STUDIES OF YIELD CHARACTERS IN CEREALS WITH PARTICULAR REFERENCE TO OATS.

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CONTENTS.

INTRODUCTION.

In all the programmes designed to improve the yields of crops it may be expected that a stage will be reached eventually when further improvements of practical significance will be difficult to obtain. From the plant breeder's point of view it may be that in the absence of further desirable mutations, a better combination of inherent characters will not be possible with the gene content available. From the agronomist's point of view, limiting factors to further improvement are set by considerations of climatic conditions, limitations of cultivation methods etc. It is possible that the improvement of cereal yield in this country is approaching this stage. In recent years many new and good varieties have appeared on the market, but it is questionable whether in many cases differences between them really represent 'cash differences' to the grower.

Assuming however that further improvement is possible with the genetic material at present available, and under current agricultural methods, it may be expected that two factors will become of increasing importance in plant breeding technique. One factor is the need of a reliable means of comparing varietal yields on a small scale - a need which is being satisfactorily met by the application of statistical methods. Given a selection of promising varieties, it is now possible for the plant breeder to choose the best of them with more assurance than would formerly have been the case. The second factor is the need of a thorough knowledge of those plant characters which influence yield, and in particular a knowledge of their interaction within the plant and within the plant population. Such knowledge is still far from adequate. If further improvement is to be obtained it is no longer sufficient to carry out single plant selection with little more than empirical knowledge, i.e. that amount of tillering is an indication of plant vigour, and that number and size of grains are associated with yield of the individual plant. More information is required about the relative importance of 'yield characters' when the plants are under intense competition as members of a field crop. Also the relation between individual plant performance and plant population performance is still imperfectly understood.

A solution of these and like problems should provide the plant breeder with a sounder basis for carrying out single plant selection. Much work has already been done, and its main features will be reviewed in the next section of this paper. The experimental work to be reported had the same object in view.

REVIEW OF PREVIOUS LITERATURE.

I. Plant characters which control yield and their reactions in plant populations.

In order to consider the general conclusions reached by the numerous workers in these studies, it will be convenient to group their results in the following way:-

(1) The general effect of changes in plant population density on yield per plant and yield per unit area. Varietal differences in response to these changes.

(2) Internal plant characters which control yield: analyses of their respective importance, and their interactions when subjected to influences external to the plant. Varietal differences.

1. <u>The effect of different plant population densities.</u>

As long ago as 1919, Brenchley showed that the two chief factors in plant competition were likely to be food supply in the soil (especially nitrogen) and competition for light. Both available nitrogen and light will be expected to vary inversely with population density, and in the field these factors must be considered together.

Two main types of experiment have been used in determining the effect of different population densities. In the first case small hand-sown plots with uniformly spaced plants have been used. Plots with different uniform spacings have then been compared. In the second case ordinary field crops (i.e. with variable spacings) or drill-sown plots have been used for experimentation. Different <u>average</u> spacings have then been compared, either by taking sample footlengths (field crops), or by comparing plots with different <u>average</u> sowing rates (drill sown plots).

As might be expected there is general agreement that yield per plant shows strong negative correlation with population density. But since yield per unit area depends both on plant density and yield per plant, it is obvious that the relation between plant density and yield per unit area will be determined by the intensity of inter plant competition. Where competition is relatively little, it may be expected that yield per unit area will be positively correlated with plant density, where great - negatively correlated. Where competition increases rapidly with increasing density, it may be expected that yield per unit area will increase up to a certain optimum and then fall off with any further increase in plant density. These three possibilities have in fact been found in the results of workers with variable spacings. Positive correlations were found by Doughty and Engledow (1928), Bonnett and Woodworth (1931), Sprague and Farris (1931), and negative correlations by Yates (1936). Optimum spacings were found by Engledow (1926), Hopkins (1932), and Thayer and Rather (1937). On the other hand workers with uniformly spaced plants find that yield per unit area is little affected by comparatively large changes in population density, - a result to be expected if increase in plant competition were just balanced by increase in plant density, (Engledow (1925), Engledow and Ramiah (1930), Frankel (1935) and others).

There is therfore an apparent discrepancy between results from the two types of experiment, yield per unit area being dependent on plant population when spacing is variable, and independent of plant population when the plants are evenly spaced. An important contribution to the interpretation of this discrepancy was put forward by Smith (1937). Doughty and Engledow (1928) had assumed that since in their results the highest yielding footlengths in a wheat field were those most densely populated, average yield of the whole field would have been greatly increased by thicker sowing of the more thinly sown areas. Smith pointed out that such an assumption was not justifiable because individual footlengths are not necessarily independent of neighbouring footlengths. In the case of evenly spaced plants, inter plant competition must be of similar intensity throughout the plot, but in a drilled plot the intensity may be expected to vary according to variations in population density. For every footlength sampled the average density of the adjacent footlengths will tend to equal the mean density of all footlengths in the plot, so that the ratio

$$p/q = \frac{\text{No. of plants in sampled footlength}}{\text{Mean No. of plants in adjacent footlengths}}$$

will be high when p is above the average, low when below. Smith suggested that apparent positive correlations observed by Doughty and Engledow between yield per footlength (y) and p may be due to a true positive correlation between y and the ratio p/q. In that case, y would be independent of plant density, and thus Doughty and Engledow's results could be harmonised with results from experiments with evenly spaced plants. (In the latter case p = q and y is constant for all spacings).

The most satisfactory confirmation of this hypothesis that yield of a sample footlength depends on the ratio of its population density to the densities of surrounding footlengths (i.e. $y \propto \frac{p}{q}$), would be the demonstration of significant partial correlations, $r_{yp.q}$ (+) and $r_{yq.p}$ (-). Although these were not demonstrated by Smith, his experimental evidence lends support to the theory. He was able to show for wheat drilled at densities between 3 and 10 plants per foot that by calculating regressions y on q for each level of p, and so obtaining adjusted values of y for p = q at each level, the regression y on p was greatly reduced. In other words, when the effect of adjacent footlengths was removed yield per footlength tended to become independent of footlength density. In another experiment Smith showed that in a direct comparison of 'variable' and 'uniform' sowings:

(a) In the variable sowings the most densely sown footlengths gave the highest yield.

(b) Uniform sowings at rates comparable with the most densely sown footlengths in (a) gave no better yields than the average yield of the variable sowings.

This shows conclusively that the most densely sown footlengths in (a) gained in yield from adjoining less dense areas, and offers an interpretation of the positive correlation between p and y which was found by Doughty and Engledow.

As a result of these experiments Smith concluded that variations in population density have little effect on average yield. Whether this holds true for all cereal varieties and for all agricultural conditions is perhaps open to doubt. The hypothesis necessarily assumes that competition occurs between the plants in neighbouring drill rows. It may be expected that the extent of this competition will depend on soil fertility, weather conditions, and particularly on the root range of the crop in relation to sowing rate and distance between drill rows. Also it is common knowledge that wheat has a greater root range than oats or barley. Wiebe (1937) working with wheat in U. S. A., studied the effect on yield per 15 ft. of drill row, of distances between rows varying from 7 to 17 inches. He found a significant regression of 3.8% increase in yield per 15 ft. of drill row for every one inch increase in distance between rows. The regression was linear over the range studied, which suggests that inter-row competition would have persisted over still wider distances. Over the same range of distances between rows, when increase in space on one side of a row was just compensated by decrease in space on the other, the yield of that row was unaffected. It appears that as long as space available to the plants remained constant, variations in plant distribution within that space had no important effect on yield. On the other hand Rayns (1930) found in the case of barley, that plants spaced at $1\frac{1}{3}$ ins. x 7 ins. gave higher yields <u>per acre</u> than plants spaced at $2\frac{2}{3}$ ins. x $3\frac{1}{2}$ ins. - the number of plants per acre being the same in both cases. It would seem that in the case of barley, changes in plant distribution within comparatively small areas may affect yield. Also there is some evidence that competition between footlengths is only important in densely sown areas. Sprague and Farris (1931) in the case of barley found that densely sown footlengths gained in yield at the expense of adjoining less dense areas, but that thin sown footlengths were independent - presumably because the component plants had sufficient space for unrestricted development. (According to Smith's hypothesis the yield of the thin sown areas should have been negatively correlated with the density of adjacent footlengths). In Smith's own experiment (the first one cited above) only one of the calculated regressions y on q was significant, this occurring in connection with the highest values of p. That inter-footlength competition may only be important above a certain density is indicated by spacing experiments with rice in China (Peh 1937). The effect of altering both numbers of plants per hill and distance between hills on yield per plot was to give proportionate increase in yield for decreased distance between hills when number of plants per hill was low. As number of plants per hill was increased however, altering distance between hills had less effect. Finally, an objection to the general acceptance of Smith's hypothesis (except in a modified form) is the fact mentioned previously; that both negative correlations between p and y, and cases where optimum sowing rates were indicated, have been found in experiments with drill sown crops. At the same time there appears to be little doubt that inter-footlength competition may play an important part in the yield relationships of a cereal crop.

2. Internal plant characters which control yield.

There are three ways in which the yield of a cereal plant may be affected in response to changes in plant density, or in the amount of food material available:-

(a) Variation in number of ears per plant.

(b) Variation in number of grains per ear.

(c) Variation in weight of individual grains.

There is a general agreement among workers that all three sources of variation are negatively associated with plant density, although the effect of the latter on the average grain weight is comparitively slight - often insignificant.

Engledow and Ramiah (1930) showed that for winter wheat grown in England, there is a critical period of tillering (March - April) after which no later formed tillers produce ears. On this basis it would be expected that early incidence of tillering and rapidity of tiller formation would be important indices of plant yield. This has been borne out in practice for highly fertile conditions in England by the success of the high tillering variety 'Yeoman'. It does not hold however for the less favourable conditions in Australia (Forster and Vasey 1931) and New Zealand (Frankel 1935) where the amount of tillering is less, and tiller survival rather than tiller production is an important factor in yielding ability. In England, also, Bell (1937) in studying the effect of vernalisation on winter wheat and barley varieties, concluded that tillering may be greatly reduced without necessarily decreasing the number of ears at harvest. The importance of tillering to plant yield will in fact depend on two factors operating successively: ability of the plant to form tillers, and ability of the plant to nourish until harvest the tillers formed. Either factor may be limiting, according to the level of fertility and intensity of inter plant competition which obtain at the respective stages in plant development. Only when the amount of available food material is above a certain level, will a high tillering variety be expected to have an advantage over a low tillering variety, as shown by Hudson (1934).

It seems doubtful whether any generalisation may be made as to the relative importance of ear number per plant and number of grains per ear in contributing to plant yield, <u>under conditions of field sowing</u>. Although reference to available data on evenly spaced plant experiments suggests that plant yield adjustment is brought about mainly by variation in number of ears per plant, (Engledow and Wadham 1924, Engledow 1925, Engledow and Ramiah 1930, Frankel 1935, Bell 1937, Li and Meng 1937, Hunter 1938), data from variable sowings are less consistent. In England, Engledow (1926) and Doughty and Engledow (1928) found that the majority of plants in field crops of wheat had only 1 to 2 ears. Even so their data show that plant yield adjustment was due mainly to variation in ear number per plant. Whether ear number per plant would be of chief importance for other varieties of wheat is perhaps open to question, since their data were obtained from the high tillering varieties, 'Yeoman' and 'Little Joss'. Varieties of the

'Wilhelmina' and 'Squareheads' type which are characterised by large ears rather than high tillering ability might not necessarily behave in the same way. Rayns (1930) in four years' drilling esperiments with barley, found that yield adjustment to changes in plant distrubution was due mainly to variations in ear weight, and that excessive tillering was negatively associated with this character. Since average grain weight showed little variation, it seemed probable that the most important factor in yield adjustment was variation in number of grains per ear. In U.S.A. the data of Bonnett and Woodworth (1931) showed that in the barley varieties, 'Wisconsin Pedigree' and 'Velvet', number of heads per plant only varied between approximately 1 and 1.5 over the range of densities studied (2 to 27 plants per foot). In the variety 'Spartan' over the same range of densities, there was a much larger variation (2 to 3.5 heads per plant). In all three varieties there were considerable variations in yield per head. Varietal differences with regard to method of adjustment to variation in plant density are also shown in the data of Thayer and Rather (1937). Over the same range of densities, two six-row barley varieties gave rather less variation in number of heads per plant than did two two-row varieties. With regard to number of grains per ear, however, the six-row varieties showed considerably more adjustment to variations in plant density than did the two-row varieties. The data suggest that although both are negatively correlated with plant density, number of ears per plant and number of grains per ear are to some extent alternative - the chief yield adjustment being brought about by variations in one or the other character. Sprague and Farris (1931) in a study of variable sowing rates of barley found that the principal adjustment of plant yield was due to variation in number of ears per plant, this being in agreement with the wheat data of the English workers.

There is some evidence to show that the three variables - number of ears per plant, number of grains per ear, and individual grain weight are not only dependent separately on plant density but also dependent on each other. Engledow and Wadham found that yield of any ear depended on its order of formation within the plant, the highest yielding ear being the one formed earliest (on main axis) and the lowest yielding ear belonging to the latest formed surviving tiller. This was to be expected, since although there was a considerable lag in time between the formation of the first and last formed tiller, there was at most a difference of a few days between their respective ear emergences. Similarly Bonnett and Woodworth found that although there was only a slight negative association between plant density and average grain weight, this association was more pronounced when only grain weight from the main axis ear was considered. Increase in grain weight (associated with decreasing plant density) was partially neutralized by increase in the number of surviving tillers with small grains. Sprague and Farris found that though increase in plant number per foot resulted in increased number of grains per foot, no further increase in yield per foot occurred at the higher densities. At the higher densities therefore increase in grain number must have been compensated by decrease in grain weight. Such interactions will be discussed more fully in a later section of this paper.

II. Varietal differences in manner of yield production.

The data reviewed in the previous section provide evidence of the manner in which the cereal plant adjusts itself to variation in available food supply. It appears likely that although there is an underlying uniformity in plant reaction, varietal differences exist in the manner of adjustment. Which of the plant characters - ear number per plant, number of grains per ear, and size of grain - is the most important attribute of high yielding ability for any selected fertility level, remains to be considered.

From a study of ten Australian varieties Smith (1935) concluded that size of grain was of primary importance in selecting for yield. This character was found to be positively correlated with grain number per ear, and the latter was negatively correlated with ear number per plant. This is in agreement with the findings of Forster and Vasey in Australia and Frankel in New Zealand whose data showed that large eared low tillering varieties were the most successful. In U. S. A. Bridgeford and Hayes (1931) in studying sixty one varieties of spring wheat found that yield was positively correlated with plant height, plumpness of grain, and 1000 grain weight, but was uncorrelated with number of ears per row. Plant height was correlated with number of grains per ear. In England, as far as the writer is aware, no similar data are available, but a consideration of trends in plant breeding achievement suggest that similar relationships hold. In oat breeding, improvement in yield has been accompanied by loss in tillering ability and increase in yield per panicle; a change over from a 'dual purpose' type like 'Potato' to a high grain yielding type like 'Star' or 'Onward'. In wheat breeding, two trends are evident. On the one hand are varieties like 'Yeoman' and 'Holdfast', characterised by high tillering ability and adapted to conditions of high fertility, and on the other hand are large eared varieties of the 'Wilhelmina' type which give high yields over a wide range of soil conditions.

The evidence as a whole indicates that increase in yield per ear and increase in number of ears per plant are alternative, and to a large extent mutually exclusive methods of breeding for yield.

A consideration of the foregoing literature suggests at least three further lines of enquiry which might be expected to have an important bearing on plant breeding procedure, and on which the evidence is still inconclusive:-

1. How far can individual footlengths in a drill sown cereal crop be considered independent units?

If as Smith suggests, yield is independent of absolute plant number over a wide range of densities, it implies that current cereal varieties at present rates of sowing are able to tap fairly completely the available soil resources. In this case it may be expected that any improvement in yield will only be obtained by (a) increasing the level of soil fertility by better cultivation and manuring, or (b) breeding new varieties which are more economical consumers of the available food material, - i.e. varieties which have a high ratio:

$$\frac{\text{Grain yield per plant}}{\text{Total vegetative material per plant}}$$

If on the other hand, individual footlengths may be considered independent units - even over only a part of the range of densities occurring in the field - then average sowing rates, and the relative ability of plants to adjust themselves to variations in population density will still be important considerations in plant breeding and agricultural procedure.

2. Which is the more important index of yielding ability for different cereal varieties: number of ears per plant, or yield of grain per ear?

It is possible that for some varieties size of ear may be more important than number of ears per plant <u>under field conditions</u>. In this case detailed studies of tillering ability of rather widely spaced plants in a breeding plot, might profitably be sacrificed to more detailed observations of ear yielding ability at spacings corresponding to accepted average sowing rates in the field.

3. What are the interactions of plant characters which influence yield?

Until these characters are more fully understood, it is possible that plant improvement in one direction may be counter-balanced by deterioration in another.

These questions in particular formed the basis of the experiments about to be described.

EXPERIMENTAL WORK 1937 - 38.

I. Materials and methods.

Spring sown oats form particularly interesting material for detailed studies of yield, since the growing conditions of this crop in Scotland contrast strongly in several respects with the conditions of winter wheat growing in England - the latter crop having so far received most attention from previous workers in this country. Apart from the differences in length of growing period between the two crops, there are contrasts in soil temperature and tilth at time of sowing, rate of sowing, root range, and length of day during the growing period. Winter wheat is usually sown on a relatively rough seed bed (particularly on the heavier soils) while the seed bed for spring oats has had the full action of frosts during the preceding winter, and is usually in a fine state of subdivision. Cereal sowing rates in Scotland are commonly much higher than in England, and the difference between rates of 5 or 6 bushels per acre (spring oats in the Lothians) and an average of 1½ to 2 (winter wheat in Eastern England) is only partially offset by the lower bushel weight of oats.

Reference has been made previously to the extensive root range of wheat. The root range of oats is much less, and the difference between the two crops in this respect may be expected to be at a maximum where wheat is winter sown and oats spring sown. Long day conditions prevail over most of the growing period of the oat crop, while the growing period of the winter wheat crop nearly always includes both shortest and longest day.

Two types of experiment were attempted; population studies in which sample footlengths from drilled plots were studied at weekly intervals from sowing to harvest, and developmental studies in which individual plants were examined at corresponding intervals until ear emergence.

Population studies.

These were similar in technique to the 'census studies' used by Engledow in sampling field crops of wheat. Instead of field crops, however, replicated drilled plots which formed part of routine variety trials were sampled in each season. These trials consisted of thirty varieties replicated in randomised blocks (4 blocks in 1937 and 5 in 1938).

Each plot was 19 ft. long and 7 drill rows wide, the drill rows being spaced 9 ins. apart, and was thus approximately 1/440 acre in area. A discard row of spring wheat surrounded each plot.

Sowing was carried out with a special single coulter hand-drill of the forced feed type, the aperture being adjustable for different sowing rates. The wheels were 9 ins. distant from the coulter on either side, so that by careful 'wheel to coulter' drilling an even 9 ins. spacing between rows was possible. A weight of seed calculated to give a sowing rate of 2½ million grains per acre* for each variety was sown on each plot. The weight required for each variety was calculated from its 1000 grain weight. Although by this method approximately equivalent numbers of seeds could be sown per plot, an extra control was necessary to ensure that the seeds were as evenly distributed as possible over the 7 drill rows. Since a rate of 2½ million grains per acre corresponds to a density of about 43 grains per foot of drill row at 9 ins. spacing, the number of grains required to be sown for each revolution of the

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* 4 - 5 bushels per acre.

drill wheel could be calculated. A preliminary testing of the sowing rate was accordingly carried out.

The drill was jacked up and the number of seeds discharged at each revolution of the drill wheel was counted. The sowing aperture of the drill was only capable of coarse adjustment, but it was found possible to fix settings which approximated to the required rate. As expected, for any fixed setting there was a very high variability in sowing rate between successive revolutions of the drill wheel, the coefficient of variation being of the order of 15% at or near the required sowing rate.

Footlengths for study were chosen at random from the five inside rows of each sampled plot, with the restriction that the end footlengths of each row were omitted from sampling. The sample footlengths were therefore situated at distances from 1 to 17 ft. from one end of each plot, and could be selected before the plants appeared above ground. As soon as the seedlings were visible after sowing, the selected footlengths were pegged out. Weekly plant counts were undertaken until the extent of tillering made these impracticable. Numbers of shoots per footlength

TABLE I.

TABLE I.

Precision of panicle sampling, Block I. (1938)

Total number of spikelets per panicle.

Potato

Variance	D.F.	S.S.	M.S.	½ log e	'z'
Between foot-lengths	9	9585.89	1065.10	3.4854	0.6395 signif. at 1%.
Within foot-lengths and between plants	90	26671.10	296.35	2.8459	
Between plants	99	36256.99	-	-	

Sampling error = $\sqrt{296.35}$ = 17.2 (52.9% of mean)

Marvellous

Variance	D.F.	S.S.	M.S.	½ log e	'z'
Between foot-lengths	9	1456.25	161.81	2.5431	0.9323 very signif.
Within foot-lengths and between plants	87	2181.19	25.07	1.6108	
Between plants	96	3637.44	-	-	

Sampling error = $\sqrt{25.07}$ = 5.0 (42.9% of mean)

N.B. On footlength of Marvellous had only 7 panicles so that the samples included the whole footlength.

were counted weekly until ear emergence, and then no further data were collected until the footlengths were harvested. After harvest, for each footlength separately, number of panicles, average number of 20 1-grained, 2-grained, etc., spikelets, and yield of grain were recorded.

The average number of spikelets per panicle was estimated from ten panicles in each footlength. The panicles were shuffled carefully and laid on a bench. Panicles were then selected at random by grasping a spikelet in the bunch and withdrawing the panicle to which it was attached. An indication of the adequacy of the size of sample is available. In the 1938 season the total number of spikelets was recorded separately for each sampled panicle in Block I, so that a comparison of 'between' and 'within' footlength variance was possible. Data are given in Table I. It can be seen that in spite of the rather high sampling errors in the two varieties, real differences exist between the samples, of a higher order than the plant to plant variation. Since the method of sampling was constant over the two seasons, it is felt that Table I can be considered representative of all the panicle sampling.

Precautions were also taken in sampling the spikelets for weighing, that as far as possible all the spikelets in the footlength had equal chances of being selected, and all weighings were checked. It should be mentioned too, that the plants in the foot-lengths were harvested by pulling up by the roots, and were then allowed to dry out for three weeks in the laboratory before sampling. By this time the pales were quite bleached and brittle and the grains 'hard ripe'. The twenty spikelet samples were selected in each case from the entire footlength and placed in paper bags in open trays before weighing.

The 1937 experiment may be considered as preliminary to the more detailed experiment of 1938. Although carried out on a small scale its results are worth more than brief notice since in spite of the very different seasonal conditions they support the results obtained in 1938. Four varieties were examined, replicated (as part of the total 30 variety trial) in four plots. Only one footlength was sampled in each of the five (inside) drill rows of each plot, making a total of twenty footlengths per variety. The varieties chosen were well known commercial varieties, commonly grown in Scotland, and exhibiting a range in agriculturally important characters:-

'Potato'	-	An old 'land' variety with moderate grain yield and high yield of straw. Panicles furnished with many small spikelets of which the majority are single grained. Husk very thin and grain of very good quality. Grown on the poorer soils.
'Victory'	-	(Svalöf) A high grain yielding variety but rather late for Scottish conditions. Panicles small, but spikelets mostly 2 to 3 grained. Grain moderately large, husk medium.
'Star'	-	(Svalöf) Similar to 'Victory' in many respects, but having a slightly larger and coarser grain. Also earlier and shorter in the straw.
'Marvellous'	-	(Garton's) An early variety with a very large coarse grain and 'close' panicle. Spikelets mostly 2 to 3 grained but sometimes more.

Stocks of these varieties had been 'pure lined' at Edinburgh for several generations.

In the 1938 experiment only two varieties were studied 'Potato' and 'Marvellous', these representing extremes in commercially grown crops. Each variety was replicated in five plots, and two footlengths were sampled in each of the five drill rows in each plot, making a total of fifty footlengths per variety.

Developmental studies.

These were carried out in parallel with the population studies, and consisted of a preliminary examination of the four varieties 'Potato', 'Victory', 'Star', and 'Marvellous' in 1937, followed by a more critical study of 'Potato' and 'Marvellous' in 1938. In 1937, plots of the four varieties in which the plants were spaced at 2 ins. x 9 ins. were sampled at approximately weekly intervals until ear emergence. The plants were dissected into their component tillers, and then the main shoot and primary tillers were analysed further in each case, by removing the leaves in order from the base of the shoot until the growing point was exposed. The younger leaves were removed with dissecting needles by aid of a mounted lens. Number of tillers, number of tiller buds, and number of leaves formed on the main shoot were recorded. In the case of the later samples, notes were also taken of the stage of development of the panicle initials and the number of internodes elongating on the main shoot. In 1938 the procedure was modified in that samples were not taken from plots with spaced plants, but from drill sown plots. These plots were situated within a few yards of the variety trial which was providing data for the population studies and they had been sown at the same rate ($2\frac{1}{2}$ million grains per acre in rows 9 ins. apart). Also they had been sown only five days later with the same hand drill. It was felt therefore that the developmental study data should be strictly comparable. Each sample was composed of 20 plants selected at random from the plot, and the subsequent analysis was confined to the main shoots.

In both seasons the relative development of the spikelets (number of florets and stage of development of the floral parts) of the different varieties was determined by examination under the low power of the microscope.

TABLE II.

TABLE II.

1937 season: Analysis of variance in seedling emergence.

	D.F.	S.S.	M.S.	½ log e	
Between varieties	3	781.94	260.65	2.9816	'z' insignif.
Blocks	3	70.24	23.41	-	
Error	9	3561.21	395.69	2.9904	
Within varieties and between plots	12	3631.45	302.62	-	
Between plots	15	4413.39	294.23	-	
Within plots and between footlengths	64	23002.00	359.41	2.9422	
Between footlengths	79	27415.39	347.03	-	

II. Population studies.

1. The 1937 season.

Sowing was carried out under good conditions on March 29th, the soil being moist after an above average rainfall during January and February. Seedling emergence was uniform, but damage by birds reduced the plant population of one plot of 'Victory' considerably. In spite of this it can be seen from the analysis of variance (Table II) that none of the sources of variation, including variation between plots, exceeded the variation between footlengths in the same plot. There remained the possibility however, that the increased variation between plots (due to the low plant numbers in the 'Victory' plot) might obscure real differences in average seedling emergence between varieties. This was tested by substituting a 'missing plot' value (Yates 1933) for the actual value of the low plant number plot. The following figures show that although the 'between plot' variance is reduced to about half by the substitution, there is no evidence of real differences between varieties in average seedling emergence:-

TABLE III.

TABLE III.

Variation in number of seedlings per footlength. Comparison of 1937 and 1938 data with data from four English wheat fields (Doughty & Engledow 1928).

Season	Crop	No. of ft.lengths	Mean plant No. per ft. length	Variance	Coefficient of variation
1928	Wheat	190	16.5	31.4	33.9
-	-	342	17.7	43.2	37.3
-	-	286	18.0	51.8	40.0
-	-	149	11.9	34.8	49.6
1937	Oats	80	38.8	359.4	49.0
1938	-	100	33.5	209.2	43.2

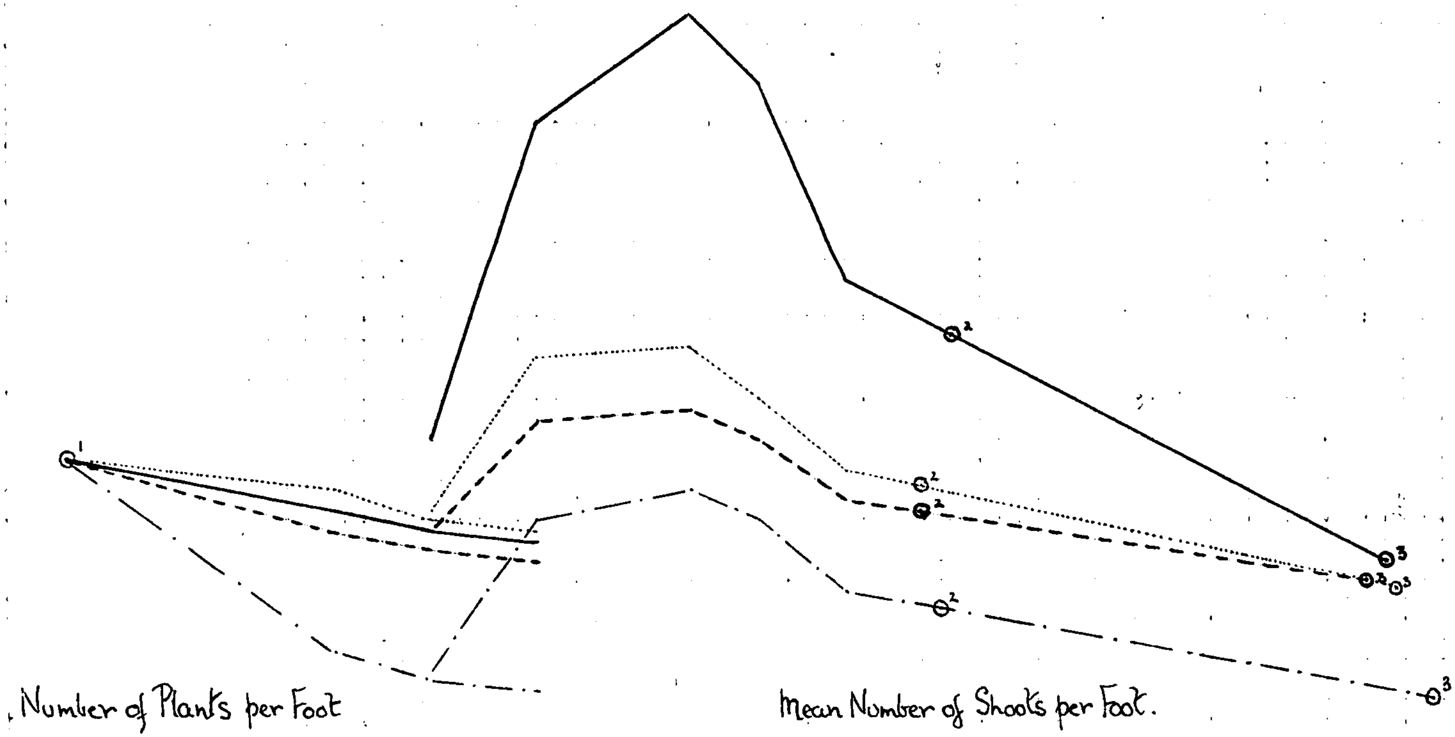
N.B. Wheat data adapted from table given by Smith (1937)

	Variance (actual data)	Variance (substituted plot)
Between varieties	260.65	17.65
Blocks	23.41	76.41
Error	395.69	215.36
Between plots	294.23	148.03

The question arises as to how far conditions in these replicated plots are comparable with ordinary field conditions. In Table III, the inter-footlength variation in both 1937 and 1938 seasons is compared with that occurring in wheat fields according to Doughty and Engledow (1928). The oat footlengths were twice as densely sown as the wheat footlengths, and the variance was correspondingly larger, but their relative variability (coefficient of variation) is of the same order. It would seem that the data are comparable as regards sowing conditions, with the exception that spacing between drill rows was 8 ins. in the case of the field sowings and 9 ins. in the case of the replicated plots.

DIAGRAM I.

A summary of shoot and panicle production in 1937, with relevant weather conditions.



	APRIL	MAY	JUNE	JULY	AUGUST.
	46·1	51·3	55·6	58·0	58·7
	+2·4	+2·4	+1·4	+0·3	+1·6

<u>Tiller and panicle production - a comparison of the four varieties from sowing to harvest.</u>

In Diagram I the relevant data are summarised. For each of the four varieties, mean number of plants per footlength, and shoots per footlength are given at different stages between sowing and harvest. Mean date of ear emergence and mean date of ripening are also shown. For each month the average rainfall and temperature are given; also the deviations from the normal monthly average.

Plant counts had to be abandoned after the middle of May owing to the rapid increase in tillering. Shoot counts were begun at the onset of tillering (beginning of May) and continued till harvest. Considering in the first place points of similarity in the behaviour of the four varieties, it can be seen that there is a decrease in plant number from sowing onwards, but that the greatest loss occurs before the commencement of tillering. As shown by the maximum shoot number attained, the peak of tiller production is reached by about the same date in each variety. <u>Perhaps the most striking point illustrated by the diagram is that in no case is the number of panicles</u>

at harvest as great as the number of plants still alive at the last plant count in May.

With regard to inter-varietal differences, the relatively low plant number of 'Victory' is accounted for by the plants lost due to bird damage in one of the plots. At the first plant count the mean plant number for the four 'Victory' plots was 33.50, but the mean of the three undamaged plots was 38.53. If allowance is made for this initial low plant number of 'Victory', it can be seen that the curve illustrating shoot production is very similar in the three varieties, 'Star', 'Victory', and 'Marvellous'. In the case of 'Potato' on the other hand, tillering is much more extensive, and the maximum number of shoots formed per footlength (June 2nd) is significantly greater than in the other three varieties. But although tiller production is greater in 'Potato', shoot survival is less than in the other varieties, so that at harvest the number of panicles in all four varieties show no significant differences.

Dates of ear emergence show insignificant differences, and the main difference in date of ripening lies between the late ripening variety 'Victory' and the other, earlier varieties. Inter-varietal

TABLE IV.

TABLE IV.

1937 season: Summary of inter-varietal differences from sowing till harvest.

	Potato	Victory	Star	Marvellous	Standard error	Varietal order
Mean plant no. (1st plant count)	40.45	33.50	41.55	39.65	4.45	S P M V
Mean maximum shoot no.	65.65	41.30	48.60	45.55	3.58	P>S M V
Mean panicle no.	38.25	31.05	36.60	36.80	3.94	P M S V
Days sowing to ear emergence	92.0	90.5	89.0	89.0	0.75	P V S=M
Days sowing to ear ripening	135.0	142.0	137.0	134.0	0.88	V>S P M

differences are summarised in Table IV. In the sixth column (Varietal order) of this table, the four varieties are arranged in order of decreasing magnitude reading from left to right. Their initial letters, P, V, S and M are used as abbreviations to represent the names of the four varieties, and significant differences (at 5%) or equality between them are indicated by the > or = sign respectively.

Since in the case of wheat much importance has been attached to tillering ability, the low shoot survival in all four varieties was rather unexpected. As the number of panicles at harvest was less than the number of surviving plants at the last plant count in May, some of the loss must have been due to whole plant casualties after that date. It was therefore important to decide which contributed most to the low panicle number: loss of whole plants or loss of tillers. The correlations presented in Table V give evidence on this point. They show clearly, that not only the number of plants tillering, but also the number of shoots lost, is proportionately greater in the low density than in the high density footlengths. Also there is a strong positive correlation between the number of plants tillering

TABLE V.

TABLE V.

The relation between plant population, tillering, and shoot loss in the 1937 season.

Correlation between:-	Correlation coefficients			
	P	V	S	M
No. of plants at last plant count (May 17th) and percentage of plants which had begun tillering at the same date.	-.9502	-.8028	-.9035	-.7544
No. of plants at last plant count (May 17th) and percentage shoot loss between maximum shoot production (June 2nd) and harvest.	-.9173	-.7884	-.8460	-.7829
No. of plants which had begun tillering by May 17th and no. of shoots lost between June 2nd and harvest.	+.7027	+.8779	+.7519	+.9360
No. of plants at last plant count and no. of panicles at harvest	+.9955	+.9995	+.9750	+.9973

(All correlations significant at 1%).

and the number of shoots lost subsequently in each footlength. These correlations together with the fact that in none of the varieties did the number of panicles exceed the number of plants surviving at the last plant count, suggest that tillers formed were for the most part lost before harvest and that panicles represented surviving main shoots. There is an alternative possibility. If whole plant casualties were high and occurred at random, there might be a tendency for more shoots to be lost from the sparsely populated footlengths, where the loss of a single plant might mean the loss of several shoots. However the high, almost perfect correlations between plant number at the last plant count and panicle number at harvest would scarcely be expected if random plant loss were the main contributing cause of shoot loss. On the other hand if tiller loss were the main factor this high correlation might be expected. Further evidence is provided by Diagram I (page 35). If the curve representing number of plants per footlength at successive stages were extra-polated, it would in the case of each variety correspond fairly closely at harvest with the observed number of panicles per footlength. Since observations in the field gave no reason to suppose any rapid increase in plant mortality after the last plant count, it would seem to be a reasonable assumption that on the average each surviving plant produced one panicle at harvest. Finally, in the most sparsely populated footlengths (about 12 plants per foot or less) direct observation was possible. In these footlengths it could be seen that in most cases all plants alive at the last plant count were still alive at harvest; that the latest formed tillers degenerated; and, that the main shoots (with occasionally one of the earlier formed tillers) produced panicles at harvest. By analogy it would be expected that in the more densely populated footlength only main shoots would survive. Since panicle number was less than plant number at the last plant count, whole plants must also have been lost from these footlengths, but this loss must have been comparatively slight.

As has been seen previously, varietal differences in tillering capacity lie chiefly between 'Potato' and the other three varieties. Since maximum tillering is reached at about the same time in all four varieties, this difference must be due to early incidence of tillering and/or rapidity of tiller formation on the part of 'Potato'. The importance of the latter is illustrated in Diagram I (page 35). Differences observed in earliness of tillering incidence were small and of doubtful significance. The greater number of tillers produced by 'Potato' was therefore due chiefly to more rapid tiller formation over approximately the same time interval.

Panicle characters in the four varieties, and their relative contributions to yield.

Since in all four varieties the majority of plants only produced one panicle each, tillering could have made no important direct contribution to plant yield. Number of panicles at harvest was determined by the number of plants surviving, which in turn was dependent to a major extent on the sowing rate and fluctuations in seed delivery from the drill. Plant adjustment to variations in amount of available food material must have been brought about almost entirely by intra-panicle variation. Before examining intra-panicle adjustment to different population densities however, it will be convenient to consider average differences between varieties as regards the manner in which yield was built up.

TABLE VI.

TABLE VI.

1937 season: Summary of inter-varietal differences in panicle characters which contribute to yield.

	Potato	Victory	Star	Marvellous	Standard error	Varietal order
Average no. of 1-grained spikelets per panicle	25.98	3.15	3.14	1.79	1.54	P>V S M
Average no. of 2-grained spikelets per panicle	0.71	13.96	10.90	10.09	1.09	V S M>P
Average no. of 3-grained spikelets per panicle	0.00	0.02	0.00	0.04	0.02	M V S=P
Average weight of 20 1-grained spikelets (gms).	0.590	0.750	0.792	0.846	0.020	M S V>P
Average weight of 20 2-grained spikelets (gms).	-	1.516	1.600	1.702	0.034	M>S V
Average weight of grains per foot-length (gms).	21.65	26.25	28.45	29.90	2.53	M S V P
Average weight per plot (lbs).	7.24	8.76	8.80	9.22	0.41	M S V>P

These are summarised in Table VI.

The table shows that although 'Potato' had on the average almost double the number of spikelets occurring in the other varieties, nearly all these spikelets were single grained. On the other hand, most of the spikelets in 'Victory', 'Star' and 'Marvellous' were two grained. Spikelets having more than two grains were rare in the 1937 season, and they were only found in 'Victory' and 'Marvellous'. The result of these differences in spikelet constitution was to give 'Victory' the largest number of grains per panicle and 'Marvellous' the least, viz:

Victory	Potato	Star	Marvellous
31.13	27.40	24.94	22.05

With regard to spikelet weight 'Potato' falls well behind the other varieties, while 'Marvellous' makes up for its lack of spikelet numbers by its heavy spikelet weight. We have therefore what appear to be alternative methods of building up panicle yield. At one extreme 'Potato' has many small single grained spikelets, and at the other 'Marvellous' has relatively few, mainly double grained, heavy spikelets. 'Victory' and 'Star' occupy intermediate positions. The net result was to give small differences in yield of grains per footlength between 'Victory', 'Star' and 'Marvellous', but a rather larger difference between these varieties and 'Potato'. Although this last difference was insignificant in the case of the sampled footlength data, it was probably real. This was supported by data available from the average weight of the four plots in each variety (determined in the routine analysis of the whole variety trial). It can be seen that the 'sample' data are in good agreement with the 'whole plot' data, and that with the lower error of the latter there is a significant difference between 'Potato' and the other three varieties.

An interesting point is illustrated in Table VI with regard to average spikelet weight. In all varieties, two grained spikelets are a little more than twice as heavy as the single grained spikelets. Since the secondary grains in a spikelet are always smaller (often considerably smaller) than the primary (basal) grain, this must mean that the primary grain of a two grained spikelet is appreciably heavier than that of a single grained spikelet. <u>Per se</u> breeding for increased yield by increasing the number of grains per spikelet would be of doubtful value, since the increment obtained in additional small grains would tend to be lost in threshing. There remains the possibility however, that increased number of grains per spikelet may in some cases be accompanied by a more than proportional increase in primary grain weight, so that in spite of the loss of additional small grains there may still be a net increase in grain yield. These considerations of course take no account of demands for milling - unevenness in grain size being undesirable from this point of view.

Of the two methods of intra-panicle adjustment to variations in population density, viz., variations in number of grains per panicle and variations in grain weight, only data from the former are available. (Spikelet weight samples were not taken separately from each footlength but only from the bulked material from each of the four plots per variety in the 1937 season). The replicated arrangement of the plots made it possible to introduce a refinement into correlations between number of panicles per footlength and number of grains per panicle, by eliminating major differences between plots. Analyses of variance and covariance are presented in

TABLE VII.

TABLE VII.

1937 season: Analyses of variance and covariance between number of panicles per footlength (p) and number of grains per panicle (g).

	D.F.	Sum of squares		Covariance	Correlation coefficient	Regression g on p
		p	g	pg		
Potato						
Between plots	3	920.95	755.59	- 552.14	-	-
Within plots and between footlengths	16	6956.80	2071.43	-2958.51	-0.7796	-0.4025
Between footlengths	19	7877.75	2827.02	-3510.65	-	-
Victory						
Between plots	3	1563.40	693.42	- 631.47	-	-
Within plots and between footlengths	16	4533.55	3099.64	-2911.60	-0.7882	-0.6422
Between footlengths	19	6096.95	3793.06	-3543.07	-	-
Star						
Between plots	3	129.60	549.52	- 91.44	-	-
Within plots and between footlengths	16	3391.20	1891.46	-1992.66	-0.7872	-0.5876
Between [illegible]	[illegible]	[illegible]	[illegible]	[illegible]		

Table VII. In all four varieties there are highly significant negative correlations between number of panicles per footlength (p) and number of grains per panicle (g). These partial correlations are of the same order in all four varieties, but their corresponding regressions (g on p) show considerable differences. On the small number of degrees of freedom available, it was not worth while attempting to analyse further these varietal differences, but the general statement may be made that with increase in number of panicles per footlength there was a tendency for a more rapid decrease in number of grains per pancile in 'Star' and 'Victory' than in 'Potato' and 'Marvellous'. 'Marvellous' in particular showed little change in number of grains per panicle over the range of plant densities studied.

2. The 1938 season.

Sowing was carried out on 25th March, - only four days earlier than in the previous season. Soil conditions however were greatly different. After heavy rainfall in the previous January (almost double the average for the month), the months of February and March were abnormally dry (less than

TABLE VIII.

TABLE VIII.

1938 season: Analysis of variance
in seedling emergence.

	D.F.	S.S.	M.S.	½ log e	'z'
Between varieties	1	529.00	529.00	3.1355	
Blocks	4	550.16	137.54	-	1.4641 (at 5%)
Error	4	113.20	28.30	1.6714	
Within varieties and between plots	8	663.36	82.92	-	
Between plots	9	1192.36	132.48	-	
Within rows and between plots	40	7972.60	199.32	2.6475	
Between rows	49	9164.96	187.04	-	0.0237 (insign)
Within rows and between footlengths	50	10461.00	209.22	2.6712	
Between foot-lengths	99	19625.96	198.24	-	

half the normal rainfall in each month). Prior to sowing high winds had dried out the recently worked soil surface, and this resulted in a very slow and uneven germination. In Table VIII an analysis of variance of seedling emergence is given. As in the previous season the varieties 'Victory' and 'Star' had occupied intermediate positions between the other two varieties in most characters studied, they were dropped from the experiment, and attention was paid in greater detail to 'Potato' and 'Marvellous'. The table shows that within each variety seedling emergence was uniform, there being no significant differences in variances within rows, or between rows of the same plot, or between plots when block differences were eliminated (= 'error' line in table). There was however a significant difference in average seedling emergence between varieties. Inspection of the data showed that 'Potato' had a higher seedling emergence than 'Marvellous'.

There were three possible reasons for this difference, - error in sowing rate, differential damage by birds, and different germination capacity of the seeds of each variety. Error in sowing rate was unlikely, since in addition to adjusting the drill aperture as previously described, equivalent numbers of seeds were sown on each plot. Owing to this checked method of sowing it was unlikely that any error in drill adjustment, or miscalculation in weight of seed sown, would have escaped notice. Damage by birds was not so marked as in the previous season, but the impression gained was that the 'Marvellous' plots were attacked more frequently than the 'Potato' plots - possibly owing to the larger sized grain of the former variety. If this were the case it would be expected that variation between the 'Marvellous' footlengths would be greater than that between 'Potato' footlengths, and that there would be more low density footlengths in 'Marvellous' than in 'Potato'. This is in agreement with observed figures:-

<u>Within rows and between footlengths.</u>

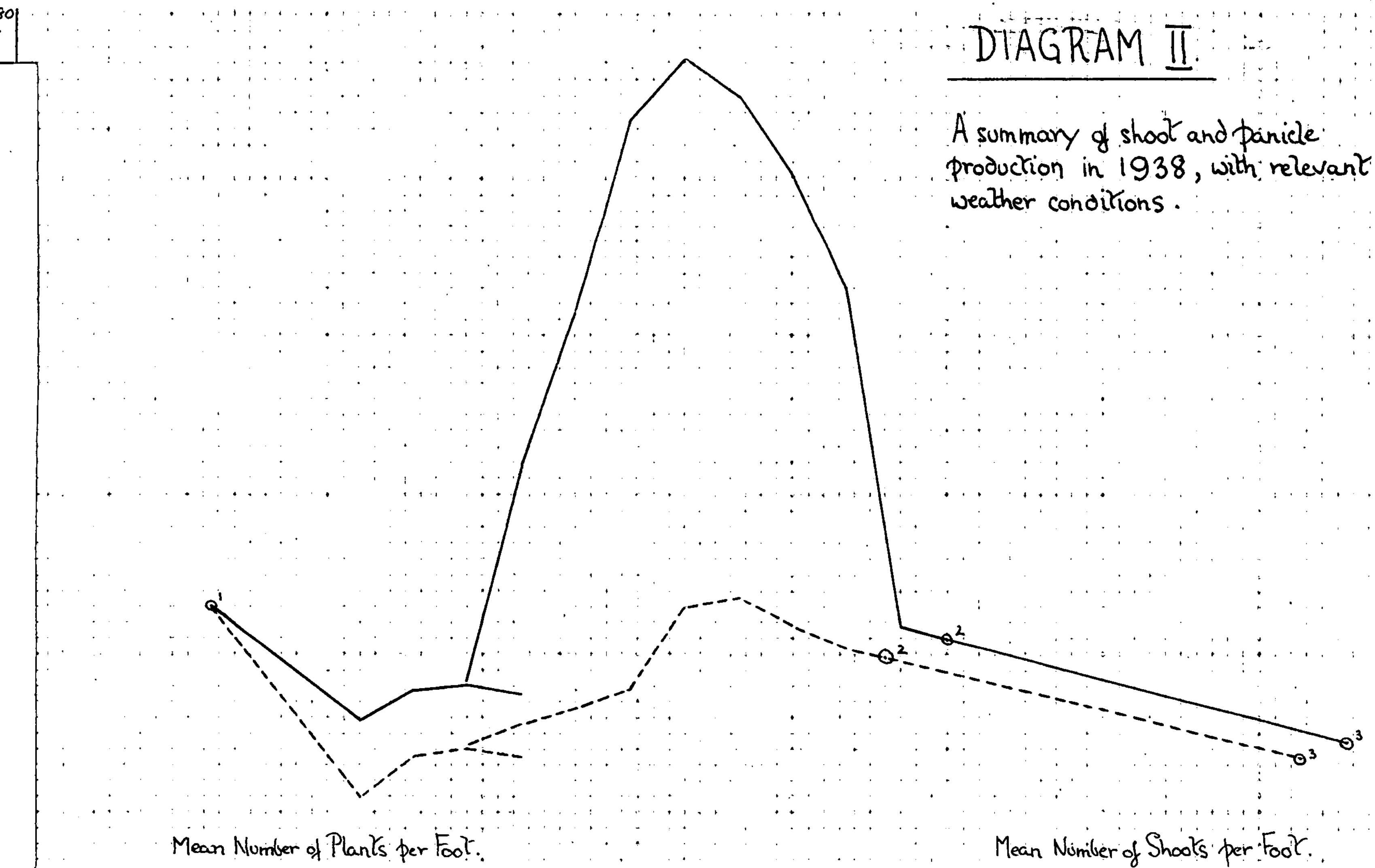
	D.F.	S.S.	Variance	$\frac{1}{2}$ log e	
Marvellous	25	6261.50	250.46	2.7617	
Potato	25	4199.50	167.98	2.5620	0.1997 (insig.)
Total	50	10461.00	-	-	

There were three 'Marvellous' footlengths with less than 10 seedlings but all 'Potato' footlengths were more densely populated. But as there was no significance in the above variation differences, it is unlikely that bird damage was sufficient to account for the low seedling emergence of 'Marvellous'. The third possibility was thought to be the chief cause - different germination capacity.

The fact that owing to drought, seedling emergence was slow and irregular, also that the plant stand was lower than in the previous season, in spite of equivalent sowing rates (see Table III, page 33) suggests that germination may not have been complete. It is known, too, that 'Potato' germinates more readily than thicker skinned varieties and is often a source of trouble during wet harvests in Scotland. It is extremely unlikely that the abnormally dry soil conditions which persisted until May prevented many of the thick husked 'Marvellous' grains from germinating. If this be accepted, the 1938 experiment may be considered a valid comparison of the two varieties, inasmuch as their sowing conditions were equivalent at the beginning of their life histories.

DIAGRAM II.

A summary of shoot and panicle production in 1938, with relevant weather conditions.



MARCH	APRIL	MAY	JUNE	JULY	AUGUST.
47·7 +7·4	46·1 +2·4	49·0 +0·1	54·8 +0·6	57·5 −0·2	57·2 +0·1
0·57 29	0·15 10	4·18 204	2·87 143	2·43 86	1·15 not available

Tiller and panicle production - a comparison with the 1937 data.

In Diagram II are summarised equivalent data to those of the 1937 season given in Diagram I (page 35). The effect of the different seasonal conditions is at once apparent in comparing the curves both for plant number and shoot number per footlength. In the 1938 season the dry sowing conditions resulted in a delayed germination, so that plant number increased up till the third plant count on 27th April. At the fourth (last) plant count plant number had fallen off again as in the 1937 season. At all plant counts plant numbers were less than in the 1937 season, which as has been seen previously, suggested that more grains failed to germinate.

The 1938 season drought in February, March, and April, was followed by heavy rainfall in May and June. In May the rainfall was over twice the normal for the month. The effect of this rainfall during the tillering period is shown by the much higher shoot production in 1938 than in 1937, in the case of 'Potato'. In 'Marvellous' maximum shoot production was less than in 1937, but the much lower plant density must be taken into account. The months of

TABLE IX.

TABLE IX.

The relation between plant population, tillering and shoot loss in the 1938 season.

Correlation between:-	P	M
No. of plants at last plant count (May 4th) and percentage of plants which had begun tillering at the same date.	-0.7581	-0.6201
No. of plants at last plant count (May 4th) and percentage shoot loss between maximum shoot production* and harvest.	-0.7927	-0.6493
No. of plants which had begun tillering by May 4th and no. of shoots lost between maximum shoot production* and harvest.	+0.8962	+0.6813
No. of plants at last plant count and no. of panicles at harvest.	+0.9603	+0.9735

* May 25th in 'Potato' : June 1st in 'Marvellous'.

All correlations significant at 1%.

July and August in 1938 were dry, so that with the exception of unfavourable conditions at sowing time, the weather in this season must have approached the ideal. The effect of this will be seen later in considering numbers and weights of spikelets per panicle.

In spite of the extensive tillering of 'Potato' in the 1938 season, the number of panicles at harvest was again below the number of plants surviving at the last plant count. In 'Marvellous' number of plants and panicles were almost identical. That shoot loss - as in 1937 - was due to degeneration of the majority of tillers is indicated by the correlations given in Table IX. These agree with their equivalents in 1937 (see Table V, page 40) although on the whole they are not so high. They are however, highly significant in all cases. (It was noticed that in the most sparsely populated foot-lengths there was a certain amount of tiller survival - probably higher than in the previous season. But this was to be expected since plant populations as a whole were lower, and especially so in the case of 'Marvellous'). In spite of conditions favourable to tillering, it is evident that in the majority of footlengths tillers made no appreciable direct contribution to panicle number at harvest.

It has been shown that in the 1937 season, amount of tillering was determined chiefly by the rate of tiller production within a time interval which is almost identical for the four varieties studied. This holds true for the 1938 season. Incidence of tillering showed no significant difference in earliness as between varieties. Maximum tillering was reached a little later in 'Marvellous' than in 'Potato' but reference to Diagram II (page 54) shows that the effect of this must have been small in comparison with the effect of inter-varietal difference in rate of tiller production. A comparison of Diagrams I (page 35) and II (page 54) suggests that the heavier May rainfall in 1938 enhanced the difference in tillering rate between the two varieties. But, allowance being made for the slightly later sowing date in 1938, there is little seasonal difference in time of tillering incidence or time of maximum shoot production. Inter-varietal differences in time of ear emergence and time of ripening are increased in the 1938 season, and though insignificant in 1937, they are markedly significant in 1938. The growing season - particularly

TABLE X.

TABLE X.

1938 season: Summary of intervarietal differences from sowing till harvest.

	Potato	Marvellous	Standard error	Varietal order
Mean plant no. (1st plant count)	35.78	31.18	1.06	P>M
Mean maximum shoot no.	77.36	43.34	1.64	P>M
Mean panicle no.	34.30	33.50	0.96	P M
Days sowing to ear emergence	95.0	87.2	0.80	P>M
Days sowing to ear ripening	146.0	140.0	0.00	P>M

in the case of 'Potato' - is longer in 1938 than in 1937. In both varieties this seems to be due mainly to a longer period between ear emergence and time of ripening, and is rather unexpected as July and August were drier than average in 1938, and wetter in 1937. Inter-varietal differences in 1938 are summarised in Table X.

Panicle characters in relation to yield.

(a) Inter-varietal differences.

Inter-varietal differences are summarised in Table XI. These may be best considered in relation to equivalent data for 1937 - (See Table VI, page 44). Varietal order is similar in both tables and will not be considered further. A marked seasonal effect is apparent with regard to yielding capacity. In both 'Potato' and 'Marvellous', number of spikelets per panicle, number of grains per spikelet, and spikelet weight are higher in the 1938 season. This was probably a direct result of the heavy rainfall during the tillering and shooting period followed by fairly dry conditions after ear emergence - a presumably ideal combination of weather conditions. In 'Potato' the majority of spikelets in 1938 as in 1937 were single grained, but in 'Marvellous' three and even

TABLE XI.

TABLE XI.

1938 season: Summary of inter-varietal differences in panicle characters which contribute to yield.

	Potato	Marvellous	Standard error	Varietal order
Average no. of 1-grained spikelets per panicle	26.07	1.98	0.78	P > M
Average no. of 2-grained spikelets per panicle	5.77	6.76	0.79	M P
Average no. of 3-grained spikelets per panicle	0.00	4.02	0.21	M > P
Average no. of 4-grained spikelets per panicle	0.00	0.15	0.09	M P
Average weight of 20 1-grained spikelets (gms).	0.613	0.980	0.007	M > P
Average weight of 20 2-grained spikelets (gms).	1.074	1.931	0.012	M > P
Average weight of 20 3-grained spikelets (gms).	-	2.930	-	M P
Average weight of grains per foot-length (gms).	29.02	36.37	0.91	M > P
Average weight per plot (lbs).	9.36	10.58	0.41	M P

four grained spikelets occurred in 1938. It would appear that the inter-varietal difference in spikelet fertility in favour of 'Marvellous' was increased in the 1938 season, although in total number of spikelets per panicle there was, if anything, a greater proportional increase in the case of 'Potato' than in the case of 'Marvellous':-

Potato	Marvellous	Season
31.84	12.91	1938
26.69	11.92	1937

On the other hand there is a greater seasonal increase in <u>spikelet weight</u> in the case of 'Marvellous' than in the case of 'Potato'. In short, it appears that 'Marvellous' reacted to the more favourable conditions in 1938 by increase in both spikelet weight and number of grains per spikelet; 'Potato' mainly by increase in the number of spikelets.

It will be remembered that in the 1937 season, two grained spikelets were a little more than twice as heavy as single grained spikelets. In 1938 they were slightly less than twice as heavy. However, as the primary grains in both varieties were markedly bigger than the secondaries, there was little doubt

TABLE XII.

TABLE XII.

1938 season: Analyses of variance and covariance between number of panicles per footlength (p) and number of grains per panicle (g).

	D.F.	Sum of squares p	Sum of squares g	Covariance pg	Correlation coefficient	Regression g on p
Potato						
Between rows	24	4226.00	4329.13	-3672.10	-	-
Within rows and between footlengths	25	3324.50	3648.17	-2131.60	-0.6122	-0.6412
Between footlengths	49	7550.50	7977.30	-5803.70	-	-
Marvellous						
Between rows	24	2091.12	2033.76	-1036.41	-	-
Within rows and between footlengths	25	5320.00	2271.05	-2740.50	-0.7888	-0.5151
Between footlengths	49	7411.12	4304.81	-3776.91	-	-

Partial correlations significant at 1%

that the primary grains of two grained spikelets were heavier than single grained spikelets in 1938 as well as in 1937.

(b) The relation between number of panicles per foot, number of grains per panicle, yield per foot, and average spikelet weight.

In Table XII analyses of variance and covariance between number of panicles per foot and number of grains per panicle are presented. As in the previous season the replicated arrangement of the plots made it possible to eliminate to some extent the effect of soil heterogeneity. The partial correlations represent the average amount of association between the two variables, when differences between rows (and plots) are eliminated. As in the previous season, they are, in both varieties significant negative correlations. The corresponding partial regressions were higher than in the 1937 season, and especially so in the case of 'Marvellous'. It would seem that in this variety the more favourable growing conditions in 1938 were responsible for a greater inter-plant competition. In 'Potato' this effect was not very marked.

TABLE XIII.

TABLE XIII.

Fitting of regression curves: yield per footlength (y) on number of panicles per footlength (p)

Potato

Regression formulae	D.F.	S.S.	M.S.	½ log e	'z'
(1) $Y = \bar{y} + a(p-p)$	1	254.54	-		
Difference	1	43.99	43.99	1.8920	0.5351 insig.
(2) $Y = \bar{y} + a(p-p)+b(p-p)^2$	2	298.53	-		
Difference	1	79.82	79.82	2.1899	0.8330 at 5%
(3) $Y = \bar{y} + a(p-p)+b(p-p)^2+d(p-p)^4$	3	378.35	-		
Difference	1	22.18	22.18	1.5495	0.1926 insig.
(4) $Y = \bar{y} + a(p-p)+b(p-p)^2+d(p-p)^4+e(p-p)^5$	4	400.53	-		
Residual	21	316.91	15.09	1.3569	
Total	25	717.44	-		

Formula used in Diagram IV --- (3)

Constants : a = + 0.462137, b = + 0.018762, d = - 0.000043

Marvellous

Regression formulae	D.F.	S.S.	M.S.	½ log e	'z'
(1) $Y = \bar{y} + a(p-p)$	1	1356.67			
Difference	1	149.03	149.03	2.5020	0.7933 at 5%
(2) $Y = \bar{y} + a(p-p)+b(p-p)^2$	2	1505.70			
Difference	1	97.18	97.18	2.2883	0.5796 insig.
(3) $Y = \bar{y} + a(p-p)+b(p-p)^2+c(p-p)^3$	3	1602.88			
Residual	22	670.86	30.49	1.7087	
Total	25	2273.74			

Formula used in Diagram IV --- (2)

Constants : a = + 0.542890, b = - 0.006290

Using a similar method of analysis, the relation between <u>number of panicles per foot</u> and <u>yield of grain per foot</u> was also determined. The following partial correlations were obtained:-

Potato	+0.5957	(significant at 1%)
Marvellous	+0.7724	(significant at 1%)

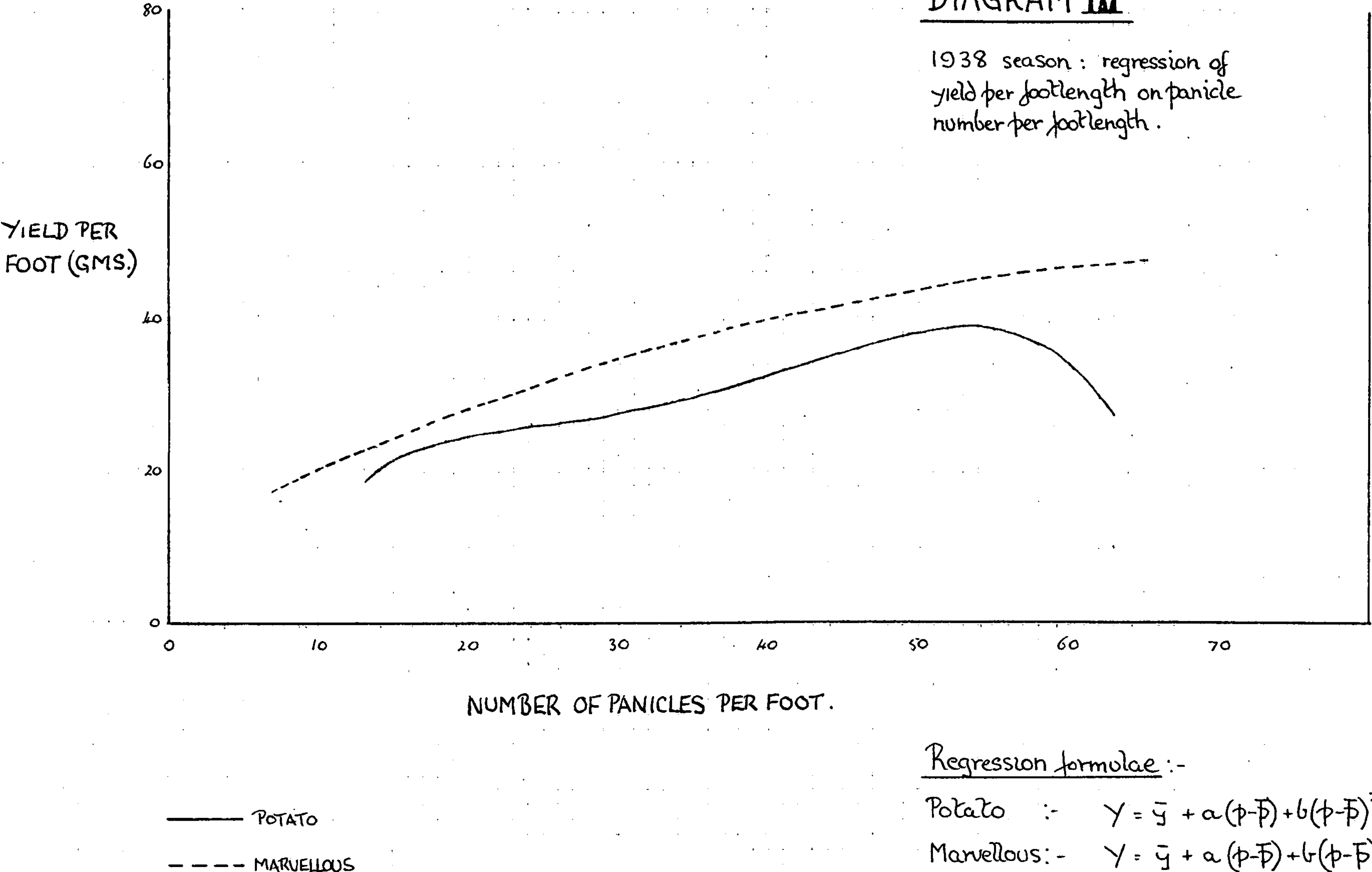
It was thought worth while to consider this association in more detail. Plotting the actual data suggested non-linear relationships between the variables in both varieties. Regression curves were therefore fitted by using polynomial equations of the form

$$Y - \bar{y} = a(x - \bar{x}) + b(x - \bar{x})^2 + c(x - \bar{x})^3$$

according to the method given by Tippett (1931 p. 155), where y is the dependent, and x the independent variable. Details of the fitting are given in Table XIII, and the curves obtained in Diagram III. In the case of 'Marvellous' equations up to the third order were calculated and the small residual obtained shows that the data were satisfactorily represented. Since the regression was not fitted to a significantly better degree by a third order than by a second order

DIAGRAM III

1938 season : regression of yield per footlength on panicle number per footlength.



Regression formulae :-

Potato :- $Y = \bar{y} + a(p-\bar{p}) + b(p-\bar{p})^2 + d(p-\bar{p})^4$.

Marvellous :- $Y = \bar{y} + a(p-\bar{p}) + b(p-\bar{p})^2$.

equation, the latter was plotted in Diagram III. In the case of 'Potato' fitting was not quite so satisfactory, as the ordinary polynomial was not found to be a suitable form. By eliminating the third (cubic) term from the general equation however, a curve was obtained which, as far as could be judged by reference to the actual data and by the analysis of variance in Table XIII (page 65), represented adequately the main trend. Equations up to the fifth order were calculated, but the regression was fitted satisfactorily by the fourth order equation.

Diagram III requires little comment. The effect of the large grain size of 'Marvellous' is shown by the fact that at all densities 'Marvellous' outyields 'Potato'. In 'Marvellous' yield increases steadily, but less and less rapidly, with increasing panicle number per footlength. In 'Potato' there is an optimum density at about 55 panicles per foot.

It might be expected that <u>average spikelet weight</u> would be affected particularly by two factors: plant spacing, i.e. the degree of inter-plant competition, and competition within each panicle. The best available estimates of these factors are <u>number of panicles per foot</u>, and <u>number of grains per</u>

TABLE XIV.

TABLE XIV.

1938 season: Correlations between number of panicles per footlength (p), number of grains per panicle (g), and weight of 20 one-grained (w_1), two-grained (w_2), and three-grained (w_3) spikelets.

	'Within row' correlations							
	D.F.	pg	gw_1	gw_2	gw_3	pw_1	pw_2	pw_3
Potato	24	-0.6122	-0.4872	+0.1220		+0.2660	-0.1218	
Marvellous	24	-0.7888	-0.1376	-0.2760	-0.0930	+0.1922	+0.1051	-0.0210

	Partial correlations						
	D.F.	$pw_1.g$	$pw_2.g$	$pw_3.g$	$gw_1.p$	$gw_2.p$	$gw_3.p$
Potato	23	-0.0467	-0.0600		-0.4255	+0.0604	
Marvellous	23	+0.1374	-0.1906	-0.3176	+0.0232	-0.3159	-0.1873

Significant correlations (at 5%) underlined.

panicle respectively. Accordingly correlations between these three characters were determined. When variation between rows was eliminated, the variation within rows in respect of average spikelet weight could be compared with the 'within row' variance previously estimated in the case of number of panicles per footlength and number of grains per panicle (see Table XII, page 63). The correlations obtained are given in Table XIV. In neither 'Potato' nor 'Marvellous' were significant correlations found between number of panicles per foot and average weight of one-grained, two-grained, or three-grained spikelets. In 'Marvellous' no significant correlation was found between number of grains per panicle and average spikelet weight, but in 'Potato' there was a significant negative correlation between number of grains per panicle and average weight of one-grained spikelets.

It was possible that the absence of correlation between plant spacing and average spikelet weight might be due to a masking effect of grains per panicle: i.e., panicle number per foot and number of grains per panicle being themselves negatively correlated might exert opposite effects on average spikelet weight. This was tested by calculating partial correlations in the usual way, (Fisher 1936 p. 189). These are also presented in Table XIV (page 69). It can be seen that when the effect of grain number per panicle is held constant in the case of 'Potato', there is still no sign of association between the other variables. In 'Marvellous' there is also no significant association, though significance is approached in the case of the negative correlation between panicle number per foot and average weight of three-grained spikelets. When the effect of panicle number per foot is held constant in the case of 'Potato', there is a significant negative correlation between number of grains per panicle and average weight of single-grained spikelets. Since the great majority of the spikelets in this variety are single-grained, it is evident that spikelet weight was affected by inter-spikelet competition within the panicle. In the case of 'Marvellous' no significant association could be found, though the negative correlation between number of grains per panicle and average weight of two-grained spikelets approached significance. To sum up - under the conditions of the experiment, average spikelet weight in 'Potato' appeared to be influenced by inter-spikelet competition within the panicle, but not by competition between plants. In 'Marvellous' there was a tendency which may or may not have been real for average spikelet weight to be affected both by competition between plants and between spikelets within the panicle.

(c) The effect of adjacent footlengths.

The regression curves in Diagram III (page 67) suggest that under the conditions of the experiment, the optimum population density for 'Potato' lay between 50 and 60 plants per footlength, since in this region the highest yielding footlengths occur. On the same basis it might be assumed that 'Marvellous' was undersown, as the regression curve shows a steady increase in yield at the highest densities.

The validity of such a conclusion has been shown by Smith to depend on the absence of competition between neighbouring footlengths and has been discussed fully in an early part of this paper. The existence of inter-footlength competition was tested critically in the 1938 season. At the fourth plant count (May 4th) the numbers of plants in the four footlengths immediately adjacent to each sample footlength, i.e.

TABLE XV.

TABLE XV.

1938 season: Correlations between number of panicles per footlength (p), number of plants in adjacent footlengths (q), and yield per footlength (y).

	'Within row' correlations			
	D.F.	py	qy	pq
Potato	24	+0.5957	+0.0695	-0.0849
Marvellous	24	+0.7724	-0.3169	+0.3371

	Partial correlations		
	D.F.	py.q	qy.p
Potato	23	+0.6052	+0.1500
Marvellous	23	+0.9846	-0.9654

Significant correlations (at 5%) underlined.

two in neighbouring, and two in the same row, were also counted. The average plant number (q) of the four adjacent footlengths was used as an estimate of the effective density of the surrounding plant population. In order to test the relative effects of the plant density of sample footlengths (p), and plant density of adjacent footlengths (q) on yield per sample footlength (y), the direct correlations, py, qy, and pq, were calculated. Now if the adjacent footlength densities have any appreciable effect on yield, the partial correlation, qy.p should be negative and significant. The actual correlations obtained are shown in Table XV. As in previous calculations, all correlations were based on 'within row' variance (cf. Tables XII, page 63, and XIV, page 69).

Table XV shows clearly that there is a marked varietal difference with regard to competition between neighbouring footlengths. In 'Potato' the partial correlation (qy.p) is quite insignificant and actually has a positive instead of a negative value. In 'Marvellous' the partial correlation qy.p is negative and very high. It is, in fact, of the same order as the partial correlation py.q which indicates that in this variety, footlengths are by no means independent. These results imply that 'Marvellous' has a greater power of tapping the soil resources than 'Potato' - either because it possesses a greater root range, or because its root system has a superior capacity for absorbing soil nutrients. In the light of Smith's hypothesis (1937) it was of interest to discover whether both densely and sparsely populated footlengths were affected by adjacent footlength competition. Accordingly in 'Marvellous', densely and less densely populated footlengths were considered separately, and the relative effects of p and q on y were estimated. This was done by selecting two sets of footlengths, (1) above 40 plants per foot and (2) below 30 plants per foot. For each set the partial regressions py.q and qy.p were calculated. They were as follows:-

Density of 'p' footlengths	No. of 'p' footlengths	Partial Regressions py.q	Partial Regressions qy.p
Above 40 plants per foot	13	+0.4863	-0.5697
Below 30 plants per foot	16	+1.1371	-0.4845

The regressions show clearly that both sets of 'p' footlengths were affected by the density of the adjacent footlengths, 'q'. But while the yield of the 'above 40' footlengths was about equally affected by unit changes in p and q, the yield of the 'below 30' footlengths was dependent mainly on p.

The effect of inter-footlength competition may now be considered in connection with the regression curves in Diagram III (page 67). In 'Potato' since footlengths have been shown to behave as independent units, the falling off in yield at densities above 55 panicles per footlength is evidence that in this variety local over-populated areas existed which were unable to take advantage of adjacent less dense areas. It would seem that in this variety uniformity in sowing would be more important that in a variety which had a greater effective root range. Under the conditions of the experiment, footlengths with less than 45, or more than 55 plants per foot represented a loss of potential yield. Not only a higher, but also a more uniform sowing would have been necessary to exploit to the full the available soil resources. Quite apart from changes in sowing rate, a decrease in distance between the drill rows might be expected to bring more soil within the root range of the plants. Too wide a spacing between the drill rows results in the paradox of over-populated footlengths in an under-sown crop.

In 'Marvellous' apparently, the available soil resources were much more fully, if not completely exploited. If the sample footlengths had been surrounded by footlengths of the same density it is likely that the regression curve in Diagram III (page 67) would run almost horizontally at densities of above 40 panicles per foot. At the lower densities the regression curve would also tend to be flattened out, but not completely so, since as plant density decreased y would tend to become more dependent on p and less dependent on q. In other words if the effect of adjacent footlengths could be omitted, y would only be dependent on p at the lower densities.

It must be concluded then that neither of the varieties gave complete support to Smith's hypothesis that average yield is independent of plant population. In the case of 'Potato' inter-footlength competition did not occur, and accordingly average yield was determined by the yields of the <u>independent</u> footlengths. Within each footlength yield was largely dependent on the plant population. In the case of 'Marvellous' the data as a whole showed that competition existed between footlengths. Further analysis suggested that the yield of a more densely populated footlength was about equally and oppositely affected by changes in plant densities within and around the footlength. This would indicate that a state of equilibrium existed between densely sown footlengths and their neighbours, and that average yield would be little affected by changes in plant numbers. On the other hand, the yield of a less densely populated footlength was influenced more by changes in plant number within the footlength than by changes in density of the surrounding areas. Below a certain density therefore, lack of plant numbers could not be completely compensated by increased development of plants in the surrounding areas, and increase in plant numbers in these foot-lengths would be expected to increase average yield. In fact the evidence obtained from this variety is in agreement with Smith's hypothesis only in so far as the more densely sown footlengths are concerned.

III. Developmental studies.

1. General developmental plan of the oat plant.

The object of these studies was to observe any inter-varietal differences in the developmental plan of individual plants and to relate any such differences to those occurring in the behaviour of varietal populations. The development of the individual cereal plant has been studied rather fully by several workers, Engledow and Wadham (1923), Hudson (1934), Bonnett (1935-7). Since the present studies gave general agreement with these previous findings, it will only be necessary to summarise the main features of the course of development before dealing with inter-varietal comparisons.

There are three phases in the development of the oat plant which occur in orderly succession:-

(1) Tiller production.

(2) Production of spikelets.

(3) Production of florets within each spikelet.

During the second and third phases, elongation of the stem internodes ('shooting') takes place, and at the close of the third phase flowering begins. Within each phase there is an orderly sequence in production of the various organs; e.g. in phase 1 the earliest formed tiller occurs in the axil of the first formed leaf on the main stem; in Phase 2 the earliest formed spikelet is the apical spikelet of the main axis panicle; and in Phase 3 the earliest formed floret is the basal floret in the apical spikelet. In other words the earliest formed organ, if uninjured, retains its leadership through all stages of development.

Within each phase there is an over production of organ initials. For example, in Phase 1 more tiller buds are formed than the plant can subsequently nourish. With the onset of Phase 2 there is apparently a diversion of the plant energies from the formation of tiller buds to the production of spikelet initials, so that the tiller production phase comes to a close. From analogies with similar phenomena occurring in other plants, it would seem likely that this diversion is due to competition for food materials between tiller bud initials and the newly formed spikelet initials. In this competition first choice of the food materials goes to the spikelet initials so that further production of tiller buds is inhibited, (cf. Mason 1922, Pearsall 1923, Murneek 1926). That the tiller buds are under intense competition is shown by the fact that with the onset of spikelet production not only is further tiller bud production inhibited but growth of tillers already formed is checked. Only the earlier formed tillers survive and in fact there is an orderly degeneration of the later formed buds - the latest formed being the first to degenerate. This was observed both in 1937 and 1938.

A similar competition effect occurs in Phase 3. Up to eight florets were formed in the apical spikelet of the main axis panicle, but the later formed ones degenerated in reverse order to their order of formation and only 2 - 3 florets persisted until the flowering stage.

Bonnett (1937) stated that the oat panicle is a determinate inflorescence, which would imply that the number of spikelets per panicle would remain fairly constant in each variety, and that variation would be restricted to the number of florets per spikelet. However although the number of spikelets formed may be constant for each variety, the present results give indirect evidence that the number surviving is a variable quantity. It has been shown in a previous section that the increased yield of 'Potato' in the 1938 season as compared with that of the 1937 season was due chiefly to seasonal variation in the total number of spikelets per panicle. Seasonal variation in this respect was also shown by 'Marvellous'. Degenerate spikelets are frequently found at the base of oat panicles after ear emergence, and it would seem likely that in Phase 2 (spikelet production) there is also a competition between spikelets with the resulting tendency for the degeneration of those latest formed.

2. <u>Inter-varietal differences.</u>

In the 1937 season a preliminary examination was made of the four varieties 'Potato', 'Victory', 'Star' and 'Marvellous'. The examination was not designed to obtain a quantitative comparison of the four varieties, but only to furnish an idea of inter-varietal differences with a view to further study. Only ten plants of each variety were examined at each stage and notes were taken of the relative development of the plants in each variety. It will be remembered that the plants in this season were obtained from plots in which all plants were evenly spaced. Probably due to this even spacing it was found that remarkably little variation existed at each stage

TABLE XVI.

TABLE XVI.

1937 season: Development of the main axis during the tiller production phase in four oat varieties. (Sown 12.4.37).

Date	Number of leaves formed				Total number of buds formed				Number of buds developing				Number of inter-nodes elongating			
	P	V	S	M	P	V	S	M	P	V	S	M	P	V	S	M
3.5.37	3	3	3	3	-	-	-	-	-	-	-	-	-	-	-	-
14.5.37	7	7	7	6	3	3	3	2	2	2	2	1	-	-	-	-
24.5.37	9	8	8	8	5	3	3	3	4	2	2	2	-	3	3	3
29.5.37	9	8	8	7	5	4	4	3	4	3	3	2	-	3	3	3
5.6.37	9	8	8	7	6	4	4	3	3	3	3	3	4	4	4	4
14.6.37	9	8	8	7	5	4	4	3	5	4	4	3	6	6	6	6

between plants of the same variety. Marked varietal differences were exhibited which were confirmed in the following season in a more precise examination. It was therefore considered worth while to summarise the results (see Tables XVI and XVII).

Table XVI summarises inter-varietal differences in the first phase of development. 'Star' and 'Victory' showed no appreciable differences, and together occupied a position intermediate between 'Potato' and 'Marvellous'. 'Potato' produced more leaves and tiller buds on its main axis than did 'Marvellous', and also more of its tiller buds continued to develop. There was a marked difference in the time at which the tiller production phase was concluded. In 'Potato' maximum tiller bud production was reached by June 5th, and at about the same time there was a rapid elongation of the stem internodes which marks the onset of the second phase of development. In 'Marvellous' maximum tiller bud production was reached 1 to 2 weeks earlier - this also coinciding with the beginning of internode elongation. In 'Marvellous' then, it appears that the first stage of development was restricted, and that the second phase was initiated relatively early.

TABLE XVII.

1937 season: Summary of panicle development in four oat varieties. (Sown 12.4.37.)

Date	Potato	Victory & Star	Marvellous
3.5.37	Panicle initial undifferentiated.	Panicle initial undifferentiated.	Panicle initial undifferentiated.
14.5.37	Panicle initial elongating.	Panicle initial elongating. Transverse ridges formed.	Panicle initial elongating. Transverse ridges formed.
24.5.37	Transverse ridges formed.	Primary panicle branches formed.	Primary panicle branches formed.
29.5.37	Primary panicle branches formed	Floret differentiation beginning in apical spikelet. Glumes extend around florets.	Floret differentiation beginning in apical spikelet. Glumes extend around florets.
5.6.37	Floret differentiation beginning in apical spikelet. Glumes extend around florets.	Apical spikelet not completely enclosed by glumes. 5 florets present in apical spikelet. Anthers differentiated in basal floret.	Apical spikelet completely enclosed by glumes. 6 florets present in apical spikelet. Anthers differentiated in basal floret.
14.6.37	Apical spikelet completely enclosed by glumes. 6 florets present in apical spikelet. Anthers differentiated in basal floret.	Apical spikelet completely enclosed by glumes. 6-7 florets present in apical spikelet. Bi-lobed stigma distinguishable in basal floret. Paleae do not completely enclose basal floret. Spikelet stalks elongating	6 florets in apical spikelet. Bi-lobed stigma distinguishable in basal floret. Paleae completely enclose basal floret. Spikelet stalks elongating.
17.6.37	6 florets present in apical spikelet. Younger florets not yet degenerating.	7 florets present in apical spikelet. Younger florets not yet degenerating.	3 florets remain in apical spikelet: remainder degenerated.

At all stages the developing panicle of 'Marvellous' was larger than those of 'Victory' and 'Star' on the same date. 'Victory' and 'Star' showed no marked difference in panicle size. Size of panicle in 'Potato' was much less than in the other three varieties.

In Table XVII differences in the second and third phases of development are compared. Again no differences could be observed between 'Star' and 'Victory'. As in the first phase, they occupied an intermediate position between 'Potato' and 'Marvellous'. In comparing the latter varieties it can be seen that apart from differences in size of panicle initials which were well marked at each stage, 'Marvellous' was about a week ahead of 'Potato' in degree of panicle development. It has been shown in a previous section that there was no significant difference between varieties in time of ear emergence in 1937, so it would appear likely that 'Potato' passed through and completed the same stages of development as 'Marvellous' during a shorter period of time.

In 1938 examination was restricted to the two varieties which exhibited most contrast in 1937 - 'Potato' and 'Marvellous'. A more thorough examination was carried out, twenty plants of each variety being examined at each stage. These were selected at random from plots drilled at the same rate as the plots used for population studies in the same season. As expected the results showed more variability than those obtained in the previous season from evenly

TABLE XVIII.

TABLE XVIII.

1938 season: Development of the main axis during the tiller production phase in 'Potato' and 'Marvellous'. (Sown 30.3.38).

Date	Number of leaves formed		Total number of buds formed		Number of buds developing		Number of inter-nodes elongating	
	P	M	P	M	P	M	P	M
5.5.38	6.50	6.00	2.70	2.65	1.40	0.55	-	-
13.5.38	7.25	6.85	3.05	3.00	2.35	0.70	-	3.00
20.5.38	8.00	7.00	4.05	3.00	2.10	1.10	-	5.00
27.5.38	7.94	6.70	4.19	2.85	1.81	1.45	4.81	4.85
6.6.38	7.70	6.10	4.15	2.95	1.45	0.95	5.75	5.05
13.6.38	7.25	6.15	3.80	2.80	1.45	0.85	6.25	5.15

TABLE XIX.

1938 season: Summary of panicle development in 'Potato' and 'Marvellous'. (Sown 30.3.38).

Date	Potato	Marvellous
5.5.38	Panicle initial shows transverse ridges.	Primary branching commenced in panicle initial.
13.5.38	Primary branching commenced in panicle initial.	Spikelet differentiation beginning. Apical spikelet differentiated into glumes and florets. Outer and inner paleae of basal floret distinguishable.
20.5.38	Spikelets differentiated. Florets developing in apical spikelet.	Glumes surround apical spikelet. Apical spikelet has 5 to 6 florets. Anthers distinguishable in basal floret.
27.5.38	Glumes surround apical spikelet. Apical spikelet has 5 florets, anthers forming in basal florets.	Glumes completely enclose apical spikelet. Stalk of apical spikelet elongating. Apical spikelet has 7 florets. Basal floret partly enclosed by paleae. All organs in basal floret differentiated. Stigma bifid.
6.6.38	Glumes completely enclose apical spikelet. Stalk of apical spikelet elongating. Apical spikelet has 6 florets. Basal floret partly enclosed by paleae. All organs in basal floret differentiated. Stigma bifid.	Apical spikelet has 7 to 8 florets. Basal floret completely enclosed by paleae. Apical floret undifferentiated.
13.6.38	Apical spikelet has only 2 to 3 florets remaining, the rest having degenerated.	Apical spikelet has only 4 florets remaining (4th floret degenerating). Basal floret has green stamens and horns of stigma hairy.

As in the previous season the panicle of 'Marvellous' was markedly larger than that spaced plants. They are summarised in Tables XVIII and XIX. The main varietal differences are in agreement with those found in the preliminary experiments. Table XVIII shows that as in 1937 more vegetative parts (leaves and tiller buds) were produced by 'Potato' than by 'Marvellous', and that the tiller production phase was brought to a close about a fortnight earlier in 'Marvellous' than in 'Potato'. Internode elongation though commencing later in 'Potato' than in 'Marvellous' was carried out much more rapidly. More internodes had elongated at the time of the last examination (June 13th) than in 'Marvellous' in spite of a later start. The impression gained from the previous season's data, that the varieties differed in the relative proportion of the growing period which was occupied by the first phase of development, was therefore confirmed.

Table XIX agrees well with the corresponding table for the previous season (Table XVII, page 85). In the early stages 'Potato' was about a week behind 'Marvellous' in degree of panicle development. In the later stages the 'Potato' panicle developed more rapidly, and at the last examination (June 13th) had reached a similar degree of development to 'Marvellous'.

At this stage in both varieties degree of panicle development did not differ appreciably from that found at ear emergence. Ear emergence occurred about a week later in 'Potato' than in 'Marvellous' (see Table X, page 59). This was apparently due to the production of more internodes on the main axis by 'Potato' than by 'Marvellous' in 1938.

DISCUSSION.

In the first section of this paper attention has been drawn to three lines of enquiry which should prove to be of interest in connection with cereal breeding technique. The results obtained from the population and developmental studies here reported can now be considered in relation to these enquiries.

1. Competition between adjoining footlengths in a drill sown crop.

Smith's hypothesis that yield is to a large extent independent of variations in plant population, rests on the assumption that over the range of densities normally occurring in a cereal crop, there is an intense competition between adjacent footlengths in addition to local inter-plant competition within each footlength. This assumption may be justifiable in the case of wheat which is known to have a wider root range than oats or barley. That it cannot be accepted universally is indicated by the present experiment. The results obtained in the 1938 season show that the intensity of competition between adjoining footlengths may show wide differences even between varieties of the same cereal (oats). In

'Potato' inter-footlength competition was insignificant, and it was therefore to be expected that both average sowing rate and uniformity of plant distribution within the sown area, would be important factors in determining average yield. In 'Marvellous' the situation was more complex. Above a certain plant density, average yield was apparently independent of local variations in plant population. This did not hold for the less dense areas. Here although competition still occurred between adjacent footlengths, the data suggested that an increase in plant number would result in a net increase in average yield. A complete independence of plant population would only be expected when all footlengths possessed above a certain minimum of plants, and this state of affairs was not realised under the conditions of the experiment.

In 'Potato' the effective root range appears to be less than in 'Marvellous', and consequently adjustment to variations in plant density is less successful. Under the conditions of the experiment 9 ins. distance between drill rows was too great. As there was no competition between drill rows, it must be concluded that the space between the rows was incompletely exploited. A more even and higher rate of sowing would also have been desirable. The average number of plants per foot in 1938 was 35.78, but as shown in Diagram III (page 67), the optimum density lay between 45 and 55 plants per foot.

In 'Marvellous', although average yield was not completely independent of plant population, the latter appeared to be relatively unimportant. The root range in this variety was sufficient to bring about considerable adjustment to variations in plant density. However a more even spacing of the plants would have been desirable, as this would have increased the number of plants in the less densely populated footlengths, i.e. those footlengths which were responsible for reducing the potential yield.

The high power of adjustment to variations in plant density found in 'Marvellous' raises an interesting point in connection with plant breeding practice. If highly bred oat varieties (of which 'Marvellous' may be considered more typical than 'Potato') are to a large extent independent of variations in sowing rate, it implies that they are able to utilise fairly completely the available soil resources. (If this were not the case, higher rates of sowing should produce increased yield instead of increased competition between plants). The replacement of such varieties by still more vigorous types will only lead to the tapping of the <u>same</u> soil resources by fewer plants, with the result that lower sowing rates will be sufficient to obtain the same yield. From considerations of yield alone it is difficult to see any advantage in such a replacement. On theoretical grounds it would appear to be a sounder practice to select individual plants, in the early stages of breeding, on the basis of economy in grain production rather than on general vigour. This might be expressed as the ratio:

$$\frac{\text{Grain yield per plant}}{\text{Total vegetative material per plant.}}$$

or more conveniently,

$$\frac{\text{Grain yield per plant}}{\text{Maximum tillers produced per plant.}}$$

Some support for such a procedure is given by the fact that high yielding oat varieties of to-day have high values of the above ratio.

2. Index of yielding ability.

In neither of the varieties and in neither the 1937 nor 1938 seasons did tillering have an appreciable effect on yield. The majority of plants surviving till harvest produced only one panicle. Adjustment to variations in plant density was brought about mainly by variation in numbers of spikelets per panicle and numbers of grains per spikelet. In 'Potato' the most important adjustment appeared to be variation in number of spikelets per panicle; in 'Marvellous' variation in number of grains per spikelet. A possible reason for this inter-varietal difference is given by the developmental studies in the same seasons. Competition within the plant leads to a retrogressive degeneration of the later formed organs. In 'Marvellous' the plant energies were diverted from tiller production to panicle development at a comparatively early stage. It might therefore be expected that competition within the panicle of this variety would be less intense than in 'Potato' where panicle development began later, and a greater proportion of plant energies had been occupied with tiller production. In 'Marvellous' intra-panicle competition would lead to an orderly degeneration of the latest formed florets in the spikelets. In 'Potato' more intense competition would lead not only to degeneration of the younger florets but also to elimination of whole spikelets.

Spikelet weight was little affected by plant competition, and its importance as an index of yielding ability was shown by the fact that this character enabled 'Marvellous' to outyield 'Potato' at all densities. Its lack of variability also contributes to its usefulness as an index of practical value.

The failure of tillering to have any appreciable direct effect on yield was perhaps surprising in view of the importance attached to this character by wheat breeders. It is a common belief too in agricultural circles, that thin rows of a cereal crop will 'thicken' and so give a fair yield at harvest. The present results indicate that in oats at least, the excessive tillering of the thin rows is only a transitory response, and that compensation at harvest is due to increase in size of panicle. Bell (1937) and Hunter (1938) working with barley came to the conclusion that the most important index of yield was number of tillers surviving till harvest (high ear survival). The present results are in direct variance with this conclusion. Since both oats and barley are spring sown crops there would seem to be no *a priori* reason for such a fundamental difference in reaction to environment. Their work however was carried out on small nursery plots of evenly spaced plants. The plants were spaced at 6 ins. x 2 ins. corresponding with a plant population of 522720 per acre. This is rather less than one quarter of the average plant population occurring in these studies, (between 2 and 2½ million in round figures). The difference between results is probably due therefore to the difference between sowing rates employed. Which of the sowing rates is most typical of general agricultural conditions is open to question. The sowing rates employed by Bell and Hunter would, in agricultural practice, be rather low by English standards, while the high rate used in the present experiments may be considered fairly typical for the Lothians. There would seem to be a need for census studies of field crops of oats and barley, of the same type as those used by Engledow and other workers with wheat crops.

Although tillers made no direct contribution to yield by producing panicles at harvest, there remained the possibility that they might have an indirect effect by nourishing the main axis. This was suggested by the work of Dungan (1931) who found in maize that the main stalk when its leaves are removed, can receive nourishment from the tillers. On the other hand, Tincker and Jones (1931) have shown that the effect on the main axis of removing tillers in two oat varieties depended on the stage at which they were removed. 'Developmental' tillers (tillers which had not yet begun assimilation) competed with the main axis for food materials. Thus their removal tended to increase the growth of the main axis. Removal of 'vegetative' (assimilating) tillers had little effect on the main axis, except where the plants were widely spaced (8 ins.) and where removal was delayed until a later stage. At the closest spacings (1 in.) removal of neither developmental nor vegetative tillers had much effect on the growth of the main axis. Hunter (1938) found that removing tillers at various stages increased 1000 grain weight and nitrogen content of the grain in the main axis.

In the 1938 season a small experiment along the same lines was designed. 'Potato' and 'Marvellous' had all tillers removed at two stages: (1) onset of tillering and subsequently, (2) maximum tillering and subsequently. The plants were spaced at 2 ins. x 9 ins. in small replicated plots. Unfortunately, weighings could not be completed before the writer left Edinburgh, so that the experiment had to be abandoned. Observations at harvest gave the impression that the main axis panicles of the treated plants were in no way inferior to those of the controls. In 'Marvellous' there were signs of a compensatory effect - several panicles of the treated plants having occasional 5-grained spikelets.

The balance of the evidence is therefore in favour of a small amount of competition between main axis and tillers, especially in the early stages of growth. Under normal conditions of growth it seems unlikely that the main axis derives any appreciable nourishment from the tillers though when the main axis is damaged an outburst of tillering results. This relationship between main axis and tillers would be expected from the results of the developmental studies described in the previous section. At the close of the tillering phase, there was an orderly retrogressive degeneration of tiller buds commencing with the latest bud formed. It would seem that main axis and tillers are in a state of 'ordered competition', the earliest formed organ (main axis) having the first choice of food material, and the last formed (youngest tiller) being the first to be restricted in food supply. The removal of a tiller might be expected to have an effect proportional to its earliness of formation.

It must be concluded that in neither of the two seasons did tillering have an appreciable direct or indirect effect on yield. Its value to the plant under the conditions of the experiment must have been as a reserve in case of damage to the main axis, or in producing extra panicles in the extreme case where the plant population was so thin that the plants had room for unrestricted development. The important indices of yielding ability were average grain weight and number of grains per panicle. The proportion of grains which occurred in one-grained, two-grained etc., spikelets was only of secondary importance, since increase in number of small grains per spikelet (tending to lower average grain weight) was accompanied by increase in weight of the large basal grain. As a result of this association, average grain weight per spikelet tended to remain constant. It would be unwise to draw general conclusions from the results of only two season's experiments, but as they stand the data suggest strongly that the main axis panicle of the oat plant may be a better unit for selection purposes than the whole plant itself.

3. Interactions of plant characters which influence yield.

A review of the relevant literature suggested a tendency for number of ears per plant and yield of grains per ear to be alternative. This is supported by the experimental data in 1937 and 1938. The chief differences between varieties lay not in the total time available for the development of the various organs (e.g. from onset of tillering until ear emergence) but in the proportion of that time occupied with tiller and spikelet production, and the relative rates at which these organs were produced. In both seasons maximum tiller bud production coincided with the beginning of internode elongation, - the second phase (panicle development) following the first phase (tiller production) in orderly sequence. In 'Potato' the first phase was characterised by rapid tillering extending over a relatively long period of time. Consequently the time available for the second phase was restricted, and its various stages were passed through more quickly than in 'Marvellous'. In 'Marvellous' rate of tiller bud production was much slower, and the second phase commenced earlier, so that more time was available for panicle development. It would seem that increase in panicle size can only be obtained at the expense of number of tillers produced, and vice-versa, unless in some way the total period available for growth can be extended, or the metabolism of the whole plant accelerated. With regard to the former possibility, there is every indication that the length of the growing period is photo-periodically controlled. (Purves 1934, Purvis and Gregory 1937). The latter possibility remains to be explored.

The relation of grain weight to the other characters is not very clear. Smith (1935) found a close positive correlation between average grain weight and number of grains per ear. On the other hand, Bridgeford and Hayes (1931) found that plumpness of grain was negatively correlated with number of grains per ear and positively with number of ears per row.

The data from the 1938 experiment were in agreement with this, although the correlations were for the most part insignificant.

On theoretical grounds it would scarcely be expected that there would be a simple relationship between plant density and grain weight (or spikelet weight). Developmental studies have shown that intra-plant competition exists in addition to competition between plants, this having been discussed previously. The work of Boonstra (1936) and Watson and Norman (1939) has shown that a considerable proportion of the plant's dry weight (including grain yield) is added after ear emergence, and indeed by photosynthesis of the ear itself. At this stage the absorption of food materials from the soil (with the possible exception of phosphates) has drawn to a close, (Berry 1920 , Watson 1936) so that competition between plants would be expected to be of decreasing importance. It might be expected that competition between plants, and competition within each plant might act in some degree as independent limiting factors to grain development.

An attempt to separate the effects of these factors was made in the 1938 season by calculating the partial correlations: panicle number per foot and average spikelet weight, grain number per panicle and average spikelet weight. The results obtained were inconclusive, but suggested a tendency for spikelet weight to be negatively associated both with plant density and number of grains per panicle.

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