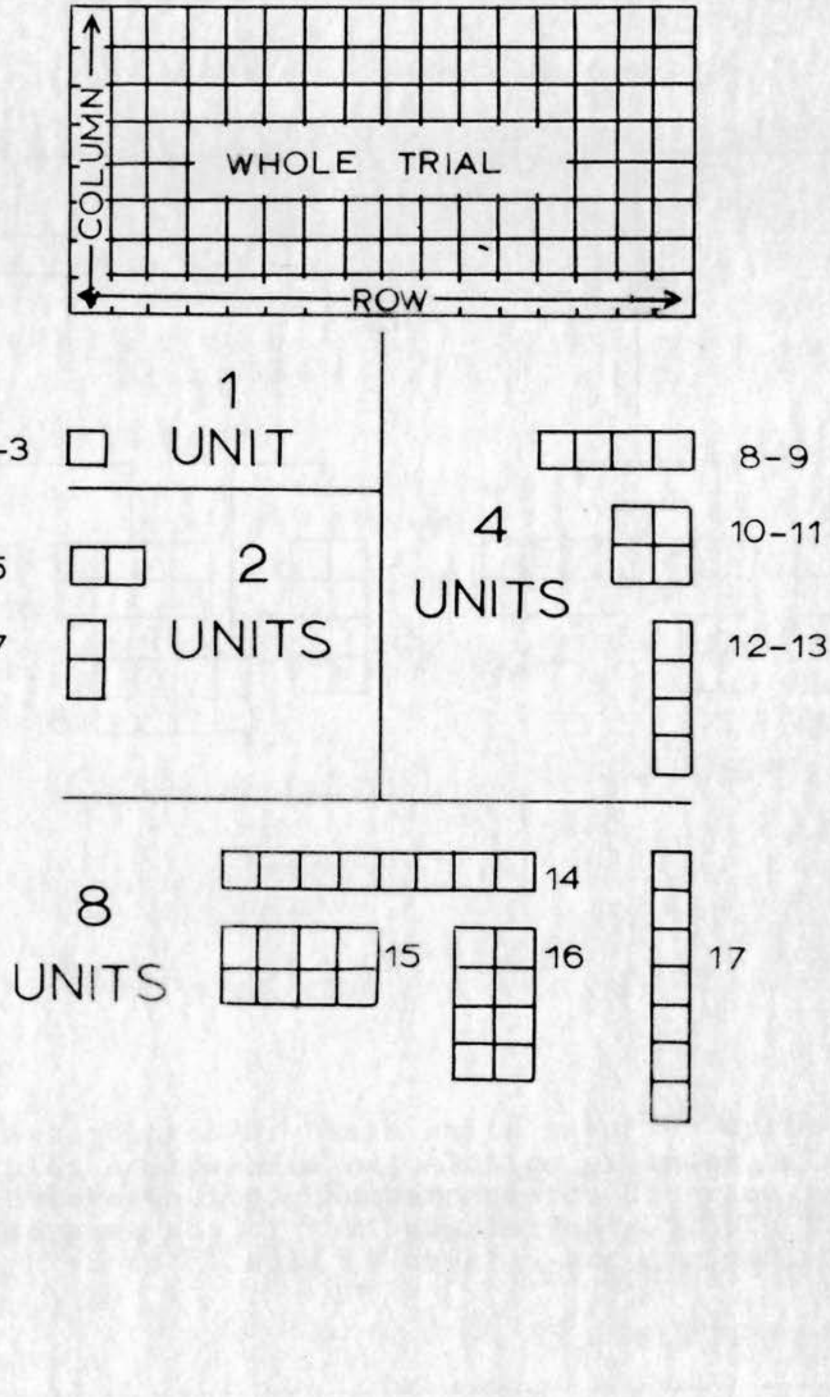

FIGURE 3.3.2a Plot sizes and shapes used for calculating coefficients of variation. Numbers beside diagrams refer to the analyses of variance in Table 3.3.2.

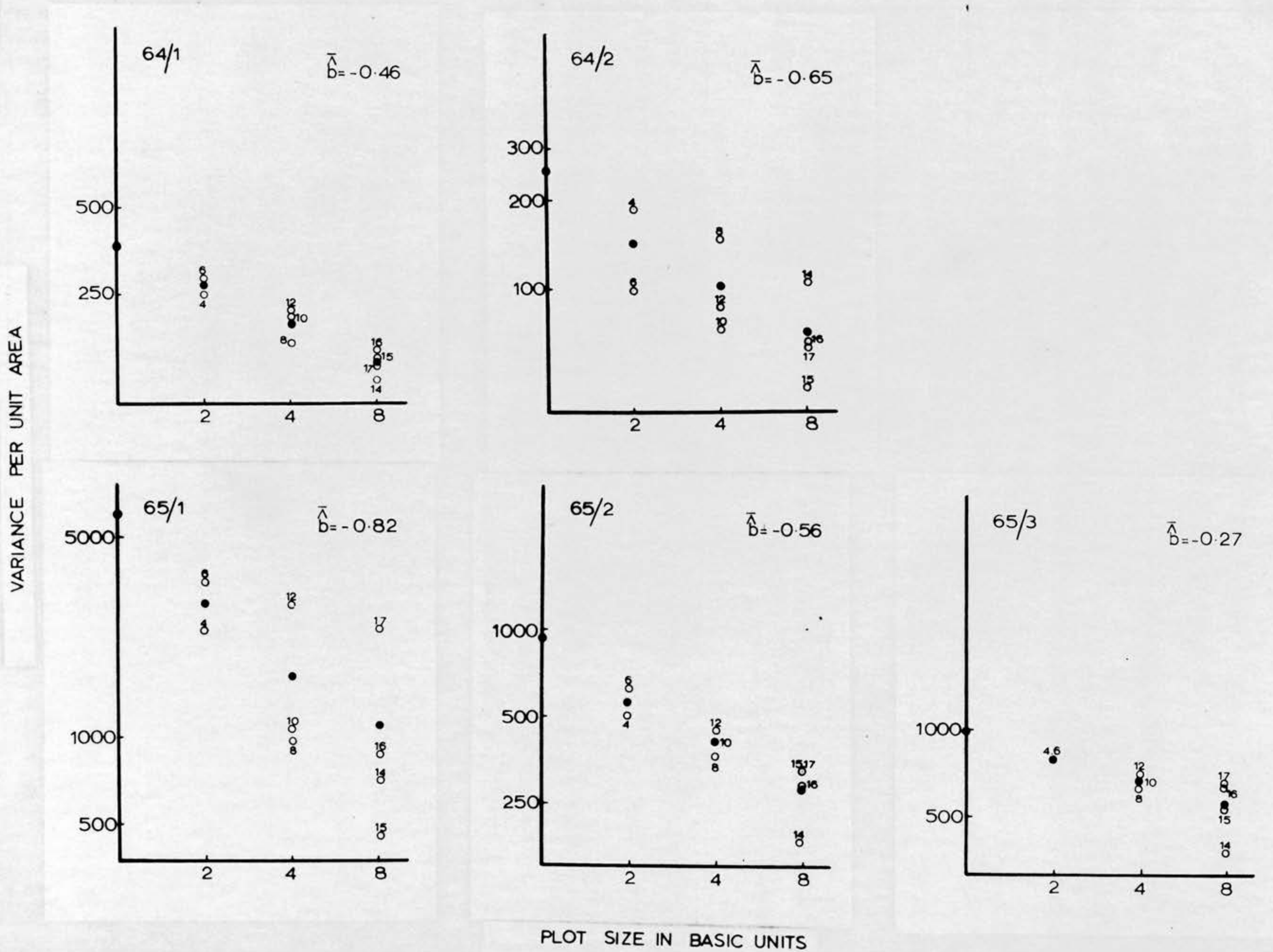

FIGURE 3.4.2 **Effect of plot size on variance. Data for single harvests on S 22.**

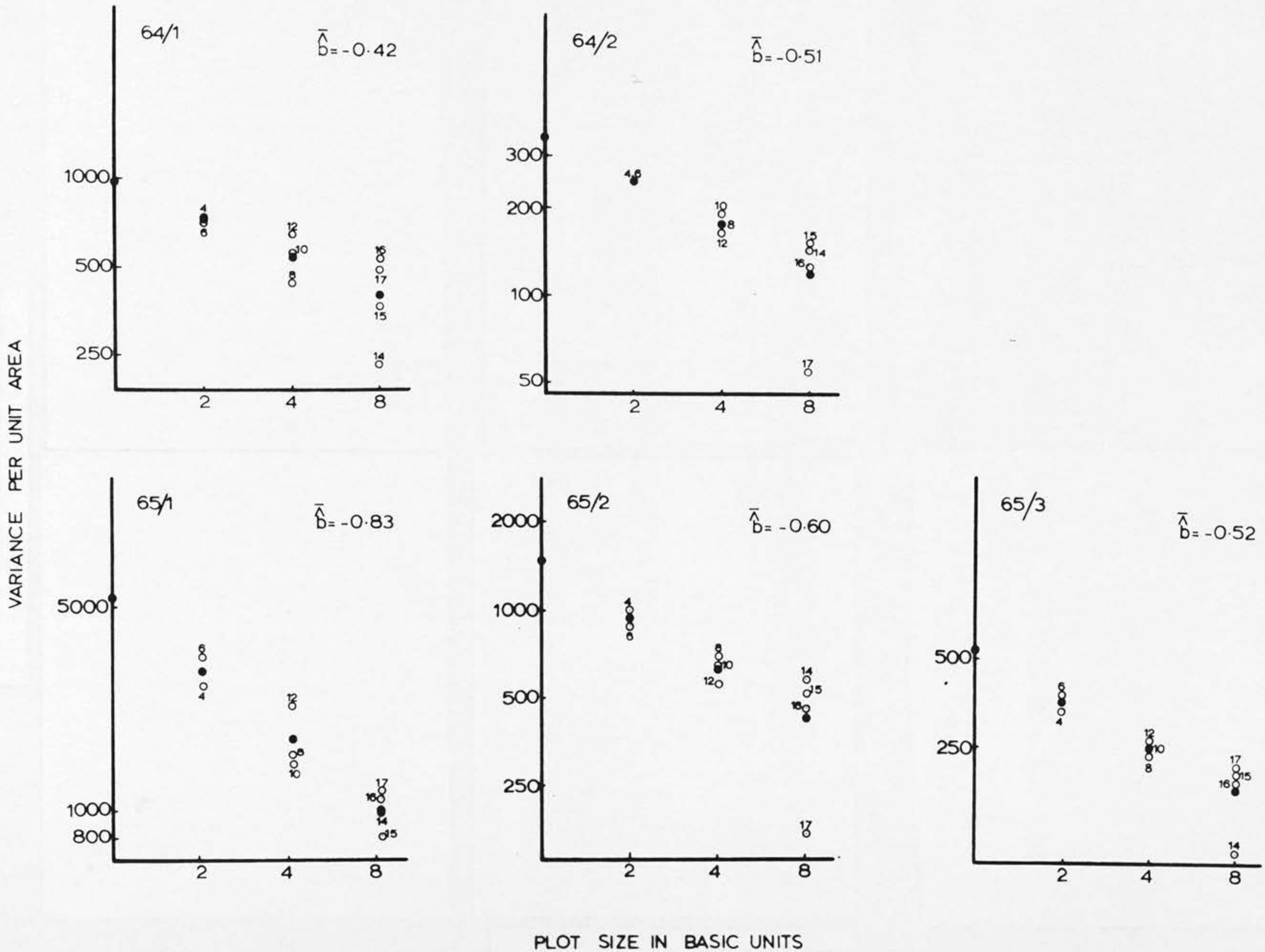

FIGURE 3.4.3 Effect of plot size on variance. Data for single harvests on Irish.

SECTION 4

A STUDY OF THE BEHAVIOUR OF FOUR HERBAGE GRASS CULTIVARS IN MIXTURE

SECTION 4.1 INTRODUCTION

This section deals with the behaviour of four herbage grasses when grown alone and in mixture with each other. The term element has been used when referring to any single component of a mixture; this has been done since some taxonomically neutral term seems desirable when referring to single components of a group which may consist of, say, different genera and different species within genera.

The assumption is often made, implicitly if not explicitly, that any one element will perform in similar fashion in pure-stand as in mixture. The validity of this assumption is of obvious interest to plant breeders, especially those dealing with outbreeding species, in the case of the herbage grasses the question is also of importance to the agronomist since it is common practice to grow mixtures of varieties, species and genera of herbage plants.

Most studies of the behaviour of mixtures have been conducted on plants grown primarily for their seed yield, mostly cereals and usually the characters measured have been those of the mature plant, either grain yield or plant weight, tiller number etc., when the plant was "ripe to harvest". There have been relatively few investigations based on vegetative behaviour of plants in mixture.

The importance of investigating the performance of mixed populations is likely to increase in the near future. On the one hand, those crops which are customarily grown in mixtures, notably the herbage grasses, have reached the stage of improvement at which the identification of particular growth habit and maturity types has become more or less routine and part at least of any further improvement must be expected to come from breeding for cultivars having closer adaptation to the microenvironment of the mixed agricultural sward. On the other hand, there is a growing realisation that pure culture is not necessarily the best system for crops such as cereals or potatoes. The cultivars of these crops are essentially isogenic lines and in the case of cereals virtually homozygous, both features which make the crops concerned particularly susceptible to environmental hazards, especially those of disease. Where great uniformity of product is essential it is probable that cultivars which are virtually isogenic lines will continue to be used but in many other cases the possible advantages of mixtures of cultivars in terms of disease resistance and perhaps complementary exploitation of the available resources resulting in greater total yield, may outweigh the loss of uniformity of product.

Borlaug (1959) has advocated the use of 'multilineal' or 'composite' varieties to control the spread of airborne diseases in self-fertilised plants, and if such varieties are to find a wide use some rapid 'survey' method of forecasting the likely behaviour of the separate "lines" in a mixture is obviously desirable.

The behaviour of the components of a mixture will be dependent on a number of factors, amongst which it might be expected that differences in density and in stage of growth would be important. In the early stages of growth of pure-stand of a herbage grass, yield is almost directly related to density (Donald 1958) but as the stand approaches maturity, yield per unit area becomes progressively less dependent on density until in mature stands it is virtually independent of density (Donald 1958, Lazenby and Rogers 1964). The effects of competition in mixed stands might therefore be expected to be slight in the early stages of growth, to become apparent sooner in higher, rather than in lower density stands but, unless the time of commencement of competition has a 'carry-over' effect, to be of much the same nature in mature stands of the same materials irrespective of density.

SECTION 4.2 LITERATURE

The most comprehensive series of experiments comparing the behaviour of elements in pure-stand and in mixture have been carried out by Sakai and his co-workers. Sakai (1955) found that elements which performed well in pure-stand did not necessarily do well in mixture with others and that in some cases found the exact opposite. Sakai also found that changes in plant density, while tending to increase the magnitude of competitive effects, did not alter the relative performance of elements. Sandfaer (1954) working with two element mixtures of barley and oat varieties also found no effect of density on competitive ability.

Allard (1961) found that mixtures of three pure lines of Lima beans tended to give lower seed yields than the mean of the pure-stands and attributed this to a negative correlation between seed yield and vegetative vigour, so that in mixture the vegetatively vigorous but low seed yielding lines were suppressing their less vigorous but better seeding associates.

Hanson, Brim and Hinson (1961) investigating seed yields of Soybean found that the competitive advantage gained by one of a pair of competing units tended to be the competitive disadvantage for the other. Eberhart, Penny and Sprague (1964) report a similar effect in maize.

The performances of mixtures as such compared with pure-stands have been reported on by a number of authors, Simmonds (1962) has reviewed the literature up to that date and summarises the results of most workers by saying "....the general conclusion that emerges may be stated thus: the performance means of mixtures are often equal to the means of components but they sometimes exceed them and occasionally even exceed the higher components; they are rarely inferior to the mean of the components." Work carried out since Simmonds' review tends to confirm this summary although Allard's findings quoted above give one reason why the reverse may hold when competitive vigour depends on some character of the plant which shows a negative correlation with the character under consideration.

Recent work mainly with mixtures of cereals tends to show that the advantages of mixtures compared to pure-stands is connected with the degree of difference between the components. In general mixtures of different varieties of the same cereal species do not show any advantage in yielding ability or quality over the mean of the varieties grown separately. Patterson _et al_. (1963) mixed oat varieties in 50/50 proportions; while they reported a decrease in the amount of lodging in the mixtures there was no increase in yield. Schlehuber and Curtis (1961) found a decrease in grain yield in two component mixtures of four varieties of hard red winter wheat. Popov and Lenkov (1962) using 1:1, 2:1, and 3:1 mixtures of common with durum wheat reported no increase in mixture yields compared to those of pure-stands. In contrast to the above a number of workers have found quite considerable gains in total yield from mixing different species of cereals or a cereal and a non-cereal species. Ilieva-Staneva (1962) obtained up to an eighteen percent increase over the yield of the higher yielding component in 50/50 mixtures of winter barley and wheat. The quality of the mixture was also better than that of either of the two components. Kolev and Ivanova (1964) working with similar mixtures confirmed these findings and also reported an increased resistance to lodging. Alexander and Genter (1962) examined the effects of growing maize and soyabeans in alternate pairs of rows and found that the yield of the maize was increased by as much as thirty percent with no reduction in theyield of the soyabeans.

The deliberate use of a mixture of two varieties to give a dual purpose crop has been advocated by Avakjan and Šumanskaja (1962) who found that a mixture of early and late ripening varieties of maize gave a useful yield of cobs while the vegetative parts of the crop were still suitable for silage. Heymann (1963) found rather similar complementary effects in mixtures of oats and barley, where although total grain yield was not increased, the feeding value of the grain was; the relatively high crude protein content of the oats being complemented by the higher starch equivalent of the barley.

Phlak, Vicherkova and Minar (1965) studied the mutual influence of barley and oats grown together and found that the barley was stimulated and the oats depressed in mixture and that some mixtures gave higher yields than either species grown alone.

There has been relatively little work done on the mechanism of the interactions between the components of mixtures. Donald (1958) grew plants of Lolium and Phalaris in the same pots and used screens between plants of the different species in such a way that it was possible to isolate either the roots or the aerial parts or both, of plants grown in the same pot. Donald found that either root or shoot competition enabled the ryegrass to be more successful than the Phalaris and that when both root and shoot competition were operative the combined effect was greater than the sum of the two effects separately. The work of Roy (1960) with rice demonstrated that interactions between different varieties can take place over a considerable distance so long as the plants concerned are growing in a liquid medium and Ivanov (1962) has demonstrated the mutual exchange of root excretions between maize and fodder bean plants although the effects on the growth of the two species were not reported. Kumagai and Tabata (1962) stated that in mixtures of oat varieties, the competitive ability of a variety was related to its water requirement and that also erect varieties tended to have greater competitive ability than prostrate ones.

In forage grasses the work of Hanson, Garber and Myers (1951) showed that mixtures of two or more Kentucky Bluegrass strains were superior to either the pure-stands or the commercial control and the authors state that this was particularly the case in combinations of an erect, high yielding strain with a compatable low-growing sod forming type and suggested that this was because of the complementary use of the available space by the two types.

Harper (1961) has carried out a series of experiments on the effects of density and of the pattern of distribution of the separate components in mixtures on competitive behaviour (Harper uses the term interference). In general Harper found that changes in density had little effect on competition so long as the densities were those at which yield per unit area becomes independent of density. The pattern of distribution, though not affecting the total yield of a mixture, had marked effects on the proportional contributions of the components.

The effects of varying other environmental factors have been studied by Sagar (1960), who found that differences in the relative time of sowing of <u>Lolium perenne</u> and <u>Plantago lanceolata</u> resulted in big changes in their relative contributions to the yield of the mixture and Williams (1964) reports a similar effect in mixtures of kale and <u>Chenopodium album</u>.

SECTION 4.3 MATERIALS and METHODS

Section 4.3.1 Materials and management

The four herbage grasses concerned were Ayrshire perennial ryegrass, Scotia perennial ryegrass, Daeno II cocksfoot and Scotia cocksfoot; these are identified as elements A, B, C and D respectively. Ayrshire ryegrass is an early flowering indigenous commercial variety, it is not particularly leafy and does not recover well after cutting; Scotia ryegrass is a variety selected from Scilly Isles material, it is rather similar in flowering time and growth habit to S.23 and is much later flowering than the other three elements. Scotia cocksfoot is a variety selected from plants growing in a small woodland clearing and might be expected to be more shade tolerant than the other three elements, there is some evidence from agricultural use that this variety does not persist or yield well in mixture with other grasses. The mean ear emergence dates for these elements at Edinburgh are:-

A	Ayrshire Perennial Ryegrass	15 May
B	Scotia Perennial Ryegrass	12 June
C	Daeno II Cocksfoot	6 May
D	Scotia Cocksfoot	8 May

Seed of all elements was sown in seed pans on 8th May, 1963 and seedlings were pricked into boxes 17" x 17" x $3\frac{3}{4}$" deep (43.2 x 43.2 x 9.5 cm.). The plants remained in these boxes for the remainder of the experiment. The plants were set out in a square grid arrangement with uniform and equal spacing between and within rows; three densities were employed having 1" (2.5 cm.), 2" (5.1 cm.) and 4" (10.2 cm.) between neighbouring plants, the resulting densities being referred to respectively as high, medium and low. Each replicate consisted of ten boxes, four of them containing the pure-stands of the elements and six containing one each of the possible two element mixtures, in the 'mixed' boxes plants of the two elements were planted alternately, so that a plant of one element had as its closest ('square') neighbours plants of the competing element and as its diagonal neighbours plants of its own element. Within each density four replicates were used, two being used for each of two different cutting regimes differing in times of cutting, these cutting regimes are referred to as "Harvest Series" 1 (HS 1) and "Harvest Series" 2 (HS 2). All boxes were harvested three times in 1963 and five times in 1964, the harvest dates are given in Table 4.3.1. At each harvest the plants were cut at ½" (1.25 cm.) above the soil surface, oven dried and the dry weights recorded. In the 'mixed' boxes, the two elements were harvested separately and in 1964 the pure-stand boxes, were treated in an analogous fashion, i.e. alternate plants were harvested separately to give two 'dummy' elements for each pure box. Immediately after each cut each box received 6.5 gms. (= 3 cwts/acre) of general fertilizer containing 12% N.

Section 4.3.2 Statistical Methods

The layout of the experiment is analogous to that of a genetic diallel containing all reciprocal progenies and parental lines.

One obvious approach to the analysis of the results is to set them out in a two-way table so that the element arrays occupy the rows and the associate arrays the columns for each replication, the pure-stand yields (reduced to the same basis as the mixed yields, in the present case to half plot yields) then occupy the NW-SE diagonal. The table can then be analysed for row (element) effects; and column (associate) effects; their interaction and the interactions of these three with replications. There are two main objections to this approach, in the first place the model on which it is based can only include an estimate of competitive effects of the one element from its effect on the other elements, it provides no estimate of the comparison between the behaviour of one element in mixture and in pure-stand; a further objection in the present case is that the design is not strictly orthogonal since the pure-stand yields are derived from whole plots and may be expected to have reduced variances from the mixed-stand yields which are derived from half plots.

Williams (1962) has published an analysis based on the analogy with the genetic diallel using plot sums and within plot differences and involving weighting the yields of pure-stand plots in inverse proportion to the variances of pure-stand plots and mixed plots. He goes on to compute an index of competition for each element based on the average effect of each element on all the others. Eberhart _et al_., (loc.

sit.) point out that the model on which this and similar diallel analyses are based is incorrect if the data are available for each individual entry. Eberhart et al., have produced a model which in effect measures deviations about the pure-stand mean and it measures competitive effects of an element as average increments from the pure-stand mean of that element; these authors define three types of competition effect:-

$\hat{k}$ the general competition effect, the average difference between all mixed plots and all pure-stand plots on a single entry basis, positive if on average elements yield more in mixture than in pure-stand.

$\hat{sk}_i$ the element by general competition effects, positive if the i^{th} element performs better in mixture than in pure-stand after allowance has been made for $\hat{k}$.

$\hat{c}_{i(i')}$ specific competition effects accounting for any further deviation in the yield of the i^{th} element grown with the i'^{th} element, not explained by $\hat{k}$ and sk_i.

Eberhart's analysis has been adopted in the present work, and has been extended slightly to incorporate certain environmental X competition effects not considered by Eberhart et al. A fuller explanation of the estimation of the various effects and of the analysis of variance is given in a statistical appendix Section 4.8.1.

A possible objection to the use of the model of Eberhart et al is that general statements about the competitive behaviour of the different elements depend on the reliance that can be placed on the estimates of the $\hat{sk}_i$'s. These estimates may be difficult to interpret if specific competition effects are large compared to the $\hat{sk}_i$'s. As will be seen when the results of this experiment are presented, the specific competition effects may sometimes be of opposite sign and of greater magnitude than the corresponding $\hat{sk}_i$'s. In such cases the characterisation of the average behaviour of elements on the basis of the direction and magnitude of their $\hat{sk}_i$ values is not entirely satisfactory. A technique recently developed by Durrant (1965) offers a wider range of alternative classifications for the behaviour of elements in mixtures according to their behaviour when grown with others which in pure-stand are higher or lower yielding. The relatively small size of the present "mechanical diallel" renders the data not really suitable for treatment by Durrant's technique, though the experiment does however furnish a useful illustration of possible applications of the method and the matter is dealt with in some detail in Section 4.4.2.

For convenience of presentation the following symbols are used when describing the performance of specific elements:-

- AA mean whole box yield of pure-stand of element A. Similarly BB, CC, DD.
- Aa mean actual $\frac{1}{2}$ box yield of pure-stand of element A. (Each box gives two estimates of Aa; their sum = AA). Similarly Bb, Cc, Dd.
- AB mean whole box yield of elements A and B in mixture. Similarly AC, ..., CD.
- Ab mean = box yield of element A when grown with element B. Similarly Ac, ..., Dc. Ab + Ba = AB.

SECTION 4.4 RESULTS

Section 4.4.1 Results in year of sowing 1963

For reasons already given, it is to be expected that the magnitude of competitive effects between elements will increase as the plots reach the point at which yield becomes independent of density. The relationship between pure-stand yield per unit area and density for each harvest in 1963 is shown in Figures 4.4.1 and 4.4.2. The scales on these figures have been chosen so that when yield per unit area is directly proportional to density the lines on the graphs are straight and of unit slope. When yield is constant irrespective of density the lines are horizontal. In both harvest series there is a clear tendency for yield to become less dependent on density in the later harvests than in the earlier. In HS 1 the yields for the first harvest show an approximately density dependent relationship for the low and medium densities but the high density is already yielding less than it would if yield were proportional to density. The same general remarks apply to HS 2 except that the decline in yield from that to be expected on a strictly proportional basis is apparent in the comparison between the low and medium densities. In both harvest series the lines for harvest three are effectively horizontal and yield per plot effectively constant no matter what the density. Harvest two is intermediate but even here the yields are largely independent of density.

The yields of all the treatments are given as bar graphs in Figures 4.4.3 and 4.4.4. In these figures each "bar" is divided into a lower, black portion and an upper, white portion. The lower part shows the yield of the element, the upper part the yield of the particular associate, the whole bar, of course, gives the yield of the mixture. The black dots show the mid pure-stand yield corresponding to each mixture. Summarised and abridged analysis of variance are given in Table 4.4.1. In HS 1, competitive effects tend to become more apparent as density increases and with successive harvests. Although significant competition effects are almost absent at the low density Figure 4.4.3 shows that some of these effects were proportionately quite large. The medium and high densities gave a similar result to each other at each harvest in the sense that elements that did well at one density also did well at the other and, in fact at the third harvest all three densities gave very similar results.

In HS 2 the three densities all gave consistent results. The easiest visual comparison is that obtained by comparing the "shape" of the black portion of corresponding diagrams for different densities and the relation that yields of single elements in mixture bear to their pure-stand yield.

Since the competitive effects from different densities are so consistent it is reasonable to make comparisons over all three densities. To avoid the complication introduced by the different yields at different densities all the data were converted to percentages of the mean yield for each harvest at each density. This, of course, removes any effect of density on mean yield but does not greatly affect the interactions involving density and the competitive effects. Expressing the data in this form also makes visual comparisons between the estimates of element by general and of specific competition effects at different harvests simpler.

Table 4.4.2 gives summarised analyses of variance for each harvest and for total yield for each harvest series. The main feature of this table is the relative absence of density X competition effects although these are present in the data for total yield in HS 1. Density X specific competition effects are completely absent in both harvest series.

The estimates of the $\hat{sk}_i$'s are given in Table 4.4.3. This table also gives the change in the estimates between HS 1 and HS 2.

Considering first the estimates for HS 1 there are marked differences between the behaviour of the different elements, 'A' having consistently the highest estimates and 'D' except in the first harvest, the lowest. The small negative values for 'C' appear at each harvest but the behaviour of element 'B' shows a sharp change between harvest one and harvest two. However the values for the different elements at harvest one do not differ significantly.

In HS 2 the behaviour of the four elements is consistent from harvest to harvest but there is a marked change compared to HS 1. Element 'C' now shows the highest values of $\hat{sk}_i$ and in fact, except for 'D', all the elements show significant changes in their average competitive behaviour. The conditions of HS 2 appear to have favoured the two cocksfoot cultivars and penalised the two ryegrasses so far as competitive performance is concerned.

The estimates of specific competion ($\hat{c}_{i_{(i')}}$) are given in Table 4.4.4 for the total harvests for both harvest series. In both cases there are a number of significant values of $\hat{c}_{i_{(i')}}$ and especially in HS 1 some of them are large relative to the values of $\hat{sk}_i$.

Section 4.4.2 Results in year after sowing 1964

In 1964 it proved impossible to harvest separately the elements of the mixtures at the high density. In the following account the high density is omitted from consideration.

Figures 4.4.5 and 4.4.6 show, in bar graph form, the yields and competitive effects in 1964.

All data for 1964 were first analysed by the method of Eberhart et al. Data for the two harvest series were analysed separately. In HS 1 there were no significant interactions between element effects and density, in HS 2 significant interactions were present but inspection of the data indicates that they are mainly due to differences in behaviour of the pure-stands at the two densities, the general competition by element by density effects and the specific competition by density effects being negligible. The analyses of variance are summarised in Table 4.4.5. The estimates of the $\hat{sk}_i$ for each harvest separately are given in Table 4.4.6 and those for the total yield together with the pure-stand totals and the specific competition effects are given in Table 4.4.7. As already mentioned the $\hat{sk}_i$ effects are difficult to interpret in the presence of numerous specific competition effects but four useful points emerge. Firstly, the largest estimates of $\hat{sk}_i$, for Scotia cocksfoot (D) in HS 1 (-22.6) and Danish cocksfoot (C) (+25.7) in HS 2 account for nearly all the variation in these two instances, the associated specific competition effects all being non-significant, the same applies to Ayrshire ryegrass (A) in HS 2. All other $\hat{sk}_i$ effects are associated with two relatively large specific competition estimates. Secondly, in HS 1 the relatively high values of specific competition estimates for all other elements in association with Scotia cocksfoot are noteworthy. The third, and probably most important point is the change in the estimates of the $\hat{sk}_i$'s between the two harvest series, the two ryegrasses being on average relatively 'good' competitors in HS 1 and the two cocksfoots being relatively poor, in HS 2 almost the reverse situation applies. Fourthly, in HS 1 the higher values of $\hat{sk}_i$ tend to be associated with the higher values of pure-stand performance, i.e. the more vigorous competitors are those with the highest pure-stand yields, the effect is not quite consistent, Scotia cocksfoot with a higher pure-stand yield than Danish cocksfoot, is, nevertheless, considerably less successful than Danish. In HS 2 there is no obvious association between pure-stand performance and average competitive behaviour.

The situation becomes somewhat clearer if we consider the actual behaviour of one element in mixture with another compared to its own pure-stand performance (Table 4.4.8). In this table each off-diagonal entry represents the difference between the yield of the i^{th} element when grown with the i'^{th} and the yield of i alone (i.e. it is equal to the sum of $\hat{k}$; $s\hat{k}_i$ and $\hat{c}_{i(i')}$. The diagonal entries are the mean pure-stand yields gms/½ plot. In Table 4.4.9 the differences of these values for the two harvest series are shown, a positive (negative) value indicating that the element i with element i′ performs competitively better (worse) in HS 2 than in HS 1.

In Table 4.4.8 a positive value is matched by a negative value for the diagonally opposite entry, i.e. in this experiment, if one element of a mixture does better than the same element in pure-stand, then its associate does worse; but in general positive values are of greater magnitude than negative i.e. any advantage of yields of mixture over pure-stand in general is due to the advantage to one element of the mixture being greater than the disadvantage to its associate.

In Table 4.4.9 there are six significant changes of competitive behaviour between HS 1 and HS 2. Four of these occur in pairs of opposite sign (i.e. one element in a mixture performing better (worse) and its associate worse (better), these are the elements of the combinations AD and CB, the remaining two significant changes are also associated with fairly large though non-significant changes of opposite sign, Bd (cf Db) and Ca (cf Ac) the change in behaviour of Bc and Bd is matched by corresponding changes in the behaviour of the pure-stand of 'B' and is probably due to factors affecting 'B' as such whether in pure-stand or in mixture. The large change in the behaviour of 'A' and 'D' in mixture with each other and the change in the relative behaviour of Ac and Ca do not obviously correspond to changes in pure-stand performance.

The relationship between pure-stand and competitive performance is shown graphically in Fig. 4.4.7 for HS 1 and Fig. 4.4.8 for HS 2. These diagrams show the differences between pure-stand and mixture yield for each element with each associate, compared with the pure-stand difference from the mid-pure stand. In HS 1 there is a fairly clear relationship between the relative pure-stand performance for the elements in each mixture and their behaviour in mixture with each other, although elements 'C' and 'D' when grown together depart from this trend. In general when two elements are grown together the heavier yielding in pure-stand increases its yield and the lower yielding suffers a decrease, these increases and decreases being roughly proportional to the pure-stand differences between the elements, although on average the increases are slightly larger than the decreases, which is reflected by the regression line cutting the vertical axis above the origin and, of course, means that mixtures have slightly higher yields than the pure-stand yields would imply. In HS 2 there is no similar relationship apparent at either density although certain elements do show a degree of consistency in their behaviour, the concentration of points for element 'A', for example, in the "S-E" sector of Fig. 2 shows 'A' to be a poor "competitor" despite its relatively good pure-stand performance, conversely 'C' is a strong "competitor" in spite of its relatively low yield in pure-stand.

The comparisons between the yield of each mixture and the mid-pure-stand yields are shown in Table 4.4.10. In most cases mixture yields exceed mid-pure-stand yields for the reasons already given, but the increases are rarely significant, although in some cases quite large; nearly 15% in one case. There are no significant values in the data for HS 1 but the behaviour of mixtures is consistent over both densities. In HS 2 there are quite large differences between the same mixtures at different densities, in particular mixtures BC and CD show marked contrasts in the data for total yield. Reference to Fig 4.4.8 indicates that this difference in behaviour at the two densities is in both cases due to the behaviour of element 'C' which at low density yields particularly well when grown with element 'B' and at high density when grown with 'D'.

SECTION 4.5 DISCUSSION

Section 4.5.1 Competitive effects as estimated from Eberhart's model

The analyses and estimates of competition effects so far presented suggest that density does not greatly affect competition between different elements in a mixture and that this is true even during the early stages of growth when it would be expected that competitive effects would become apparent earlier at the higher densities. Differences in management however, can have very marked effects; the two cutting regimes employed producing very different effects on the behaviour of the elements. In both 1963 and 1964 the environment of HS 1 favoured the two ryegrasses at the expense of the cocksfoots while that of HS 2 favoured element C (Danish cocksfoot) and was much less unfavourable to element D (Scotia cocksfoot). Since the effects of differing densities were small and generally non-significant it is convenient to examine the effects of cutting regime averaged over all three densities in 1963 and over both the low and medium densities in 1964.

In 1963 the estimates of $\hat{sk}_i$ calculated as a per cent of the overall harvest mean tended to remain fairly constant in both direction and magnitude from one harvest to another, this is especially true in HS 2 but it holds for most of the data collected on HS 1, the most notable exception being the reversal of the behaviour of element 'B' after the first harvest. (It should however be noted that the negative value of $\hat{sk}_b$ at harvest one, though large is not significant).

In 1964 there was considerable change in the estimates of the $\hat{sk}_i$'s from harvest to harvest. These estimates (Table 4.4.6) are given on the basis of their percentage of the harvest means in Table 4.5.1. In HS 1 there is a tendency for the two ryegrasses to be competitively more successful in the earlier harvests and for the earlier flowering of the ryegrasses (Ayrshire) to be more successful than the later flowering Scotia. As the season progresses the advantage turns in favour of the cocksfoots, particularly of the Danish commercial. Scotia ryegrass, holds its own though it is not so successful as in earlier cuts, while the early flowering commercial Ayrshire ryegrass is markedly less successful. Over the season as a whole the cutting regime of HS 1 favours the ryegrasses at the expense of the cocksfoots.

In HS 2 the trends from harvest to harvest are similar to those in HS 1 in the sense that the ryegrasses are less successful and the cocksfoots more so as the season progresses but by the time the first harvest was taken the advantage was already shifting in favour of the cocksfoots, the effect over the whole season being a large competitive advantage to element 'C' and a must smaller disadvantage to element 'D' than in HS 1.

In view of the relatively close relationship between pure-stand yield and competitive behaviour in HS 1 and its absence in HS 2 it is tempting to conclude that a cutting regime which maintains the plants in a more or less vegetative condition allows yielding ability per se to determine competitive ability, while a regime which allows the plants to commence stem elongation destroys this relationship. This is quite a reasonable hypothesis since small differences in the onset of stem elongation and hence of the time of maximum yield could have large effects on the competitive ability of different elements. This hypothesis would also be consistent with the results obtained by workers with mixtures of cereal cultivars which have not generally shown any consistent relationship between pure-stand performance and performance in mixtures.

The data for the total yields for 1964 are consistent with the hypothesis, the data for individual harvests are less so; moreover, although there is a marked difference in the behaviour of the elements if only total yield is considered the trend from harvest to harvest is the same in both harvest series; favouring the ryegrasses early in the season and the cocksfoots later; suggesting that the same influences are operating in both cutting regimes.

In view of the considerations outlined above it can only be said that the case for pure-stand performance being a determining factor in mixture performance where plants are maintained in a vegetative condition is unproven, the present evidence being suggestive rather than convincing.

Section 4.4.2 Alternative methods of interpreting the data

The analogy between the layout of the trials which have been described and the genetic diallel and the success of the W_r/V_r graph as a rapid means of assessing the results of a genetic diallel leads naturally to a search for similar techniques which could be applied to data from a mechanical diallel.

Harper (1964) has suggested the use of V_r/W_r graphs for detecting ecological effects analogous to the various dominance relationships in a genetic diallel. Statistically the analogy seems quite justifiable, but the interpretation of W_r/V_r graphs is much more speculative in the case of the mechanical diallel since there is no widely accepted hypothesis about the relationship of pure-stand performance of an element to that of its performance in mixtures and its effect on the performance of the mixture as such. In certain limited cases it may be that W_r/V_r graphs do detect an analogue of genetic dominance, this will be so if, in 50:50 mixtures, the differences between the departures of each element from its own pure-stand performance are in the same direction as the differences between the pure-stands; even so, the precise meaning of "dominance" in this context is difficult to visualise; it is easy, for example, to imagine a situation in which the changes of behaviour of elements due to mixture are exactly compensatory so that the mixture yields are the same as those of the mid-pure-stands, in this case the V_r/W_r graph would detect no dominance and yet those elements which showed the greater increases (or smaller decreases) in mixture compared to pure-stand would be showing "dominance" in an ecological sense.

Despite these limitations, W_r/V_r graphs may be useful when only the mixture yields are available and not the yields of the separate elements, particularly when they reveal a change in "dominance" relationships associated with a change in environment. Harper quotes an example in which at low density a situation akin to full dominance obtains whereas at higher density certain elements show strong interactions.

W_r/V_r diagrams for the total (season's) yields for the present experiment are given in Fig. 4.5.1 they show that in HS 1 "partial dominance" without interaction obtained at both densities, in HS 2 this was true at the higher density but at lower density strong interactions were present, the elements in HS 2, therefore, show a reversal of the behaviour of the <u>Linum</u> varieties in the experiment quoted by Harper.

Comparison of the graphs in Fig. 4.5.1 with Figs. 4.4.7 and 4.4.8 shows that in HS 1 the order of "dominance" on the V_r/W_r graphs corresponds to the order of "ecological dominance" as shown by the distribution of points in Fig. 4.4.7 and is also in the order of pure-stand yields. In HS 2 at high density the W_r/V_r order of dominance is still in the order of pure-stand yields but does not now correspond to the ecological dominance indicated in Fig. 4.4.8. The apparent dominance of element 'A', for example, is due to deviations in yield of mixtures containing 'A' from their mid-pure-stands in the direction of pure 'A' which are attributable to small decreases in the yield of 'A' being more than compensated for by larger increases in the yields of the associates of 'A'. In these circumstances it is difficult to attach any meaning to the statement that 'A' shows "dominance" in mixtures with the other three elements. In all these cases where "W_r/V_r dominance" is indicated, the apparent dominance of those elements having the highest pure-stand yields is an inevitable consequence of increases due to competition being greater in magnitude than are decreases.

Durrant (1965) has produced a modification of the W_r/V_r analysis in which W_r (which is strictly analogous to the W_r, the row covariance, of the genetic diallel) is plotted against W_c, the column covariance, the covariance of the element array with the pure-stand array.

The points are plotted on a graph such as that shown in Figure 4.5.2 the W_r values being measured along the vertical axis and the W_c along the horizontal. The point Z is marked along the W_c axis at a distance from the origin representing the pure-stand variance and the diagram divided into eight segments by the W_c axis, the perpendicular drawn through Z and the bisectors RZQ and MZN. The particular segment of the graph into which the point representing one element falls enables certain general deductions to be made as to how that element reacts to being grown with others and in what way it effects its associate elements.

Elements can first be classified according to whether or not they have a greater effect on their associates than their associates have on them. If they do the points representing them fall into one of the unshaded portions of the diagram, RZN or MZQ, and the more pronounced the effect the nearer do the points lie to the W_c axis. Conversely elements which are more affected by their associates but which have little effect on them, lie in the shaded areas RZM or NZQ.

The direction of the effects can be assessed from the diagram according to the displacement of the points from the W_c axis and the line SZT. Displacement above or below the W_c axis gives an indication of the effect that different associates have on the element in question. Elements falling below the W_c axis show a decrease in yield compared to their pure-stand yield when they are grown with elements which have a larger pure-stand yield than their own and/or show an increase when grown with a smaller element. Elements whose points lie above the W_c axis are increased in yield when grown with larger elements and/or decreased with smaller. It is likely that more points will lie below than above the W_c axis, that is that the values of W_r will tend to be negative.

The position of the points to the right or left of the line SZT shows the direction of the changes induced by an element in the associates with which it is grown. Elements lying to the right of the line tend to produce an increase in larger elements and/or a decrease in smaller while those lying to the left tend to produce a decrease in larger elements and/or an increase in smaller.

Although, when two elements which differ in their pure-stand yield are grown in mixture with each other, almost any outcome is possible, the most likely single effect is that the larger yielder in pure-stand will increase its yield and the smaller suffer a decrease and on a priori grounds one would expect to find more points falling into the quadrant of the diagram XZTQ than in any of the others.

An explanation of the rationale of Durrant's method is given in the statistical appendix section 4.8.

The data for 1964 for total yield for both harvest series have been examined by Durrant's technique and the resulting W_r/W_c graphs are presented as Figure 4.5.3.

In HS $_1$ all the points fall into the SE quadrant of the graph, indicating that on average all the elements show a reduced yield when in mixture with elements having a higher pure-stand yield and an increased yield with elements having a lower yield. In addition the elements 'C' and 'D' have a greater influence on their associates than their associates have on them, the reverse being true of elements 'A' and 'B'. The general picture is consistent over both densities. Since 'A' and 'B' are the higher yielding elements in pure-stand the graph indicates that increases due to competition are greater than are decreases and that the mixture yields will therefore be higher than those of the mid-pure-stands.

In HS 2 the elements seem to behave rather differently at the two densities. At the low density it appears that compensating action is occurring, the increase by one element in a mixture being balanced by a decrease in its associate. Elements 'B' and 'C' show the same type of behaviour as that demonstrated in HS 1 but elements 'A' and 'D' show a tendency to increase in yield when grown with heavier yielding elements and to decrease when grown with lower yielding elements. They themselves produce a reduction in yield of higher yielding and an increase in yield of lower yielding elements. At the medium density the different elements are not behaving in a sufficiently consistent fashion to produce a very clear pattern, the points tending to clump around Z.

In practice the method would be of greater value when dealing with rather larger diallel layouts than the one in the present example. Nevertheless the data provide a useful illustration of the method and the conclusions drawn are consistent with the actual behaviour of the elements.

SECTION 4.6 CONCLUSIONS

The present study has shown that different environmental influences can have vastly different effects on the competition behaviour of the components of physical mixtures of herbage grasses. Differences of density ranging from nine (4" spacing) to 144 (1" spacing) plants per square foot had little effect in the direction or magnitude of estimates of competitive effects if these effects were calculated on a proportional basis; that is as a percentage of the overall mean yield for any harvest at any density. In the second year of the experiment the same was true of the absolute competitive effects; that is those estimated using the original data not converted to a percentage basis.

In marked contrast to the slight effects of change in density were the large changes in competitive behaviour due to different cutting regimes. The delaying of the first cut until the plants were beginning stem elongation before flowering favoured the later growing constituents of the mixture in both years. Successively later harvests also showed a tendency to favour these same constituents.

The data for 1964 showed a tendency for mixture yields to exceed those to be expected on the basis of pure-stand yields, and although these differences were rarely significant they were sometimes quite large, as much as 14% in one instance.

The use of the W_r/V_r analysis on the yields of the mixtures and pure-stands suggests a situation which in most cases is akin to partial dominance, but the interpretation of these graphs is difficult since there is no widely acceptable theory regarding the behaviour of the constituents of a mixture as there is regarding the behaviour of the crosses of two parent lines.

The W_r/W_c analysis permits of a more detailed assessment of competitive behaviour because it considers the behaviour of each constituent of a mixture separately and considers it simultaneously as both an element and as an associate.

SECTION 4.7 SUMMARY OF SECTION 4

The performance of four herbage grasses, two cocksfoot cultivars and two ryegrass cultivars was compared in pure-stand in all possible 50:50 mixtures at three densities (1", 2" and 4" spacing) in the seeding year and at the two lower densities only in the year after sowing. Two different cutting regimes were used. Under one of these (HS 1) the plants were kept in a vegetative condition, in the other (HS 2) they were allowed to pass out of the purely vegetative phase before the first cut was taken.

In the seeding year density affected overall yield but if the yields of the different treatments were expressed as percentages of the mean yield for each density then the estimated competitive effects were unaffected by density. The cutting regimes had a marked effect on competitive ability, HS 1 tending to favour the two ryegrasses and HS 2 the cocksfoots.

In the year after sowing neither density nor cutting regime affected total yield per unit area but the cutting regimes had a similar effect on competitive behaviour to that which they had in the seeding year.

Mixture yields tended to exceed the yields of the mid-pure-stands but the differences were rarely significant.

The use of W_r/V_r and W_r/W_c graphs as aids to the interpretation of the data from "mechanical diallels" is discussed and illustrated using the data from the experiment.

SECTION 4.8 STATISTICAL APPENDIX

Section 4.8.1 Analysis of variance and estimation of competitive effects based on the model of Eberhart *et al*.

Consider the model:-

$$Y_{i_{(i')}m} = \overline{PS} + d_m + yk + s_i + ysk_i + yc_{i_{(i')}} + (sd)_{im} + E_{i_{(i')}m}$$

$$y = \begin{cases} 1 \text{ when } i \neq i' \\ 0 \text{ when } i = i' \end{cases}$$

Where:-

$Y_{i_{(i')}m}$ is the mean of observations on element i grown with element i' at density m, where i and i' = 1,...,p and m = 1,...,d

$\overline{PS}$ is the mean of all the pure-stands, s_i is the deviation of the pure-stand yield of element i from the pure-stand mean, k is the general competition effect which measures whether on a single entry (half plot) basis elements on average perform better or worse in mixture than in pure-stand, d_m is the average effect of density m, sk_i is the element by general competition effect measuring whether or not the ith element performs better or worse in mixture than average, $c_{i_{(i')}}$ is the specific competition effect on the ith element when grown in mixture with the i'th

The basic data are the yields in each replication at each density of each element grown with each of the others and with itself, these are the $Y_{i(i')}$qm required for the calculation of the total sum of squares in the usual way. Corresponding entries in the different replications are summed to produce the $Y_{i(i')}$.m The least squares estimates of the main and competition effects can then be calculated from the formulae in Table 4.8.1.

Table 4.8.2 gives some data for the present experiment, that for the total yield for the low and medium densities in 1964. The values for each replication (the $Y_{i(i')}$qm) are not given, the smallest units are summed over replications for each density (the $Y_{i(i')}$.m). The estimates of the competition effects for this set of data are given in Table 4.8.3. The sk_i and $c_{i(i')}$ effects are shown for element 'A' only.

A worked analysis of variance is given in Table 4.8.4.

Section 4.8.2 Durrant's W_r/W_c technique

For purposes of illustration it is convenient to consider a set of yields from a 2 x 2 mechanical diallel. There will be four different values, one for each of the pure-stands, and one for each component grown with the other, all being expressed on the same basis such as yield per plant or per square yard.

Let the variance of the pure-stand array be V_p. Let the elements, as defined earlier in this section, occupy the rows of the diallel table and the associates the columns. Then if all the elements behave in mixture as they do in pure-stand the row

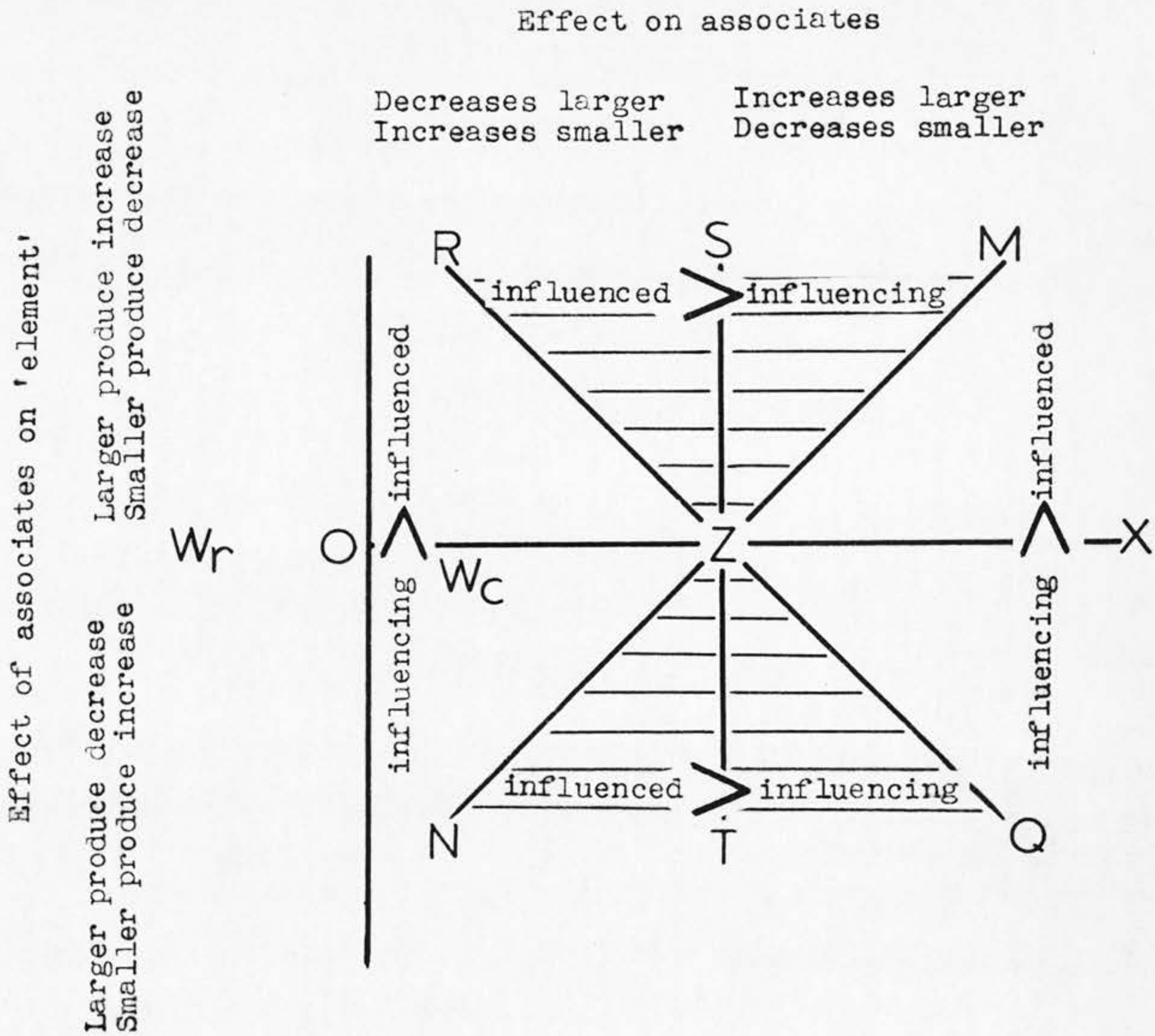

FIGURE 4.5.2 Durrant's W_r/W_c diagram. Explanation in text. Modified, with permission from Durrant (1965).

covariance $W_r = 0$, and column covariance $W_c = V_p$

If elements do not behave in mixture as in pure-stand then $W_r \neq 0$, and if the associates of any one element do not behave in mixture as in pure-stand $W_c \neq V_p$.

When only a 2 x 2 diallel is being considered there are five alterative types of behaviour possible.

1) Elements behave in mixture as they do in pure-stand. Then

$$W_r = 0 \qquad W_c = V_p$$

and on the graph the points for both elements fall at Z.

2) The two elements change in opposite directions, the higher yielding in pure-stand increasing its yield and the lower yielding decreasing when in mixture.
Then for both elements

W_r is negative. W_c is greater than V_p

and the points for both the elements fall into the SE quadrant of the graph. If the changes are compensatory so that increase in the higher yielding is the same as the decrease in the lower, then both elements lie at the same point on the line ZQ because $-W_r = (W_c - V_p)$. If one element is more affected than the other then its W_r will increase in magnitude and its $-W_r$ will be greater than $(W_c - V_p)$. Conversely the other element will have an increased value for its W_c. The point for the "more sensitive" element will be displaced below ZQ and that for the "less sensitive" to the right of ZQ.

In the case where one element is unchanged its $W_r = 0$, and W_c for the other element equals V_p.

3) As 2) but the higher yielding element in pure-stand decreases in mixture and the lower yielding increases.

Then for both elements

W_r is positive. W_c is less than V_p.

and the points for both elements lie in the <u>NW</u> quadrant.

If the changes are compensatory then again $-W_r = (W_c - V_p)$. If one element is more sensitive than the other then its W_r will again increase in magnitude (although this time in a positive direction), and its point will be displaced above the line RZ and the W_c for the less sensitive element will decrease moving its point below OZ.

4) Both elements increase in yield.

Then for the higher yielding in pure-stand

W_{r_1} is negative. W_{c_1} is less than V_p.

and the point for this element falls into the SW quadrant.

and for the lower yielding in pure-stand

W_{r_2} is positive. W_{c_2} is greater than V_p.

and the point for this element falls into the NE quadrant.

If the increases are of the same size then

$$-W_{r_1} = W_{r_2} = -(W_{c_1} - V_p) = (W_{c_2} - V_p)$$

and both points fall on the NZM on opposite sides of Z and equidistant from Z.

If either element is increased more than the other, then its

W_r increases in magnitude, displacing its point either above MZ or below ZN, while the less sensitive element has a reduced W_c, displacing its point to the left of ZN or to the right of MZ.

5) Both elements decrease in yield.

The situation is the same as in 4) except that the signs and magnitudes of the higher and lower yielding (pure-stand) elements are exactly reversed, so that the higher yielding now falls into the NE quadrant and the lower yielding into the SW.

For convenience of reference Figure 4.5.2 is reproduced in this section.

TABLE 4.3.1. Dates of Harvest

	Harvest No.	1	2	3	4	5
1963	HS 1	27 June	31 July	11 Sep.		
	HS 2	18 July	14 Aug.	2 Oct.		
1964	HS 1	2 May	18 June	21 July	25 Aug.	28 Sep.
	HS 2	20 May	3 July	28 July	28 Aug.	4 Oct.

TABLE 4.4.1. 1963 data. Summarized analyses of variances for each density and harvest series separately

HS 1						HS 2					
Density	Harvest	1	2	3	T	Density	Harvest	1	2	3	T
Low	K	NS	NS	NS	NS	Low	K	NS	NS	NS	NS
	S	**	NS	**	**		S	**	**	**	**
	SK	NS	NS	*	NS		SK	**	*	NS	*
	C	NS	NS	NS	NS		C	NS	NS	*	NS
Med	K	NS	NS	NS	NS	Med	K	NS	NS	NS	NS
	S	*	**	**	**		S	**	**	**	**
	SK	NS	NS	NS	NS		SK	NS	NS	NS	NS
	C	NS	NS	**	**		C	NS	NS	NS	NS
High	K	NS	NS	NS	NS	High	K	NS	NS	NS	NS
	S	**	**	**	**		S	**	**	**	**
	SK	NS	NS	**	*		SK	*	NS	NS	*
	C	NS	*	**	**		C	NS	NS	NS	*

K = general competition effects
S = element effects
SK = S X K
C = specific competition effects

TABLE 4.4.2. **Summarised analyses of variance for competition effects in 1963 based on original data converted to percentage of each harvest and density mean.**

Harvest	1	2	3	T	1	2	3	T
SK	NS	**	**	**	**	**	NS	**
C	NS	**	**	**	NS	**	**	**
D X S	NS	*	NS	**	NS	*	NS	NS
D X SK	NS	NS	NS	**	NS	NS	NS	NS
D X C	NS	NS	NS	NS	NS	NS	NS	NS

SK = general X element effects

C = specific competition effects

S = element effects

D = density

TABLE 4.4.3. **1963.** Estimates of $\hat{sk}_i$ expressed as percentage of mean yield for each density and harvest series. Averaged over all densities.

	HS 1					HS 2			
	HARVEST						HARVEST		
	1	2	3	T	HS2 - HS1	T	1	2	3
A	+16.11^{a}	+16.89^{a}	+19.00^{a}	+16.72^{a}	-15.21*	+ 1.51^{a}	- 4.00^{a}	+ 3.13^{ab}	+ 9.11^{a}
B	-20.56^{a}	+17.33^{a}	+12.83^{ab}	+ 9.39^{a}	-17.44**	- 8.05^{ab}	-17.00^{a}	- 4.54^{ac}	- 4.28^{ab}
C	- 2.33^{a}	- 7.67^{b}	- 4.06^{b}	- 4.50	+24.55**	+20.05	+29.44	+15.21^{b}	+11.83^{a}
D	+ 6.78^{a}	-26.56^{b}	-27.78	-21.61	+ 8.10	-13.51^{b}	- 8.44^{a}	-13.79^{c}	-16.67^{b}

T = estimates based on total yield = sum of three cuts.

HS2 - HS1 = difference between "T columns" for the two harvest series.

Within each column estimates having the same superscript do not differ significantly.

TABLE 4.4.4. 1963. Estimates of competitive effects for total yield. Based on original data converted to percentage of density and harvest series means. Averaged over all densities.

	Assoc. / Elem.	$\hat{c}_{i(i')}$ A	$\hat{c}_{i(i')}$ B	$\hat{c}_{i(i')}$ C	$\hat{c}_{i(i')}$ D	$\hat{sk}_i$
HS 1	A	-	- 7.06	- 5.89	+ 12.94**	+ 16.72[a]
	B	- 22.06**	-	+ 5.94	+ 16.11**	+ 9.39[a]
	C	- 10.17	- 4.83	-	+ 15.00**	- 4.50
	D	- 8.06*	+ 7.28	+ 0.78	-	- 21.61
HS 2	A	-	- 7.94*	- 2.61	+ 10.56**	+ 1.51[a]
	B	- 4.39	-	- 13.89**	+ 18.28**	- 8.05[ab]
	C	- 11.50**	+ 3.00	-	+ 8.50*	+ 20.05
	D	+ 6.89	+ 0.06	- 6.94*	-	- 13.51[b]

* Estimate significant at 5%
** Estimate significant at 1%

TABLE 4.4.5 Summary of analyses of variance for five harvests separately and for the sum of five harvests for each harvest series in 1964

	HS 1						HS 2					
	HARVEST						HARVEST					
Source of variation	1	2	3	4	5	T	1	2	3	4	5	T
D	*	NS	NS	NS	NS	*	NS	**	*	NS	NS	NS
K	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S (unadj. S)	**	**	**	**	**	**	**	**	**	**	**	**
SK (adj. S)	**	**	NS	*	*	**	NS	NS	**	**	**	**
C	**	**	NS	**	*	**	*	*	**	**	**	**
DS	*	NS	NS	NS	NS	NS	**	NS	NS	NS	*	**
DSK	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
DC	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

TABLE 4.4.6(a). **1964 data. Estimates of $\widehat{sk}_i$ for each harvest separately in HS 1 and HS 2. Averaged over densities. Gms. per half-box**

		HARVEST					
		1	2	3	4	5	T
HS 1	A	$+5.56^{a}$	$+9.39^{a}$	-0.09	-3.28^{a}	-3.57^{a}	$+8.01^{a}$
	B	$+2.41^{ab}$	$+10.15^{a}$	$+0.55$	$+1.81^{ab}$	$+0.38^{ab}$	$+15.35^{b}$
	C	-2.16^{bc}	-5.69^{b}	$+0.79$	$+3.05^{b}$	$+3.23^{b}$	-0.78^{c}
	D	-5.80^{c}	-13.85^{c}	-1.25	-1.58^{ab}	-0.03^{ab}	-22.58^{d}
HS 2	A	$+3.69$	-0.11	-2.99^{a}	-5.75^{a}	-6.07^{a}	-11.23^{a}
	B	-1.19	-2.72	-0.63^{b}	-1.85^{b}	-2.27^{b}	-8.66^{a}
	C	$+4.41$	$+4.80$	$+3.79^{c}$	$+6.58^{c}$	$+6.14^{c}$	$+25.72^{b}$
	D	-6.91	-1.97	-0.17^{b}	$+1.02^{d}$	$+2.20^{d}$	-5.83^{a}

Estimates having the same superscript (within one harvest) do not differ significantly.

TABLE 4.4.6. (b). As Table 4.4.6.(a) but $\hat{sk}_i$'s expressed as percentage of mean half-box yield at each harvest.

		HARVEST					
		1	2	3	4	5	T
HS 1	A	+ 31.30	+ 19.04	- 0.78	- 20.83	- 30.31	+ 7.55
	B	+ 13.57	+ 20.58	+ 4.79	+ 11.49	+ 3.23	- 14.48
	C	- 12.16	- 11.54	+ 6.87	+ 19.37	+ 27.42	- 0.74
	D	- 32.65	- 28.09	- 10.88	- 10.03	- 0.25	- 21.29
HS 2	A	+ 7.83	- 0.41	- 27.87	- 41.40	- 50.81	- 10.19
	B	- 2.53	- 10.23	- 5.87	- 13.32	- 19.00	- 7.85
	C	+ 9.36	+ 18.05	+ 35.32	+ 47.38	+ 51.39	+ 23.33
	D	- 5.29	- 7.41	- 1.58	+ 7.34	+ 18.41	- 5.29

TABLE 4.4.7. Estimates of pure stand yields and competition effects for total yield in 1964. Averaged over densities for each harvest series separately. (Gms. per half-box)

	i \ i'	A	B	C	D	$\widehat{sk}_i$	$\widehat{u_o + s_i}$
		$\widehat{c}_{i(i')}$					
HS 1	A	-	- 10.2*	- 8.3	+ 18.5**	+ 8.0[cd]	109.1
	B	-19.8**	-	+ 6.2	+ 13.5*	+ 15.4[ad]	120.9
	C	- 4.7	- 12.6**	-	+ 17.3**	- 0.8[c]	89.5
	D	+ 3.5	- 0.3	- 3.1	-	- 22.6[b]	92.0
HS 2	A	-	- 0.3	- 1.8	+ 2.1	- 11.2[a]	122.0
	B	+ 7.5	-	- 19.6**	+ 12.1*	- 8.7[a]	110.6
	C	- 5.9	+ 2.7	-	+ 3.2	+ 25.7[b]	103.7
	D	+ 19.3**	- 1.5	- 17.9**	-	- 5.9[a]	92.6

$\widehat{sk}_i$ estimates having a superscript in common do not differ significantly.

* and ** indicate that the estimates of $\widehat{c}_{i(i')}$ are significant at the 5% and 1% levels respectively.

TABLE 4.4.8. 1964 total yields. Difference between yields of each e lement in mixture with each other element and yield of element in pure stand (e.g. Ab - Aa) gms. per half-box. Pure stand yields are shown in NW-SE diagonal. Within each cell of the Table the upper left figure refers to the values for HS 1 and the lower right to HS 2. In each case averaged over densities

Elem. \ Assoc.	A	B	C	D
A	<u>109.1</u> <u>122.0</u>	+ 1.7 - 7.5	+ 3.6 - 9.0	+30.4** - 5.1
B	- 0.6 + 2.9	<u>120.9</u> <u>110.6</u>	+25.5** -24.3**	+32.7** + 7.5
C	- 1.6 +23.8**	- 9.6 +32.4**	<u>89.5</u> <u>103.7</u>	+20.4** +33.0**
D	-15.3* +17.5*	-19.1** - 3.4	-22.0** -19.8*	<u>92.0</u> <u>92.6</u>

* and ** indicate significance at 5% and 1% levels respectively.

TABLE 4.4.9. 1964 total yields. Differences between mixture and pure stand differences between HS 1 and HS 2. A positive (negative) value indicates that the ith element in mixture with the i'th does relatively better (worse) in HS 2 than in HS 1.

Elem. \ Assoc.	A	B	C	D
A	+ 12.9	- 9.2	- 12.6	- 35.5**
B	+ 3.5	- 10.3	- 49.8**	- 25.2*
C	+ 25.4*	+ 42.0**	+ 14.2	+ 12.6
D	+ 32.8**	+ 15.7	+ 2.2	+ 0.6

* and ** indicate significance at 5% and 1% levels respectively.

TABLE 4.4.10. 1964 data. Excess or deficit of mixture yield compared to mid-pure stand gms. per half-box. e.g. $\frac{1}{2}AB - \frac{1}{4}(AA + BB)$

	Mix-ture	Peak Harvest = 2nd		Sum of 5 cuts			
		Low Density	Medium Density	Low Density	%	Medium Density	%
HS 1	AB	- 3.9	+ 11.0	+ 0.9	+ 0.4	+ 1.5	+ 0.6
	AC	+ 6.4	+ 6.3	+ 5.5	+ 2.9	- 1.4	- 0.7
	AD	+ 3.7	+ 20.6	+ 4.5	+ 2.3	+ 25.9	+ 12.6
	BC	+ 10.3	+ 19.5	+ 14.6	+ 7.2	+ 17.4	+ 8.0
	BD	+ 9.6	+ 14.1	+ 13.9	+ 6.7	+ 13.4	+ 6.2
	CD	- 2.8	- 2.4	+ 1.0	+ 0.6	- 4.0	- 2.2

	Mix-ture	Peak Harvest = 1st		Sum of 5 cuts			
		Low Density	Medium Density	Low Density	%	Medium Density	%
HS 2	AB	- 4.0	- 6.4	- 2.6	- 1.2	- 6.7	- 2.8
	AC	- 4.2	+ 21.9*	+ 0.5	+ 0.2	+ 29.2*	+ 12.9
	AD	- 5.2	+ 16.9*	+ 0.1	± 0.0	+ 24.9	+ 11.8
	BC	+ 18.5	+ 1.3	+ 26.8*	+ 12.5	- 10.4	- 4.8
	BD	- 7.1	+ 11.7	- 1.5	- 0.7	+ 9.9	+ 4.9
	CD	+ 1.0	+ 11.1	- 0.3	- 0.1	+ 26.8*	+ 14.6

* indicates significant values at 5% level

NOTE. In this Table and in Table 4.8.2. the symbol E has been used to indicate summation in place of the usual $\sum$

8.1

TABLE 4.[redacted]. Formulae for least squares estimation of main and competition effects

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$$\overline{PS} = 1 / rdp \mathop{E}_{i} \mathop{E}_{i'=i} Y_{i(i')} \cdot\cdot$$

$$k = 1 / rd(p-1) \mathop{E}_{i} \mathop{E}_{i' \neq i} Y_{i(i').} - 1 / rdp \, Y_{\cdot(.)} \cdot\cdot$$

$$d_m = 1 / rp^2 \, Y_{\cdot(.)} \cdot m - 1 / rdp^2 \, Y_{\cdot(.)} \cdot\cdot$$

$$s_i = 1 / rd \mathop{E}_{i'=i} Y_{i(i')} \cdot\cdot - \overline{PS}$$

$$ds_i = \mathop{E}_{i'=i} Y_{i(i')} \cdot m - 1 / rd \mathop{E}_{i'=i} Y_{i(i')} \cdot\cdot - 1 / rp \mathop{E}_{i} \mathop{E}_{i'=i} Y_{i(i')} \cdot m + \overline{PS}$$

$$sk_i = 1/ rdp\,(p-1) \left(\left(p\left(\mathop{E}_{i' \neq i} Y_{i(i').} - \mathop{E}_{i} \mathop{E}_{i' \neq i} Y_{i(i').} \right) - (p-1)\,(pY_{i(.)} \cdot\cdot - Y_{\cdot(.)} \cdot\cdot) \right) \right)$$

$$c_{i(i')} = 1 / rd(p-1) \left(\left((p-1) Y_{i(i')\cdot\cdot} - \mathop{E}_{i' \neq i} Y_{i(i')\cdot\cdot} \right) \right)$$

Where

$$Y_{i(i')\cdot\cdot} = \mathop{E}_{m} Y_{i(i')} \cdot m \qquad Y_{i(i')} \cdot\cdot = \mathop{E}_{i'} \mathop{E}_{m} Y_{i(i')} \cdot m$$

$$Y_{\cdot(.)} \cdot\cdot = \mathop{E}_{i} \mathop{E}_{i'} \mathop{E}_{m} Y_{i(i')} \cdot m$$

TABLE 4.8.2. Original data for total yield (sum five cuts) in HS 1 1964. (Note: the data presented have already been summed over both replications.) Gms. per half-box

	Assoc. / Elem.	A'	B'	C'	D'	$\sum_{i' \neq i} Y_{i(i')}.$	$\sum Y_{i(i')}.$
Low Density	A	211.6	210.0	217.2	266.7	693.9	905.5
	B	238.4	235.0	277.4	299.9	815.7	1050.7
	C	178.4	159.7	173.1	223.5	561.6	734.7
	D	136.6	145.7	134.4	182.9	416.7	599.6
						2487.9	3290.5

$$(\text{PS sum}) = \sum_{i i' = i} Y_{i(i')}. = 806.2$$

	Elem.	A'	B'	C'	D'	$\sum_{i' \neq i} Y_{i(i')}.$	$\sum Y_{i(i')}.$
Medium Density	A	224.9	233.2	233.6	291.0	757.8	982.7
	B	243.2	248.7	308.0	314.5	865.7	1114.4
	C	172.9	160.0	184.7	215.6	548.5	733.2
	D	170.5	146.0	146.0	185.1	462.5	647.6
						2634.5	3477.9

= 843.4

	Elem.	A'	B'	C'	D'	$\sum_{i' \neq i} Y_{i(i')}.$	$\sum Y_{i(i')}.$
Total (both densities)	A	436.5	443.2	450.8	557.7	1451.7	1888.2
	B	481.6	483.7	585.4	614.4	1681.4	2165.1
	C	351.3	319.7	357.8	439.1	1110.1	1467.9
	D	307.1	291.7	280.4	368.0	879.2	1247.2
						5122.4	6768.4

= 1646.0

Replication totals I 3246.7
II 3521.7

TABLE 4.8.3. Least squares estimates of competition effects based on data in Table 4.8.2.

$$k = 5122.4/12 - 6768.4/16 = +3.9$$

$$sk_a = ((\,(16 \times 1451.7) - (4 \times 5122.4) - (12 \times 1888.2) + (3 \times 6768.4)\,))/48 = +8.0$$

$$c_{ab} = ((\,(3 \times 443.2) - 1451.7))/12 = -10.2$$

$$c_{ac} = ((\,(3 \times 450.8) - 1451.7))/12 = -8.3$$

$$c_{ad} = ((\,(3 \times 557.7) - 1451.7))/12 = +18.5$$

TABLE 4.8.4. Worked analysis of variance using data in Table 4.8.2.

$$CF = 6768^2/64 = 715800.60$$

Source of Variation	df	Sum of squares	
Total	63	SS for original entries - CF	= 47541.00
Reps.	1	$(3246.7 - 3521)^2/64$	= 1181.64
Densities (D)	1	$(3290.5 - 3477.9^2/64$	= 548.73
General Competition (K)	1	$(1646.0^2/16 + 5122.4^2)/48 - CF$	= 177.10
Elements (S)	3	$(1888.2^2 + ,\dots, + 1247.2^2)/16 - CF$	= 31899.12
Elem x Gen Comp (SK)	3	$(436.5^2 + 483.7^2 + 357.8^2 + 368.0^2)/4 + (1451.7^2 + ,\dots, + 879.2^2)/12 - CF-K-S$	= 2430.01
Specific Comp (C)	8	$(443.2^2 + ,\dots, +280.4^2)/4 - (1451.7^2 + ,\dots, + 879.2^2)/12$	= 6490.70
D x K	1	$(802.6^2 + 843.4^2)/8 + (2487.9^2 + 2634.5^2)/24 - CF - D - K$	= 3.05
D x S	3	$(905.5^2 + ,\dots, + 647.6^2)/8 - CF - D - S$	= 221.51
D x SK	3	$(211.6^2 +,\dots,+185.1^2)/2 + (693.9^2 +,\dots,+462.5^2)/6 -$ CF-D-K-S-SK-DK-DS	= 90.40
D x C	8	$(210.0^2 + ,\dots, + 146.0^2)/2 - (1451.7^2 + ,\dots, + 879.2^2)/12 - C$	= 986.71
Error (by difference)	31		= 3512.03

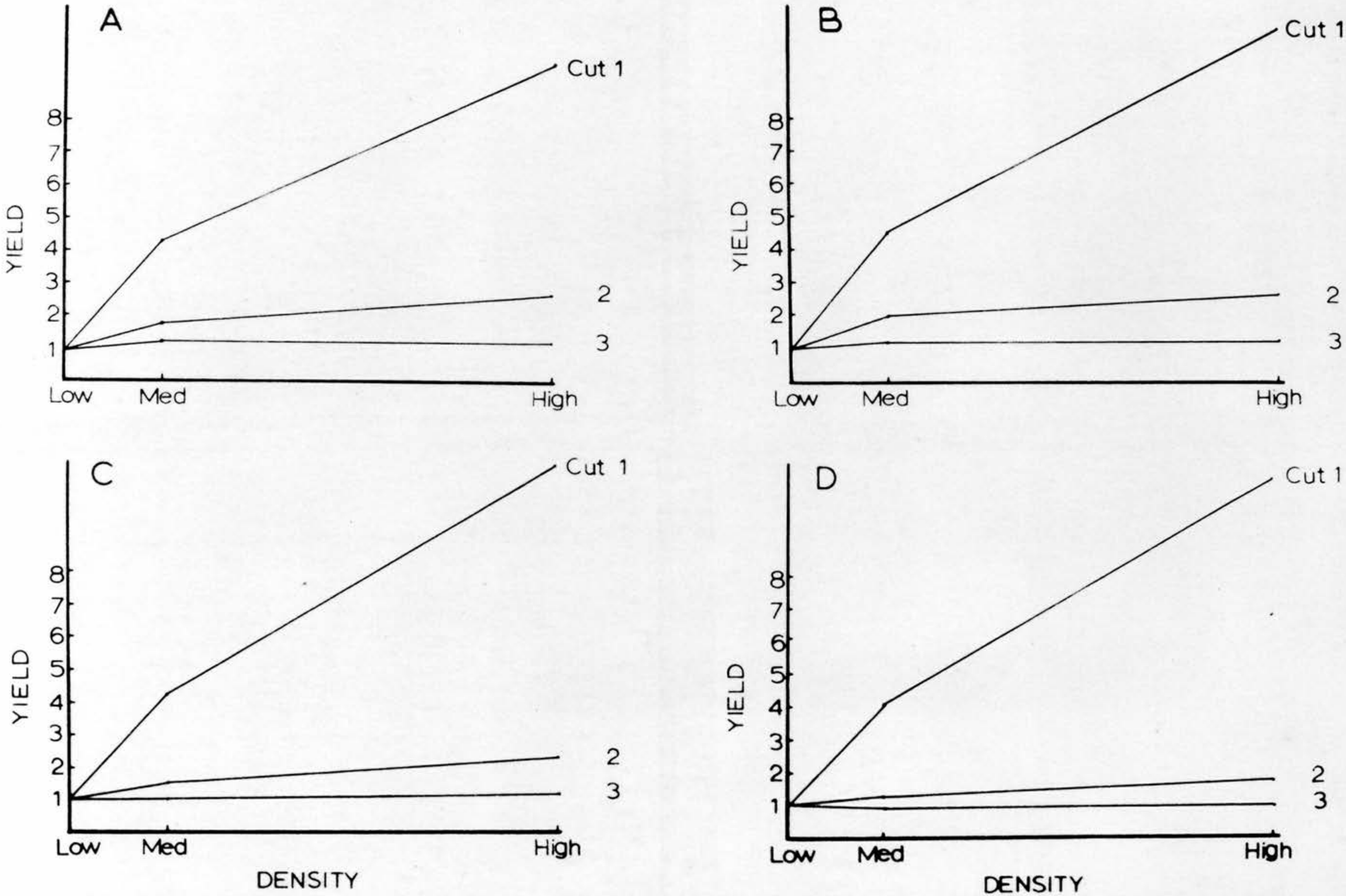

FIGURE 4.4.1 Effect of density on mean yield per unit area of pure-stands. H.S.1

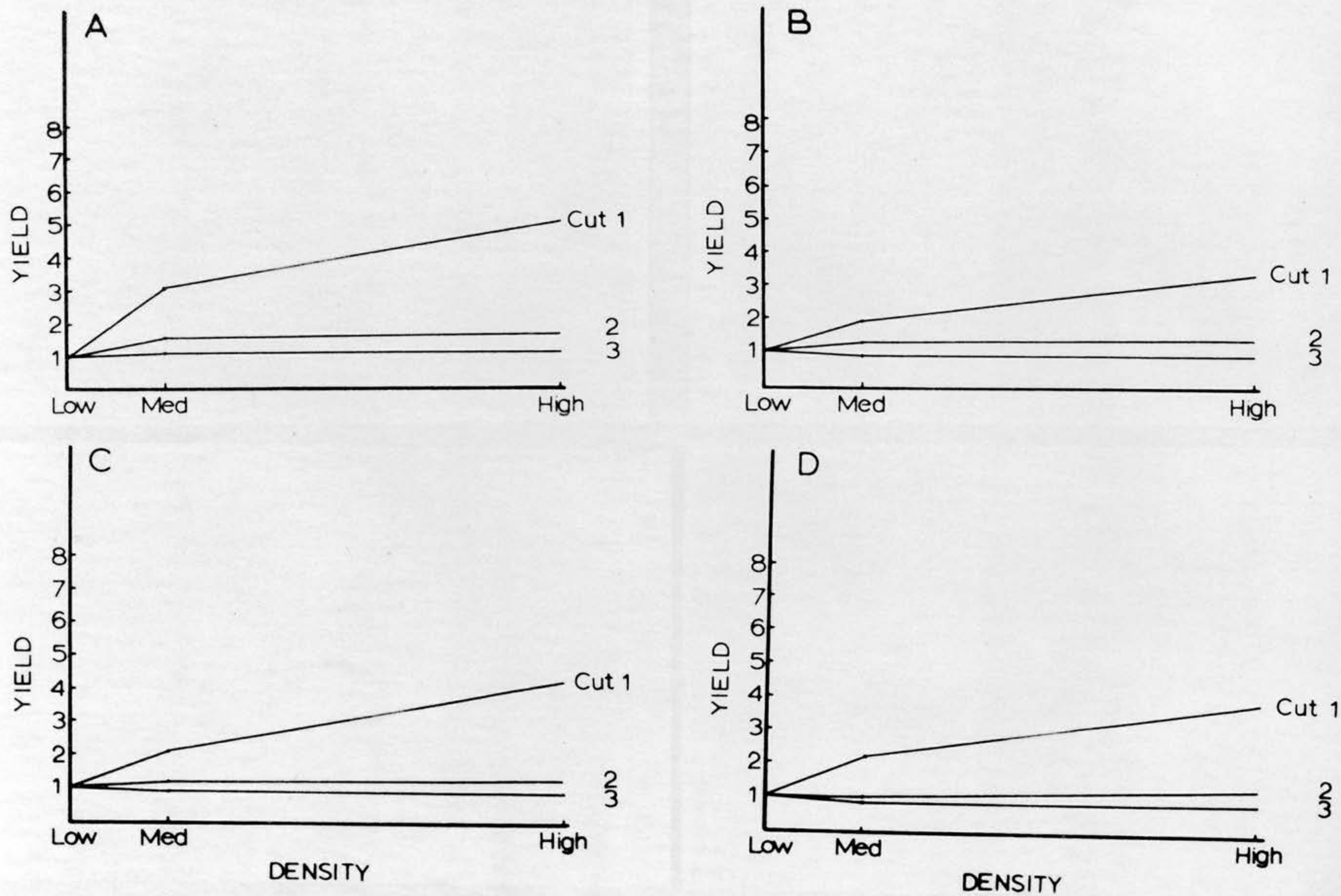

FIGURE 4.4.2 Effect of density on mean yield per unit area of pure-stands. H.S.2

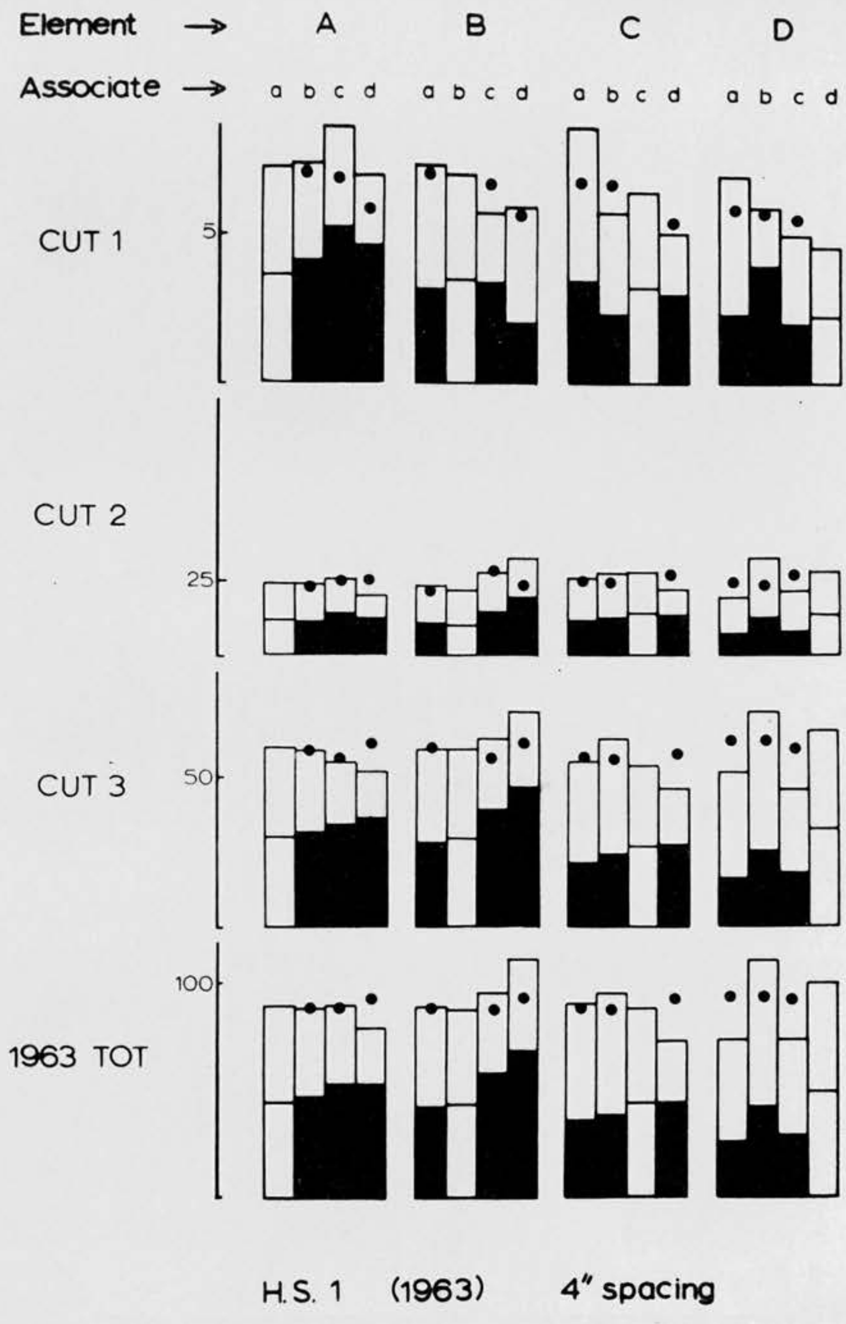

FIGURE 4.4.3a Pure-stand and mixture yields for HS 1 Low density, 1963. Each whole bar represents the whole-box (plot) yield of one mixture. The pure-stand bars are unshaded and divided into halves. The black portion of each of the remaining bars shows the yield of the element in the mixture and the white portion the yield of the associate. The black dots show the whole-box mid-pure-stand yields for each combination.

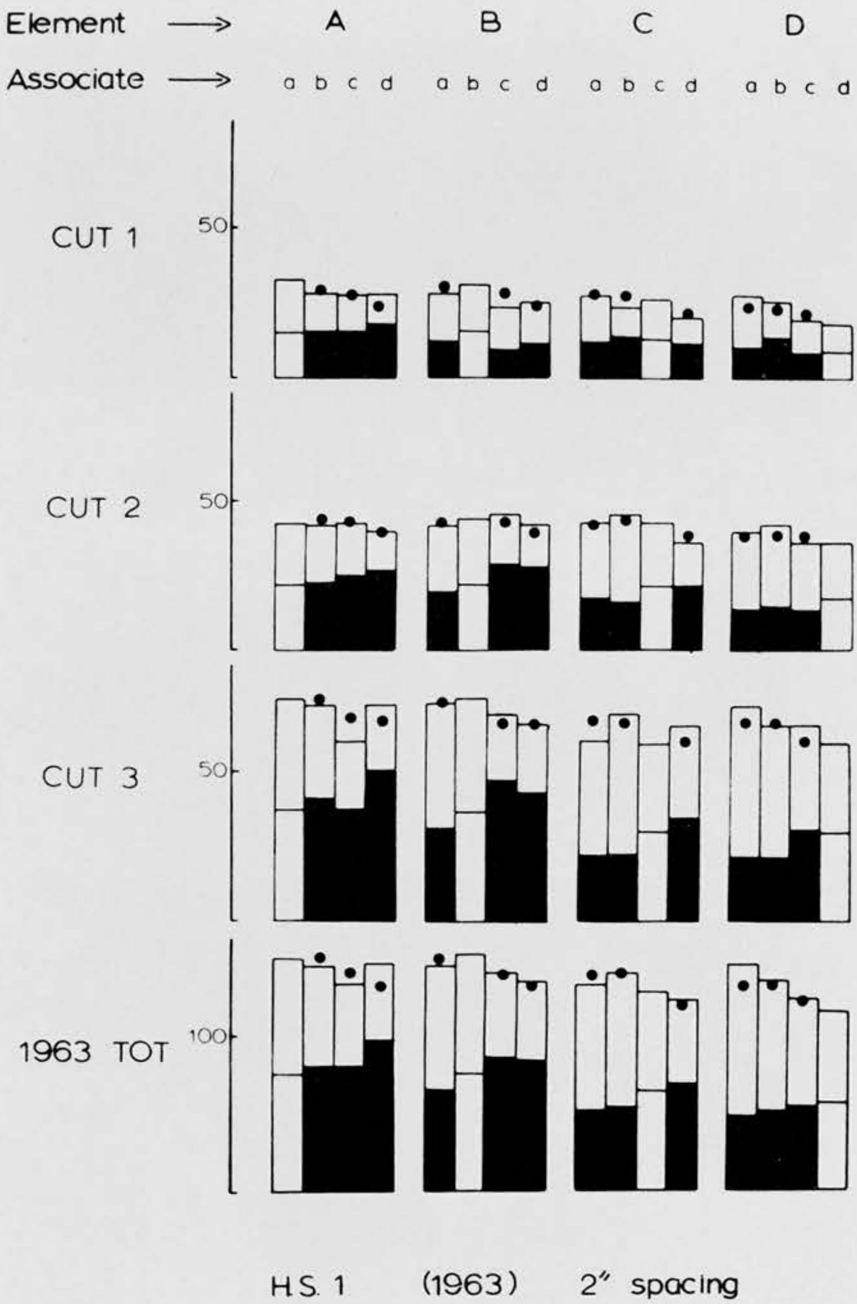

FIGURE 4.4.3b Pure-stand and mixture yields for HS 1 Medium density. 1963. Explanation, see Figure 4.4.3a.

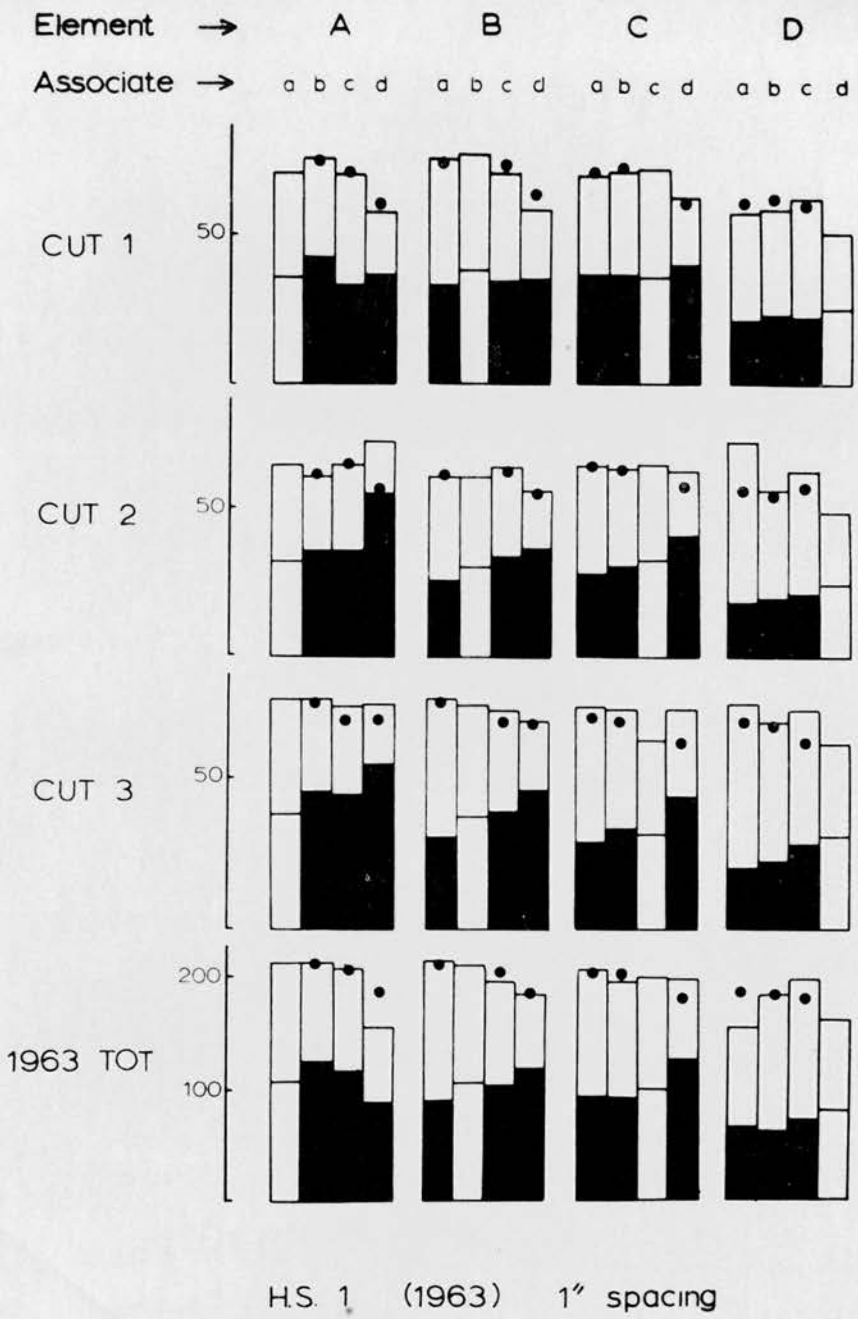

FIGURE 4.4.3c Pure-stand and mixture yields for HS 1 High density. 1963. Explanation, see Figure 4.4.3a.

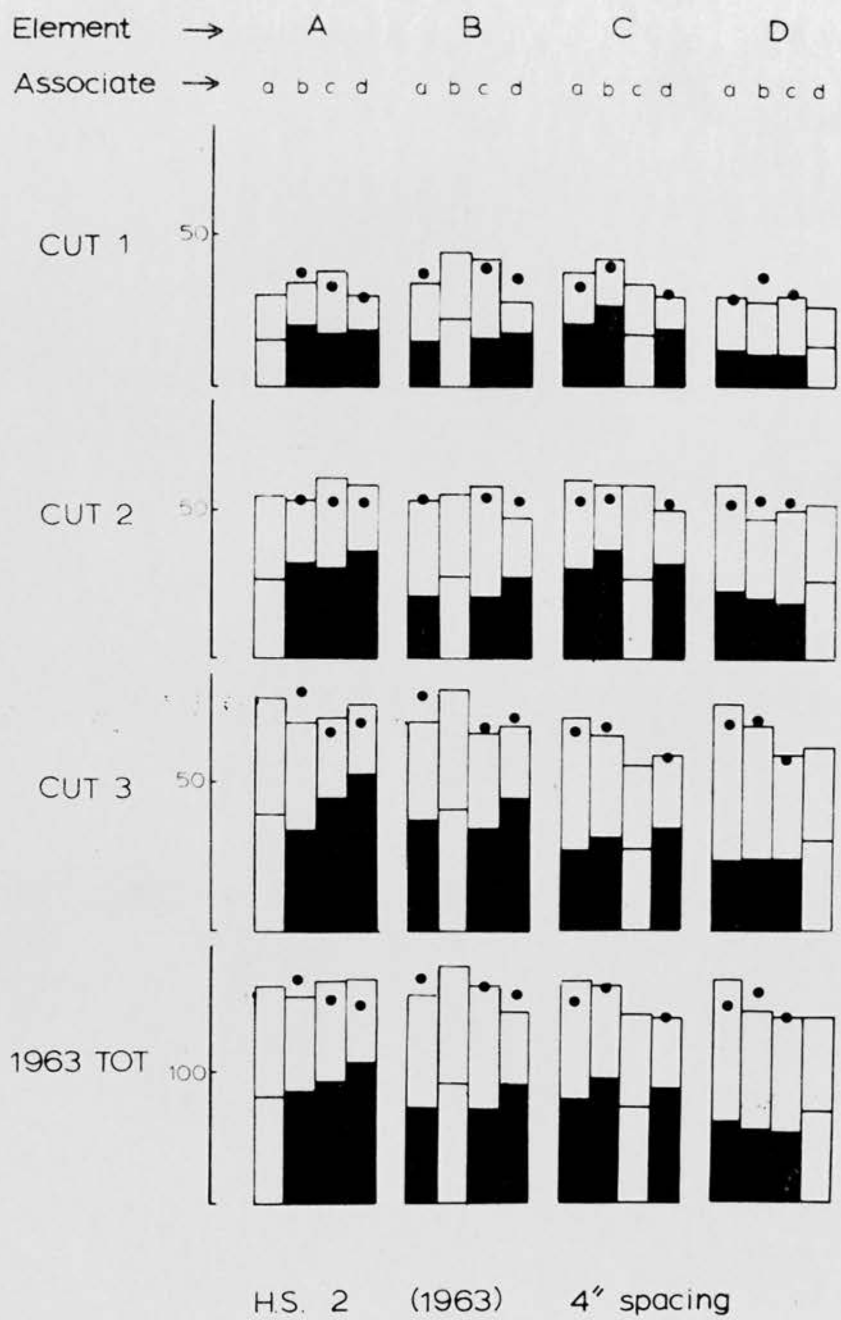

FIGURE 4.4.4a Pure-stand and mixture yields for HS 2 Low density. 1963. Explanation, see Figure 4.4.3a.

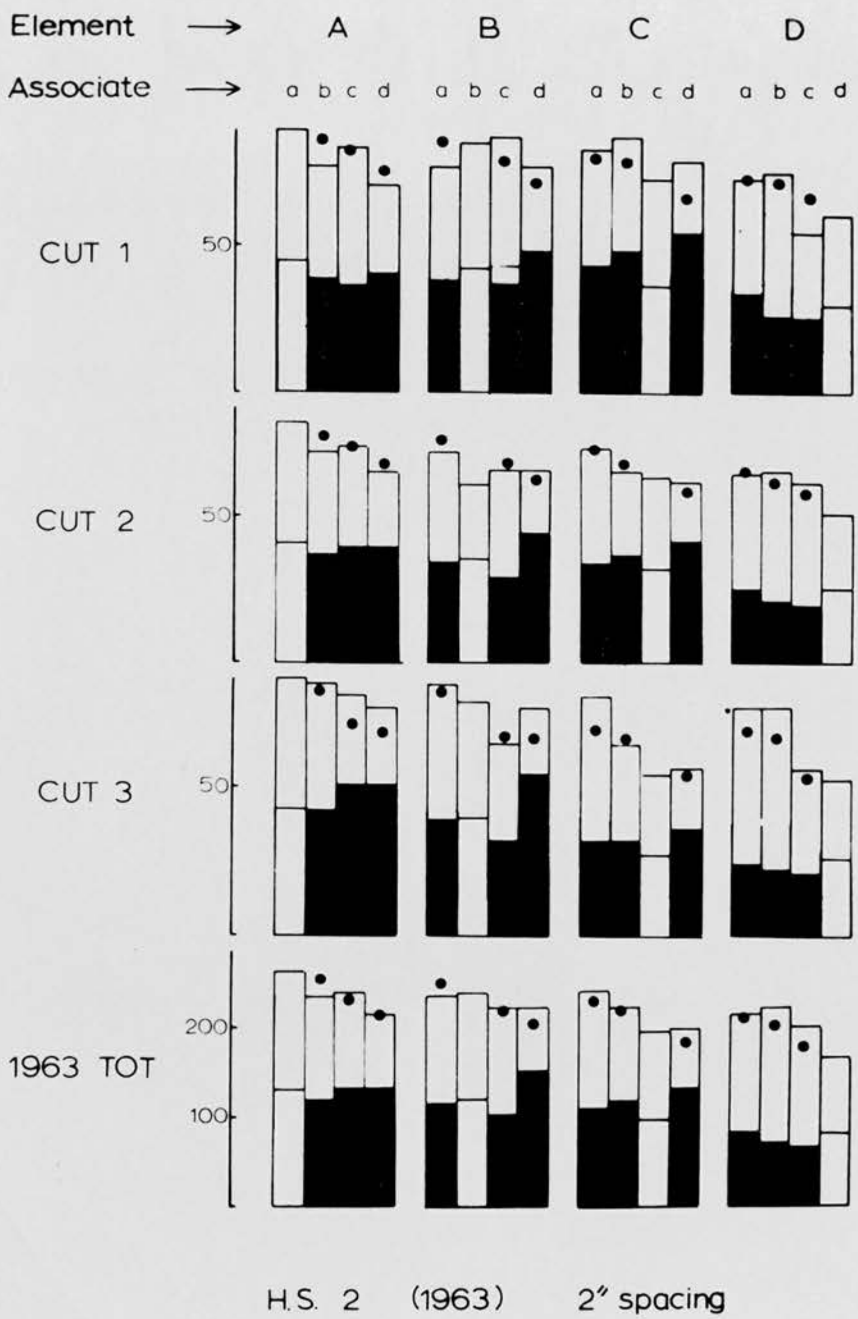

FIGURE 4.4.4b Pure-stand and mixture yields for HS 2 Medium density. 1963. Explanation, see Figure 4.4.3a.

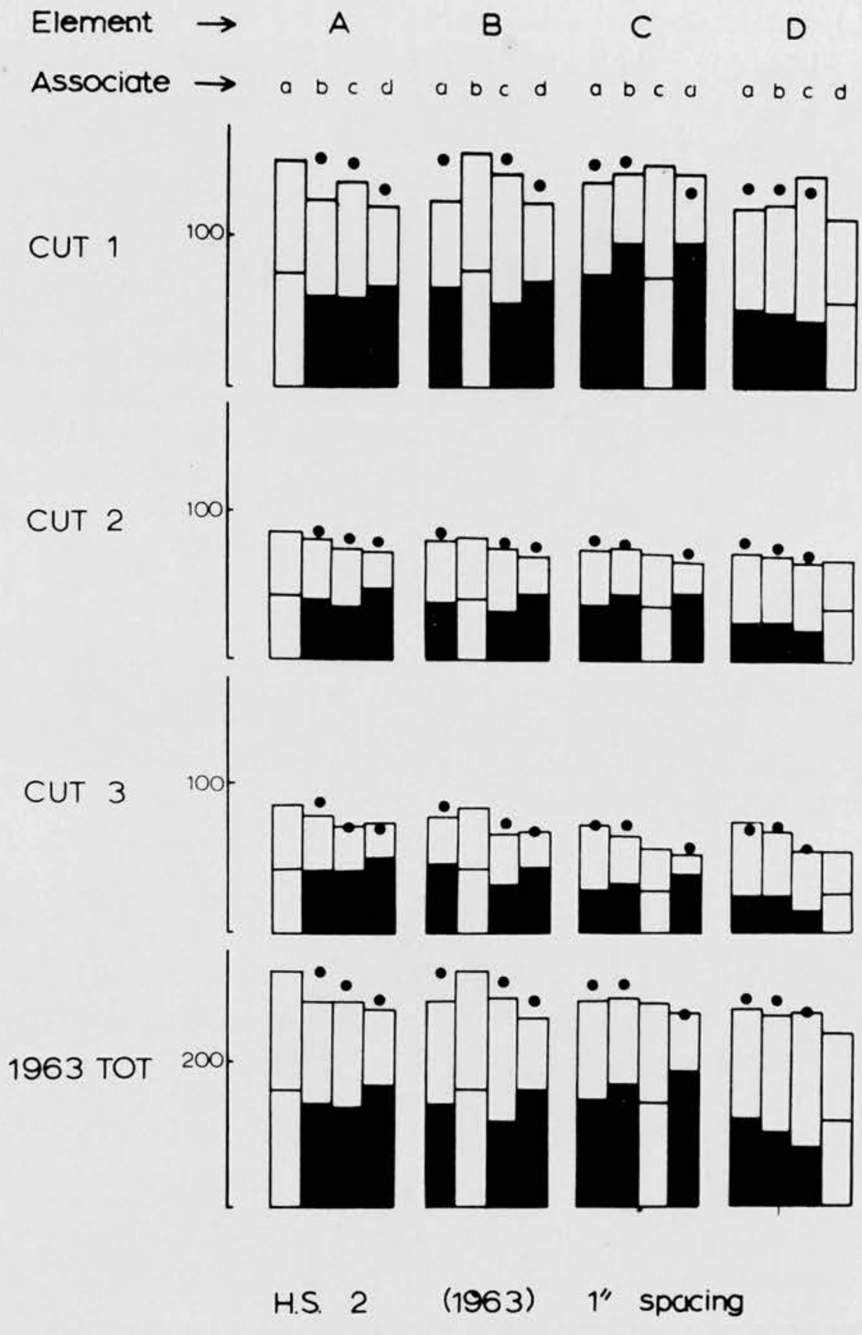

FIGURE 4.4.4c Pure-stand and mixture yields for HS 2 High density. 1963. Explanation, see Figure 4.4.3a.

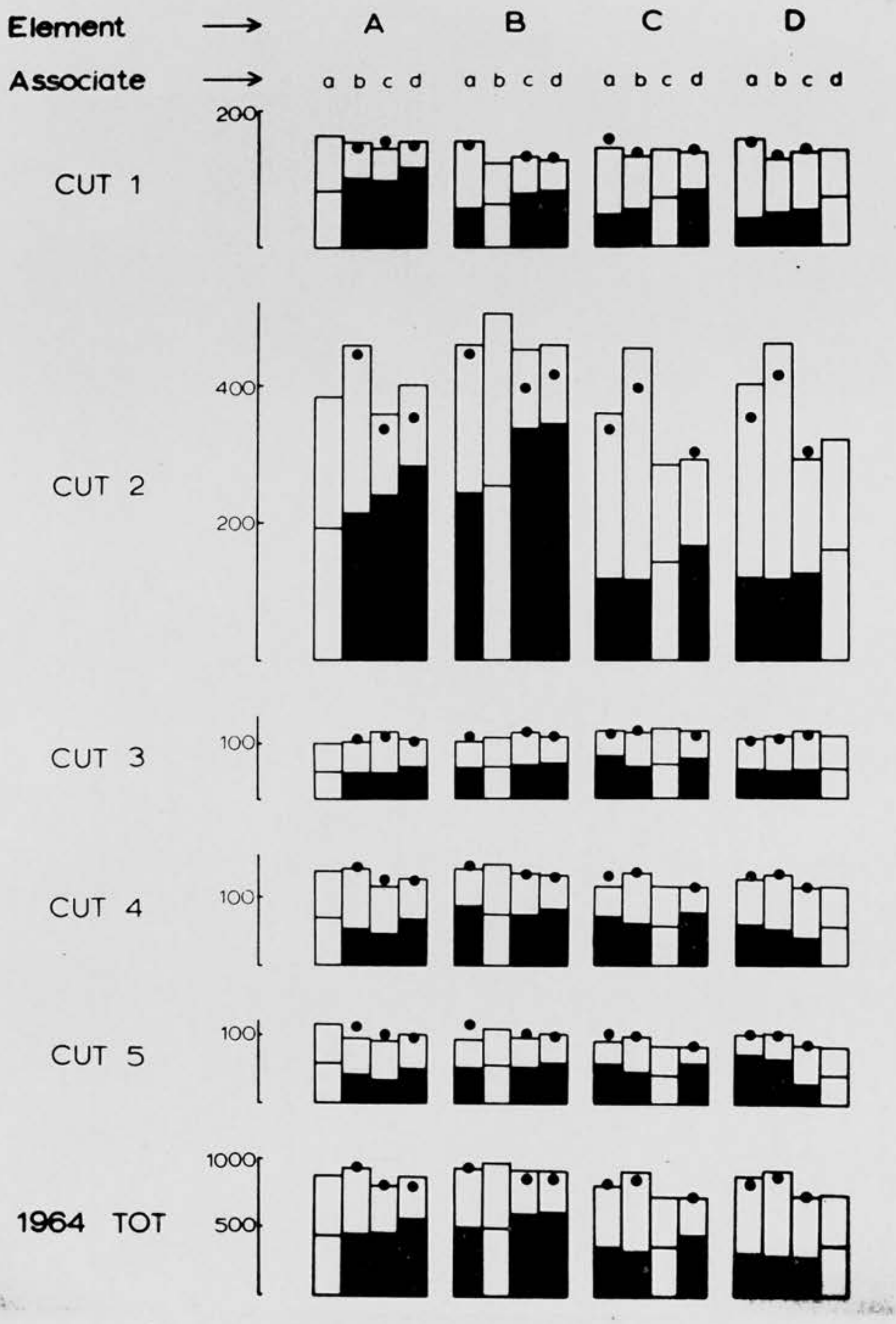

FIGURE 4.4.5 Pure-stand and mixture yields for HS 1 1964. Averaged over Low and Medium densities. Explanation, see Figure 4.4.3a.

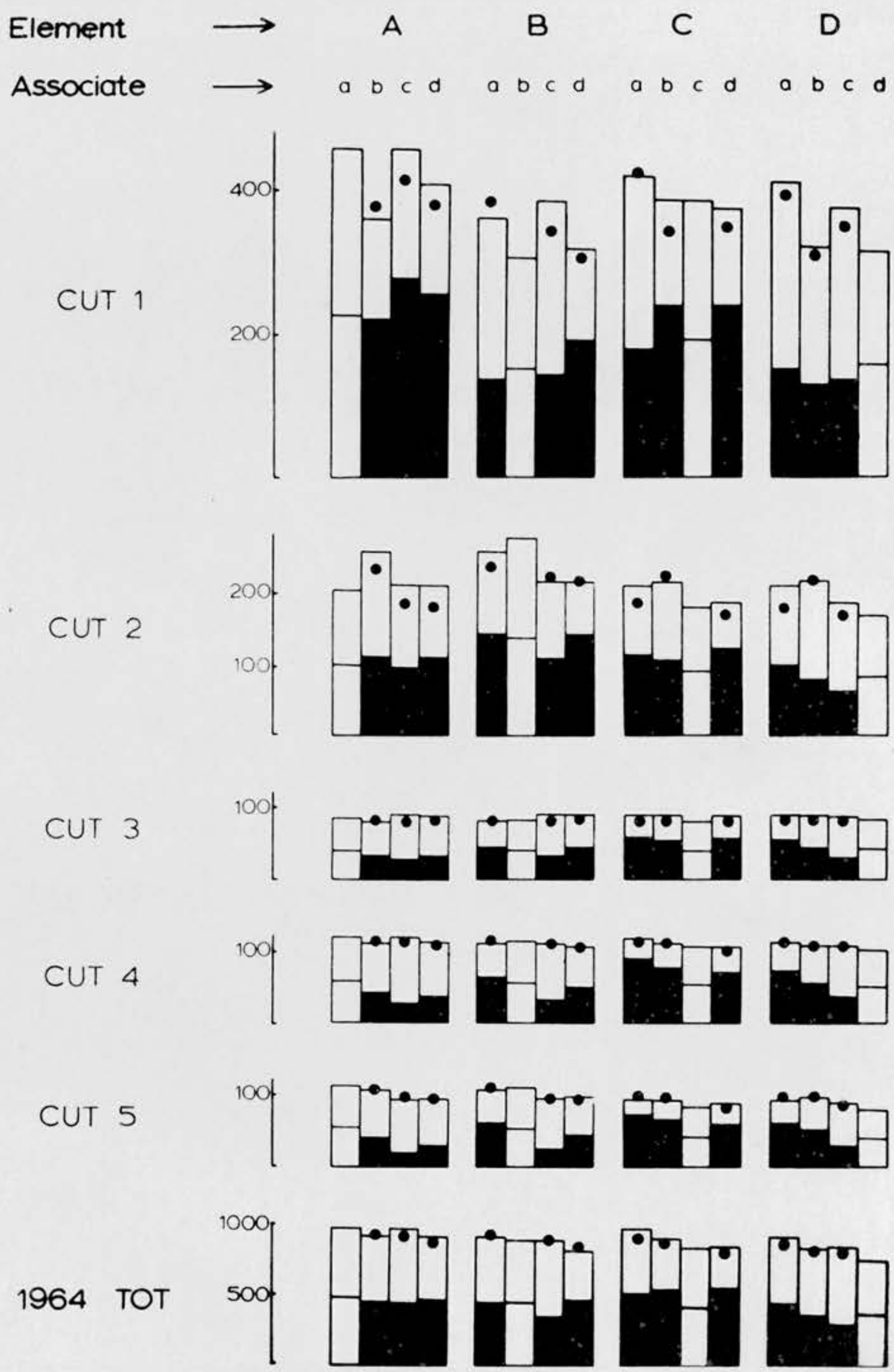

FIGURE 4.4.6 Pure-stand and mixture yields for HS 2 1964 Averaged over Low and Medium densities. Explanation, see Figure 4.4.3a

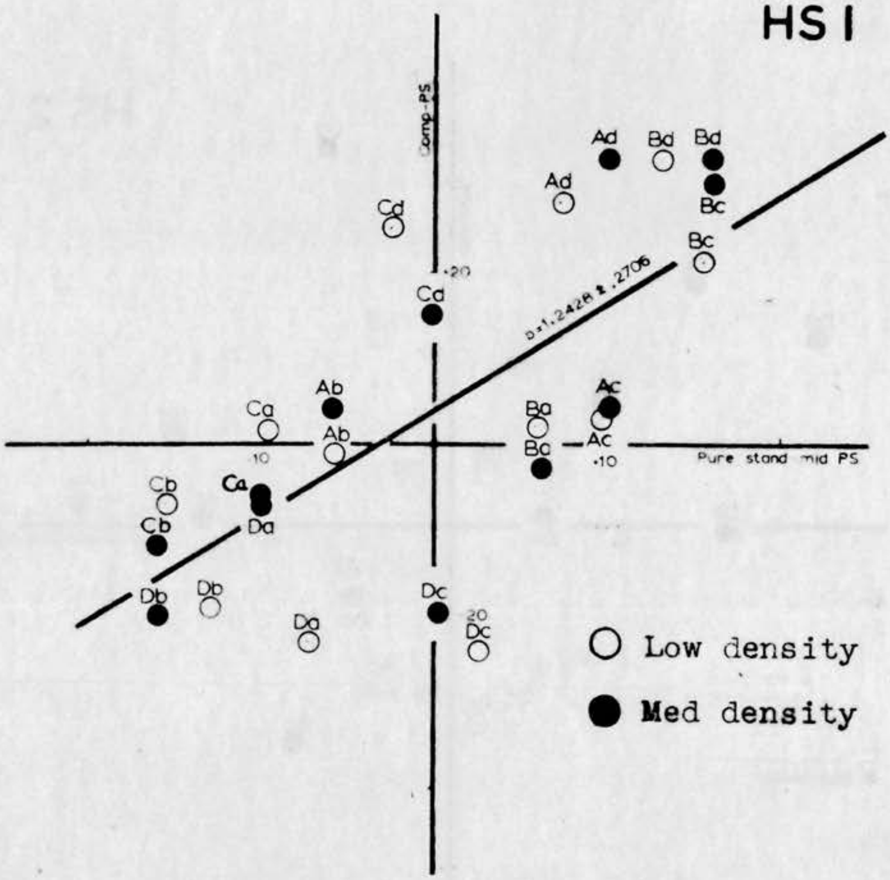

FIGURE 4.4.7 Relationship between pure-stand deviation from mid-pure-stand (horizontal scale) and yield in mixture minus PS yield (vertical) for each element in each mixture. HS 1 1964 Total yield.

e.g. $((\frac{1}{2}AA-1/4(AA+AB)))$ vs $(Ab-\frac{1}{2}AA)$

The straight line joining the two points for the two elements in a mixture, e.g. Ab:Ba cuts the vertical axis above (below) the origin by half the amount by which the mixture yield is more (less) than the mid-pure-stand.

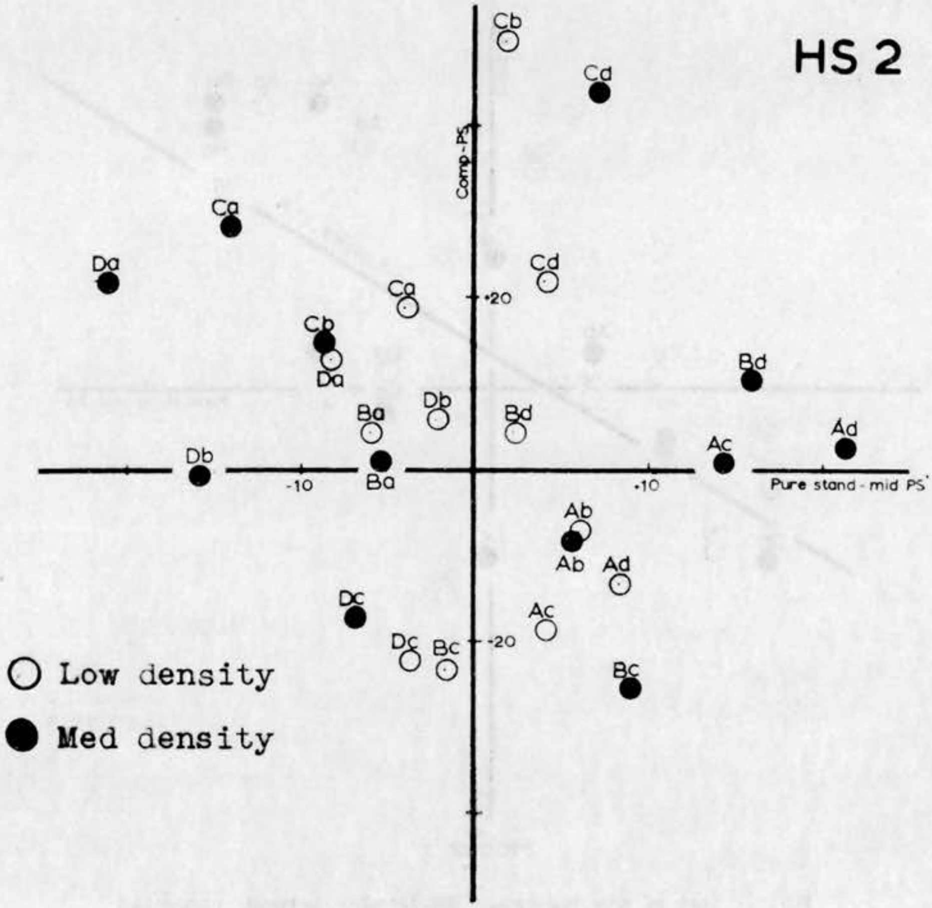

FIGURE 4.4.8 As 4.4.7 but for HS 2.

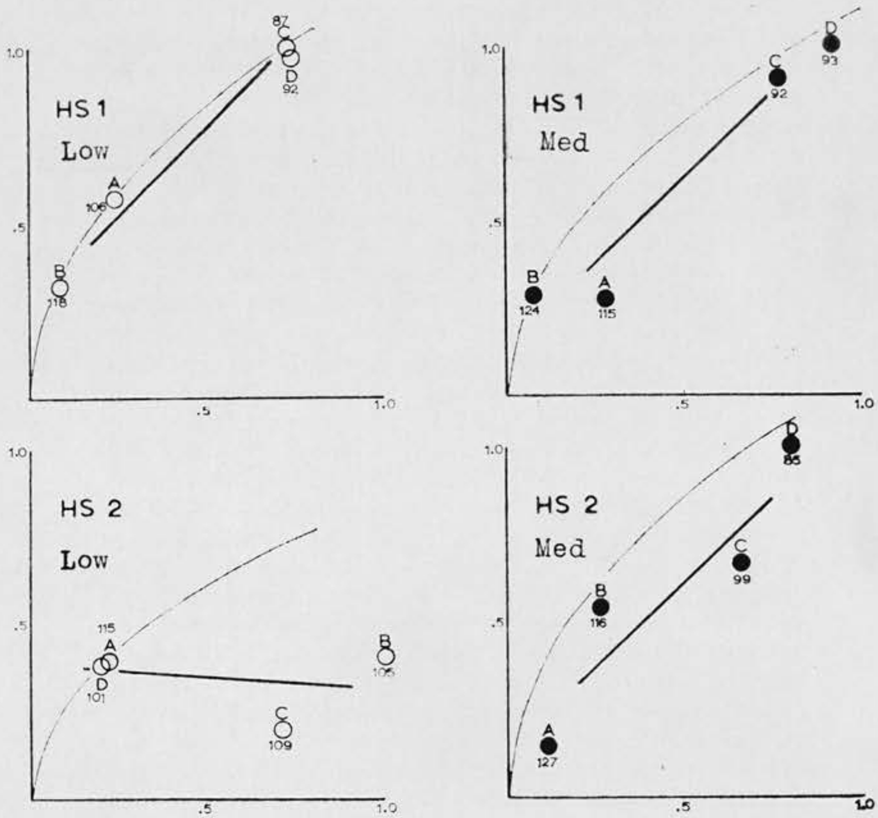

FIGURE 4.5.1 W_r/V_r graphs for total yield for each harvest-series and density. 1964. The number below each point gives the mean pure-stand yield for the element.

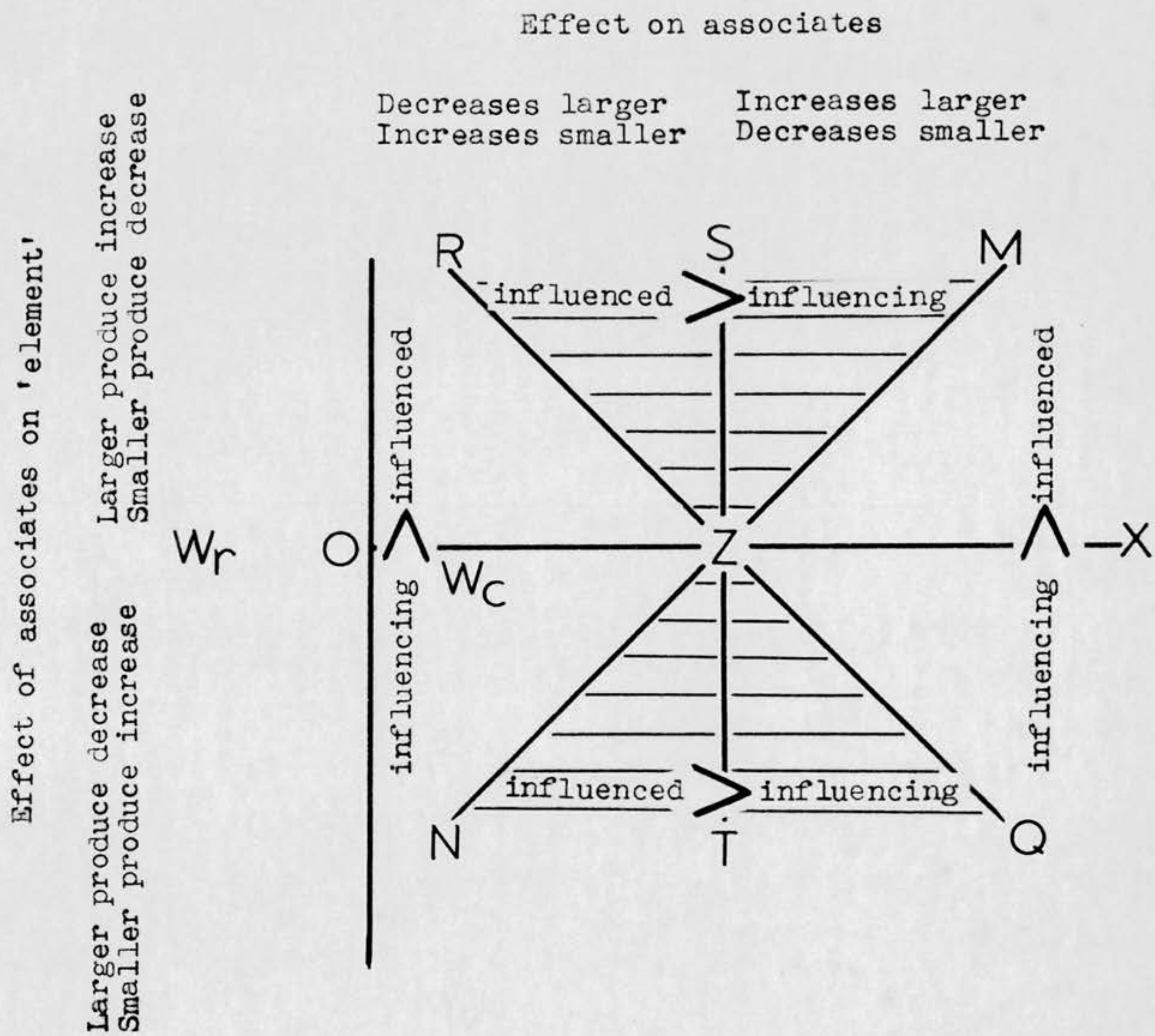

FIGURE 4.5.2 Durrant's W_r/W_c diagram. Explanation in text. Modified, with permission from Durrant (1965).

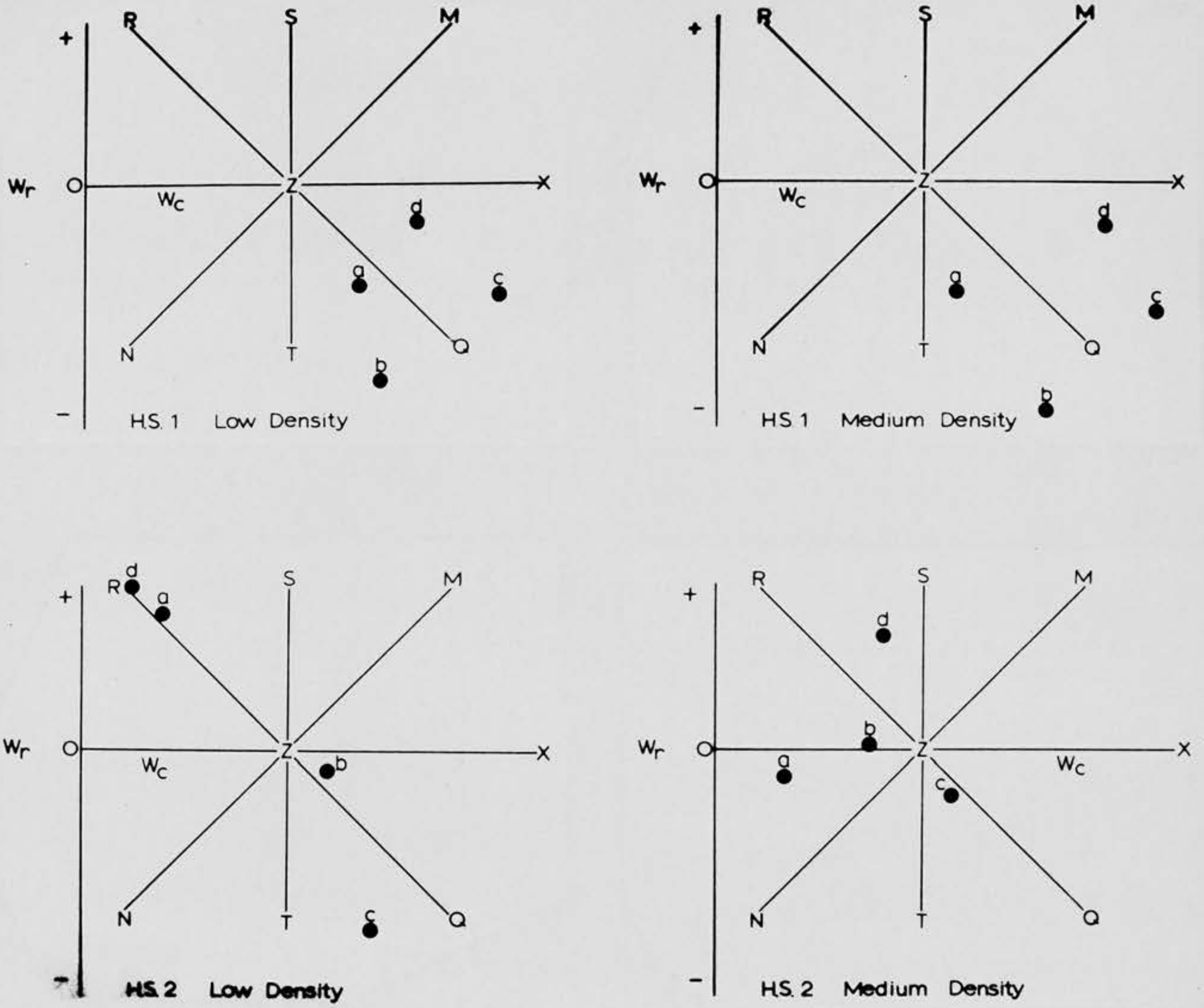

FIGURE 4.5.3 W_r/W_c graphs for total yields, 1964

SECTION 5.1 SUMMARY OF SECTIONS 2, 3 and 4

This thesis presents the results of investigations into techniques suitable for the evaluation of progenies of herbage grasses in a breeding programme. It is argued that, while sward performance must be the ultimate criterion of the excellence of a progeny, sward testing is expensive of labour and of seed, and that small sward plots are difficult to manage with the necessary degree of precision. It is also considered that a technique suitable for the assessment of the performance of progenies (or of cultivars) in mixture with others is required. The study falls into three main parts, the first of which is an investigation into the use of lower than sward densities for the prediction of sward performance. The material for this purpose consisted of fourteen populations of Italian ryegrass, seven of these populations being commercial cultivars and seven of them 50:50 mixtures of two cultivars. The performance of these fourteen populations was compared at sward and three non-sward densities.

The non-sward densities were: six inch square planting, three inch square planting and sown rows three inches apart. The plots were harvested four times in 1962. In no case were there significant interactions between sward and non-sward performance, indicating that the non-sward densities were suitable for predicting sward performance. The degree of agreement between sward and non-sward performance was assessed from the correlation coefficients between each sward and each non-sward performance in turn. There was little to chose between any of the non-swards on this basis; there was, however, a considerable difference between the coefficients found for the cultivars and the mixtures. The cultivars gave correlations for total yield (the sum of four cuts) of about + 0.9, and for three of the single harvests the values were about + 0.7. At one harvest they were rather lower at about + 0.3. The coefficients for the mixtures followed the same general trend from harvest to harvest, but were in all instances rather lower. This was probably due to the fact that the mixed plots were established from broadcast sowings of mixed seed of the two components and that some selection had occurred in favour of one of the components during the early seedling stage in the sward density.

A statistical technique is presented for assessing the "quality" of selection based on a character having a known correlation with the one for which it is actually desired to select. The correlations found indicate that any of the non-sward densities used would be suitable for the assessment of sward performance of pure-stands of cultivars or progenies but would be less suitable for the assessment of mixtures.

The six inch square planting was the easiest of the densities to manage and for that reason was chosen for use in the second stage of the study which was concerned with the choice of suitable combinations of plot and block size and number of replications. Two Italian ryegrass cultivars were used for this purpose, each being sown in a separate uniformity trial. Each trial measured eight by sixteen yards and was harvested in one square yard square plots (basic units). Seventeen different combinations of plot and block size and shape, obtained by combining the data from the basic units, were analysed as randomised blocks. The choice of suitable plot and block shape was made on the basis of the coefficients of variation and of the estimates of the index of soil heterogeneity (b) (obtained from the regression of log. plot size on log. variance).

The efficiency of a particular layout was assessed on the basis of the amount of ground required to achieve a specified degree of precision. The most efficient plot size, if no allowance was made for guard rows, was the smallest (equal to one basic unit); if allowance was made for one guard row, plots of two basic units were as efficient and, as the number of guard rows was increased, the advantage lay with the progressively larger plots. In Italian ryegrass, in which all the different populations tend to be of very similar growth habit, one guard row is probably sufficient and, on the basis of efficiency alone, plots two square yards in area would be chosen. The use of plots of this size does, however, require the use of rather many replications and in practice it is considered that the use of eight replications of plots of four square yards would be most suitable.

The estimates of the coefficient of variation from plots of the same size but of different shape varied widely, in some cases by a factor or two. A difference of this magnitude requires a fourfold increase in replication to achieve the same degree of precision and the desireability of chosing an optimal shape of plot is obvious.

Estimates of 'b' varied widely with changing plot shape and also from harvest to harvest. Graphs are presented to assist in the choice of suitable combinations of plot size and number of replications for various values of 'b'.

The third part of the study concerns the behaviour of herbage grasses grown in mixtures and its relation to pure-stand performance. Two perennial ryegrass and two cocksfoot cultivars were used for this purpose; they were grown in all possible combinations in pairs and in pure-stand, in boxes at three densities having one inch (high density), two inches (medium) and four inches (low) between neighbouring plants. In the mixed boxes alternate individuals of the two components were planted. The layout has certain analogies with the genetic diallel and the term "mechanical diallel" is sometimes used of it.

Statistical methods for the interpretation of the data are discussed and the various main and "competitive effects" estimated from the linear model of Eberhart et al. (1964).

During the seedling year density had a marked effect on overall yield but did not affect the proportional estimates of competition effects. During the year after sowing density affected neither yield nor competition.

Two replicates of the trial were subjected to a cutting regime under which the first cut was taken before the plants had begun stem elongation, later cuts being taken at roughly monthly intervals. Two other replications were allowed to approach ear emergence before being cut. Under the former regime competitive behaviour tended to follow that in pure-stand in that the higher yielding component tended to increase its yield in mixture and the lower yielding to decrease. Under this regime the ryegrasses were competitively superior to the cocksfoots although in later cuts the advantage tended to disappear. Under the alternative cutting regime there was no clear relationship between pure-stand performance and that in mixture, and the cocksfoots on the whole were competitively superior to the ryegrasses.

The use of W_r/V_r graphs in the interpretation of the data is discussed and use is made of the W_r/W_c technique recently developed by Durrant (1965).

Part of Section 4 of this thesis, that dealing with the behaviour of the plants in the year after sowing, has been published as an occasional paper in the Annual Record of the Scottish Plant Breeding Station.

ENGLAND, F.J.W. (1965) Interactions in mixtures of herbage grasses. Scottish Pl. Breeding Sta.Rec., 1965: 125-49

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REFERENCES

PLEASE NOTE:

Seven references have been omitted from the main reference list. These seven are in a supplementary list which follows the main list. The omissions are indicated in the main list by bracketed numbers.

Please refer to note on preceeding page

REFERENCES

AHLGREN, H.L., SMITH, D.C. and NIELSEN, E.L. (1945). Behaviour of various selections of Kentucky bluegrass, Poa pratensis L. when grown as spaced plants and in mass seedings.

Agron. J., 37: 268-81.

ALEXANDER, M.W. and GENTER, C.F. (1962). Production of corn and soybeans in alternate pairs of rows.

Agron. J., 54: 233-4.

ALLARD, R.W. (1961). Relationship between genetic diversity and consistency of performance in different environments.

Crop Sci., 1: 127-33

AVAKJAN, A.A. and ŠUMANSKAJA, M.G. (1962). Combined sowing of late and early-ripening varieties of maize.

Agrobiology, (Moscow) No.2(134):283-7

BORLAUG, N.E. (1959). The use of multilineal or composite varieties to control airborne epidemic diseases of self-pollinated crop plants.

Proc. 1st. Internat. Wheat Genet. Symp., (1958): 12-27.

BRIM, C.A. and MASON, D.D. (1959). Estimates of optimum plot size for soybean yield trials.

Agron. J., 51: 331-4.

CHRISTIDIS, B.G. (1939). Variability of plots of various shapes as affected by plot orientation.

Emp. J.Exp. Agric., 7: 330-42.

COCHRAN, W.G. and COX, Gertrude M. (1950). Experimental designs.

(N.Y.) John Wiley. (London) Chapman and Hall.

CREWS, J.W., JONES, G.L. and MASON, D.D. (1963). Field plot technique studies with flue-cured tobacco. I. Optimum plot size and shape.

Agron. J., 55: 197-9.

DONALD, C.M. (1958). The interaction of competition for light and for nutrients.

Austr. J. Agric. Res., 9: 421-35

(1)

DUTTA, S.K. and HEATH, E.D. (1960). Size, shape and number of plots for field experiments with tea.

Emp. J. Exp. Agric., 28:121-32.

EBERHART, S.A., PENNY, L.H. and SPRAGUE, G.F. (1964). Intra-plot competition among maize single crosses.

Crop Sci., 4:467-71.

EVERITT, P.F. (1910). Tables of the tetrachoric function for fourfold correlation tables.

Biometrika, 7:437-51.

.... (1912). Supplementary tables for finding the correlation coefficient from the tetrachoric groupings.

Biometrika, 8:385-95.

FISHER, R.A. and YATES, F. (1953). Statistical tables for biological, agricultural and medical research 4th ed.

Oliver and Boyd.

GEIDEL, H. and HAUFE, W. (1965). Mischbestände aus drei Komponenten.

Z. Pflanzensuchtg., 54:2:143-53.

GILBERT, N. (1961). Correlations in plant breeding.

Euphytica, 10:205-8

GREEN, J.O. and EYLES Jean C. (1960). A study in methods of grass variety testing.

J. Brit. Grassl. Soc., 15:2:124-32.

GREGOR, J.W. (1957). Genotype-environmental interactions and its bearing on a practical problem of international interest.

Proc. 7th Internat. Grassl. Cong., (1956):202-11.

HALLAUER, A.R. (1964). Estimation of soil variability and convenient plot size from corn trials.

Agron. J., 56:493-9.

HANSON, W.D., BRIM, C.A. and HINSON, K. (1961). Design and analysis of competition studies with an application to field plot competition in soybeans.

Crop Sci., 1:255-8.

HANSON, A.A. GARBER, R.J. and MYERS, W.M. (1952). Yields of individual and combined apomictic strains.

Agron. J., 44:125-8.

HARPER, J.L. (1961). Approaches to the study of plant competition.

Symp. Soc. Exp. Biol. 15:1-39.

HARPER, J.L. (1964). The nature and consequence of interference amongst plants.

Proc. 11th Internat. Cong. Genet., 465-82.

HATHEWAY, W.H. and WILLIAMS, E.J. (1958). Efficient estimation of the relationship between plot size and the variability of crop yields.

Biometriks, 14:207-22.

HATHEWAY, W.H. (1961). Convenient plot size.

Agron. J., 53:279-80.

HEINRICHS, D.H., LAWRENCE, T. and MORLEY, F.W.H. (1962). Breeding for improvement of quantitative characters in *Agropyron intermedium* (Host). Beauv. by the polycross method.

Can. J. Pl. Sci., 42:323-38.

HEYMANN, W. (1963). Contributions to the question of fodder grain production of spring cereals by sowing oats and barley pure or in mixture.

Albr-Thaer-Arch., 7:75-91.

ILIEVA-STANEVA, B. (1962). On the question of mixed crops of winter barley and wheat.

Selskostop. Nauka. Bulgaria, 1/7:745-50.

IVANOV, V.P. (1962). The mutual influence of the root systems of maize and the fodder bean plants.

Pl. Physiol. U.S.S.R., 9:179-88.

JENKIN, T.J. (1930). Perennial rye-grass at Aberystwyth.

Welsh J. Agric., 6:140-65.

.... (1931). The method and technique of selection, breeding and strain building in grasses.

Imp. Bur. Pl. Genet. Herb.Pl. Bull., No3:5-34.

.... (1951). Genetic problems in the breeding of forage grasses.

Ath. del Convegno di Genetica Agraria, (1950): 360-74.

.... (1955). The development of strains in grasses and clovers.

J. Nat. Inst. Agric. Bot., 7:419-33.

JUSTESEN, S.H. (1932). Influence of size and shape of plots on the precision of field experiments with potatoes.

J. Agric. Sci., 22:366-72.

KEULS, M. and SIEBEN, J.W. (1955). Two statistical problems in plant selection.

Euphytica, 4:34-44.

KNIGHT, R. (1961). The relations between tillering and dry matter production in cocksfoot (D. glomerata L.) grown under spaced and sward conditions.

Aust. J. Agric. Res., 12:4:566-77.

KOCH, E.J. and RIGNEY, J.A. (1951). A method of estimating optimum plot size from experimental data.

Agron. J., 43:17-21.

KOLEV, D. and IVANOVA, A. (1964). Growing of barley/wheat mixed crops.

Naŭc. Trudove. vĭss. Selskostop. Inst. "V. Kolarov." Plovdiv., 13:87-97.

KRAMER, H.H. (1947). Morphologic and agronomic variation in Poa pratensis L. in relationship to chromosome numbers.

J. Amer. Soc. Agron., 39:181-91.

.... (1952). Agronomic problems of strain evaluation with forage crops.

Proc. 6th Internat. Grassl. Cong., 341-5.

KUMAGAI, T. and TABATA, S. (1962). Relationship between the occurrence of competition and some characters in oat varieties.

Res. Bull. Hokkaido Nat. Agric. Exp. Sta., 79:1-4.

LAZENBY, A. (1957). The problem of assessing strains. A study in grass-breeding techniques.

(2) J. Agric. Sci., 48:294-304.

LAZENBY, A. and ROGERS, H.H. (1961). The evaluation of selection indices for yield in grass breeding.

Proc. 8th Internat. Grassl. Cong., (1960):303-7.

.... (1962). Selection criteria in grass breeding. I

J. Agric. Sci., 59:51-66.

.... (1964). II Effect, on Lolium perenne, of differences in population density, variety and available mixture.

J. Agric. Sci., 62:285-98.

LAZENBY, A. and ROGERS, H.H. (1965a). IV Effect of nitrogen and spacing on yield and its components.

J. Agric. Sci., 65:65-78.

.... (1965b). V Performance of Lolium perenne genotypes grown at different nitrogen levels and spacing.

J. Agric. Sci., 65:79-89.

.... (1965c). VI Effects of defoliation on plants growing in small plots in field and controlled environment conditions.

J. Agric. Sci., 65:397-404.

LEE, Alice. (1927). Supplementary tables for determining correlations from tetrachoric groupings.

Biometrika, 19:354-404.

LESSMAN, K.J. and ATKINS, R.E. (1963). Optimum plot size and relative efficiency of lattice designs for grain sorghum yield tests.

Crop Sci., 3:477-81.

MILES, D.G. (1961). Some significant factors in the assessment of herbage varieties.

Proc. 8th Internat. Grassl. Cong., (1960):112-5.

MURPHY, R.P. (1952). Comparison of different types of progeny in evaluating breeding behaviour.

Proc. 6th Internat. Grassl. Cong., 320-6.

NISSEN, O. (1961). Testing hay varieties of grasses as spaced plants in a pure-stand or in a mixture with a legume.

Proc. 8th Internat. Grassl. Cong., (1960):310-3.

NONNECKE, I.L. (1958). The precision of field experiments with vegetable crops as influenced by plot and block size and shape.

I Sweet corn

Can. J. Pl. Sci., 39:443-57.

NONNECKE, I.L. (1959). II Canning peas.

Can. J. Pl. Sci., 40:396-404.

NONNECKE, I.L. and SMILLIE, K.W. (1963). III Potatoes.

(3) Can. J. Pl. Sci., 44:57-65.

PATTERSON, F.L., SCHAFER, J.F., CALDWELL, R.M. and COMPTON, L.E. (1963). Comparative standing ability and yield of varietal blends of oats.

(4) Crop Sci., 3:558-60.

PHLÁK, F., VICHERKOVA, M. and MINÁŘ, J. (1965). The mutual influence of barley and oats grown in mixture.

Rostl. Výroba, 11:657-68.

POPOV, A. and LENKOV, L. (1962). On the inter-relationships of wheat varieties grown as a mixture.

Bull. Centr. Sci. Res. Inst. Plantgr. Bulg. Acad. Sci., 12:21-38.

PROUDFOOT, K.G. (1957). A comparison of total dry matter yields obtained in the first harvest year, from five strains of perennial ryegrass under single plant, pure sward and clover sward conditions.

Res. Exp. Rec. Min. Agric. N. Ire., 6:19-30.

ROBINSON, H.F., RIGNEY, J.A. and HARVEY, P.H. (1948). Investigations in plot technique with peanuts.

(5) N. Carolina Agric. Exp. Sta. Res. Bull., 86:pp19.

SAGAR, G.R. (1960). The biology of some sympatric species of grassland.

D. Phil. Thesis. University of Oxford.

SAKAI, K.I. (1955). Competition in plants and its relation to selection.

Cold Spr. Harb. Symp. Quant. Biol., 20:137-57.

.... (1961). Competitive ability in plants; its inheritance and some related problems.

Symp. Soc. Exp. Biol., 15:245-63.

SANDFAER, J. (1954). Virkningen af det naturlige udvalg ved foraedlingsarbejdet med selvbefrugtende kornarter.

Tidsskr. Planteavl., 58:333-54.

SCHEIJGROND, W. and VOS, H. (1961). Methods of appraisal of herbage species and varieties.

Proc. 8th Internat. Grassl. Cong., (1960):118-22.

SCHLEHUBER, A.M. and CURTIS, B.C. (1961). Grain yield of four varieties of hard red winter wheat in pure-stand compared to a mixture.

Proc. Ser. P-394. Oklahoma Agric. Exp. Sta., 1961 pp7.

SIMMONDS, N.W. (1962). Variability in crop plants, its use and conservation.

Biol. Rev., 37:442-65.

SMITH, F.L. (1958). Effects of plot size, plot shape and number of replications on the efficiency of bean yield trials.

Hilgardia, 28:43-63.

SMITH, H.F. (1938). An empirical law describing heterogeneity in the yields of agricultural crops.

(6) J. Agric. Sci., 28:1-23.

STAPLEDON, R.G. (1930). Nationality trials with cocksfoot.

Welsh J. of Agric., 6:130-40.

.... (1931). Methods as applied to cocksfoot grass (*Dactylis glomerata* L.) and remarks as to technique in general.

Imp. Bur. Pl. Genet. Herb. Pl. Bull., No.3: 35-45.

THOMSON, J.R. (1961). The botanical appraisal of grass varieties.

Proc. 8th Internat. Grassl. Cong., (1960):116-8.

(7)

TORRIE, J.H. (1957). Breeding for quantitive characters.

Proc. 7th Internat. Grassl. Cong., (1956):450-9.

WEBER, C.R. and HORNER, T.W. (1957). Estimates of cost and optimum plot size for measuring yield and chemical characters in soybeans.

Agron. J., 49:444-9.

WIEDEMANN, A.M. and LEININGER, L.N. (1963). Estimation of optimum plot size and shape for safflower yield trials.

Agron. J., 55:222-5.

WILLIAMS, E.J. (1962). The analysis of competition experiments.

Aust. J. Biol. Sci., 15:509-25.

WILLIAMS, J.T. (1964). A study of the competitive ability of *Chenopodium album* I. Interference between kale and *C. album* grown in pure-stands and in mixtures.

Weed Res. 4:283-95.

YATES, F., VERNON, A.J. and NELSON, S.W. (1964). An example of the analysis of uniformity trial data on an electronic computer.

Emp. J. Exp. Agric., 32:25-30.

SUPPLEMENTARY REFERENCES

(1) DURRANT, A. (1965). Analysis of reciprocal differences in diallel crosses.

Heredity, 20 : 573-607.

(2) LAZENBY, A. and ROGERS, H.H. (1960). The evaluation of selection indices for yield in grass breeding.

Proc. 8th Int.Grassl.Cong., (1959). 303-307.

(3) PATTERSON, H.D. and ROSS, G.J.S. (1963). The effect of block size on the errors of modern cereal experiments.

J. Agric.Sci., 60 : 275-78.

(4) PEARSON, E.S. (1932). The percentage limits for the distribution of range in samples from a normal population.

Biometrika, 24: 404-17.

(5) ROY, S.K. (1960). Interaction between rice varieties.

J. Genet., 57 : 137-52.

(6) SNEDECOR, G.W. (1956). Statistical methods.

Iowa State Coll. Press, Ames, Iowa.

(7) TIPPET, L. H.C. (1925). On the extreme individuals and the range of samples taken from a normal population.

Biometrika, 17 : 364-87.