ROTHAMSTED RESEARCH

Rothamsted Experimental Station Report for 1973 Part 2

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P. J. Welbank, M. J. Gibb, P. J. Taylor and E. D. Williams (1974) *Root Growth of Cereal Crops ;* Rothamsted Experimental Station Report For 1973 Part 2, pp 26 - 66 **- DOI: https://doi.org/10.23637/ERADOC-1-34632**

Root Growth of Cereal Crops

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Introduction

Studies of the growth of crops in the field have long been a major part of the work of the Botany Department at Rothamsted. This involves periodic sampling of crops growing under different experimental treatments and detailed measurement of numbers and dry weights of various parts of the plants, leaf areas, etc. From the data useful deductions can be made about attributes of the crop that contribute to final yield.

Before 1965 storage roots such as those of sugar beet were measured and in some experiments a part of the fibrous roots were dug or pulled up and included in dry matter measurements, but generally little attention was paid to the absorbing roots of the crops, either as functional organs, or as components of dry matter yield. It was difficult to measure the growth of roots in the same detail as growth of parts above ground. Work to rectify this omission began at Rothamsted in 1965. Its first objectives were to collect basic information on the rates of growth and distribution in the soil of the roots of crops. This would permit not only an assessment of the contribution of roots to the total dry matter of the crop, but also deductions about the possible effects of the size and form of root system on its overall growth. Later the work could be extended to study relationships between root growth and uptake of nutrients and water. Root measurement may also be required to determine whether factors, such as experimental treatments, pests, diseases, environmental conditions, etc., known to influence the overall growth of a crop, do so predominantly because of their effect on growth or distribution of roots. This paper reports chiefly the physical (dry weight and length) data on roots, and on the above-ground parts with which they were associated. It is confined to work on cereals. Few measurements have yet been made on other crops, many of which pose special sampling problems.

Site and soil

To facilitate soil core sampling, all the experiments described here were done at Woburn Farm in Stackyard Field. The soil, light sandy-silty loam of the Cottenham series or the very similar colluvial soil of the Stackyard series, has few stones and overlies loose sandy substrata extending below sampling depth, which are unlikely to obstruct root penetration. Although it has a tendency to form a pan at plough-sole depth, no evidence was found that root growth in our experiments was obstructed by any compacted layer. The root distributions, therefore, were probably typical of what might be found in a homogeneous and easily penetrable soil.

To facilitate cleaning the root samples, experiments were sited on land which had been fallowed for from two to five years to allow residues of previous crops to decompose.

Methods

Root sampling. To parallel the periodic samples of the above-ground parts of a crop used for growth analysis it is necessary to sample the roots growing in the soil beneath small known areas of the crop. We customarily sample shoots from areas of 0·5 to 2·0 m^2 per experimental plot, but as roots may penetrate below 1 m, sampling roots from

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https://doi.org/10.23637/ERADOC-1-8

an equal area could mean handling from 0·7 to 3·0 tonnes of soil per sample. It was therefore necessary to sacrifice some precision by greatly decreasing the area of plot sampled for roots. To permit the soil samples to be representative of the area from which shoots were sampled it was early decided to take several smaller soil samples from different positions within the area rather than a single large one.

Several different methods of sampling soil and roots were investigated.

A motor driven soil auger approximately 10 cm in diameter was used to produce loose soil samples. By digging to successively greater depths samples from different soil layers could be obtained. However, the volume of soil excavated was uncertain because the radius swept by the cutter was not well controlled and it was difficult to ensure that deeper layers were not contaminated by soil and roots from above. The need frequently to remove the auger from the hole for cleaning also made it a rather slow method and it would be quite unsuitable for strong soils.

As well as a simple soil auger, a motorised hollow auger was investigated in which an outer tube carries cutters and auger flights and rotates about a free central tube in which an undisturbed core of soil is collected. A successful machine of this type to cut undisturbed cores 15·0 cm in diameter is made by Proline Industries Pty. Ltd., Croydon Park, South Australia, but was considered too large and cumbersome for our purposes. The smaller portable design cutting 7·6 cm diameter cores tested for root sampling was less satisfactory. It was difficult to force the auger down into the soil and the core produced was somewhat irregular, apparently because stones forced the auger off-course.

A third method tested attempted to combine the processes of soil coring and washing roots free of soil by using water jets acting inside a 7·5 cm diameter soil coring tube and near its cutting edge to wash away the soil and roots from within the tube. The water, soil and roots were collected as they overflowed the top of the coring tube, and passed through a sieve to retain the roots. However, it was difficult to provide the large volumes of water at high pressure needed to operate this system on remote sites, and to prevent the water leaking round the outside of the coring tube. It would probably also have been impossible to determine sufficiently precisely the depth from which roots were extracted.

Soil core sampling. The sampling procedure eventually adopted as a routine used coring tubes hammered into the soil to cut cores of known cross-section to depths depending on the depth of root penetration, up to a maximum of approximately 1 m. While this was not deep enough to recover all roots growing beneath the sample area at later stages in growth, it represented as near an approach to this ideal as was practicable with the portable equipment used. The design of the coring tubes (Fig. 1) was based on principles given by Hvorslev (1948). They were of mild steel 7·62 cm (3·0 in.) internal diameter × 3·18 mm (0·125 in.) thick and 94 or 120 cm long, and fitted with cutting tips of heat-treated special steel ('Pax No. 2', Sanderson Kayser Ltd., Sheffield) which stands up well to hammering through stones of flint, limestone and comparable materials. The tips were made with a fine cutting angle and an Area Ratio (the ratio of the cross-sectional area of the soil displaced by the coring tube to that of the core it cuts, $= (A - B)^2/B^2$, Fig. 1) as small as practicable to minimise soil compaction by the advancing cutting edge. To facilitate removal of cores, the tubes were fitted with liners of brass or duralumin tube 1·22 mm (18 swg) thick, split lengthwise into two halves. The throat diameter of the cutting tip (7·06 cm) which determines the diameter of the core was slightly less than the inside diameter of the liners *in situ* in the coring tube so that there was a small clearance between the core and the liners to permit the core to enter the tube freely. A mild steel ring was brazed on to the top end of the coring tube to engage with the extraction gear used to pull the full tube out of the ground and also to strengthen the top of the tube against the hammer blows when being driven in.

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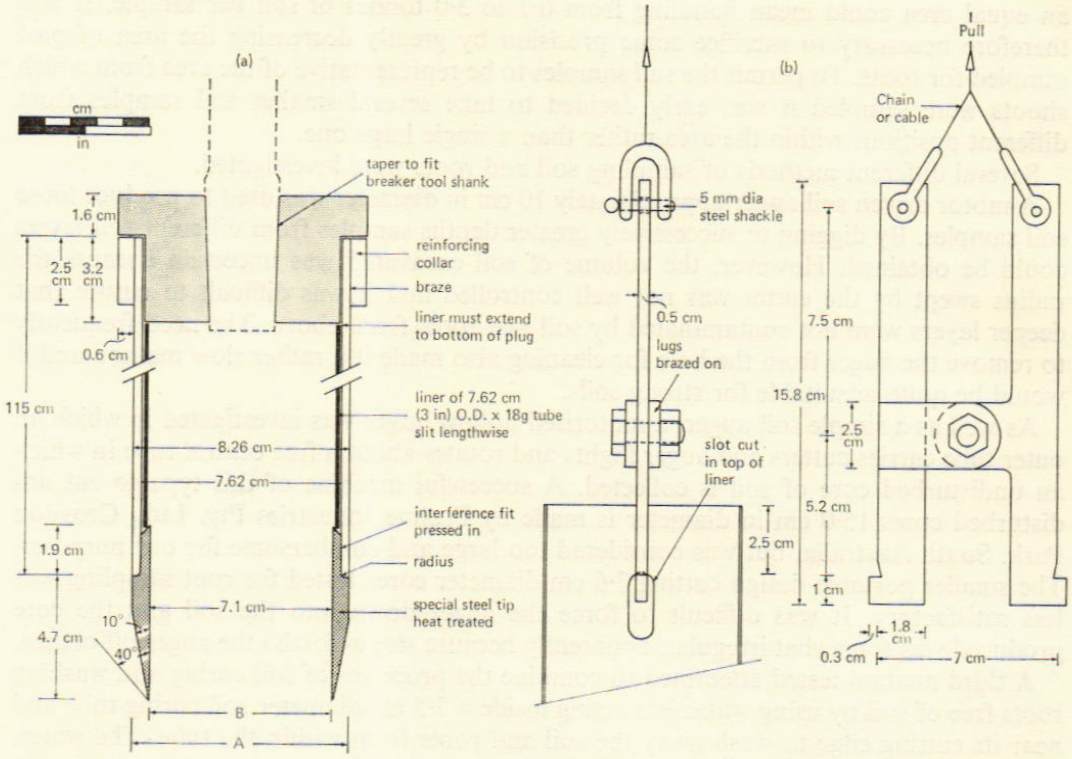

FIG. 1. (a) Coring tube and adaptor design. (b) Device for extracting tube liners.

Coring tubes were driven into the soil with a portable petrol-powered motor breaker delivering 2500 blows per minute (Plate 1). A simple adaptor had a shank fitting the tool socket of the breaker and a mild steel plug fitting the top of the coring tube. This equipment could drive a coring tube into the light sandy loam soil to a depth of 1 m in less than 30 seconds when the soil was moist, although when the soil was very dry it could take several minutes; it also took longer on heavier and more stony soils.

When the sandy loam soil was wet, tubes could be removed from it by one or two men using a tommy bar passing through holes at the upper ends of the tubes. When the soil was dry, pulls of up to about 1000 kg were needed and were obtained using a tripod and a chain hoist ('Pul-lift' made by Yale and Towne Inc.). The hoist was connected to the coring tubes by a set of gear-puller legs engaging under the ring at the top of the tube (Plate 2). This is in many ways preferable to connecting the hoist to a tommy bar passing through holes in the tube because the forces often needed to extract the tubes are sufficient to deform the edges of the holes in mild steel tubing and cause the liners to jam.

The manually operated chain hoist was barely adequate to extract tubes under the worst conditions encountered and satisfactory mechanised equipment has still to be found. Attempts have been made to use pneumatic cylinders to extract coring tubes (Ellis & Barnes, 1971), but the 12–14 cm diameter cylinder needed to provide a pull of 1000 kg with safe air pressures becomes unreasonably heavy for lifts as high as 1 m.

Soil cores encased in the liners were removed intact from the full coring tubes. To facilitate this when there was much friction between the liners and the tube the liners were attached by hooks engaging in holes at their upper ends to the steel cable of a small hand winch mounted on a field work bench (Fig. 1 and Plate 3). Each core removed from the tube was cut as it lay in one half-liner into sections corresponding to the different soil layers

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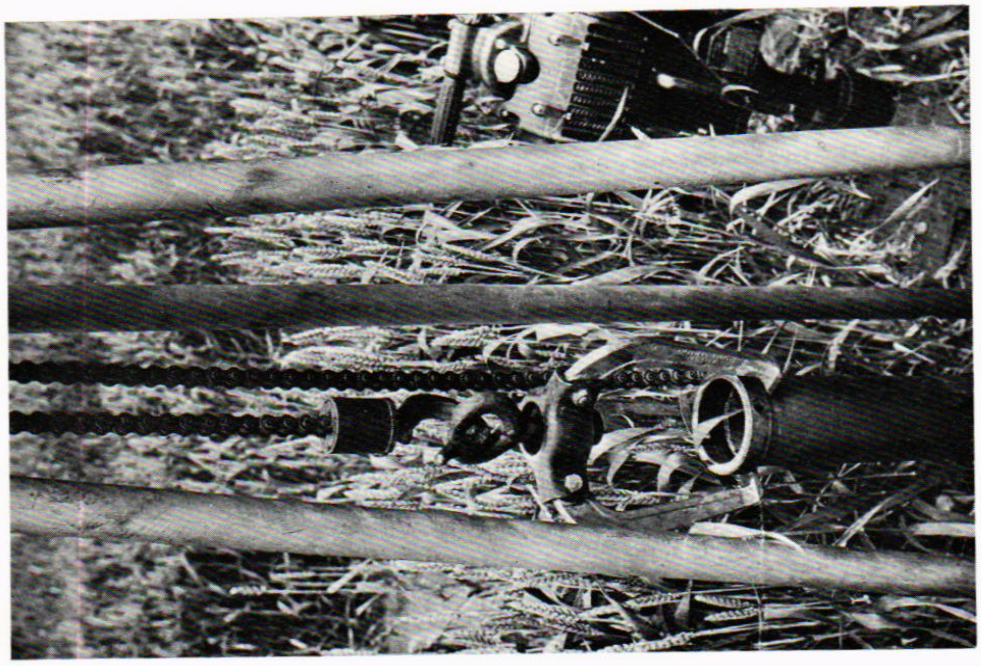

PLATE 2. Hoist and gear-puller legs attached to coring tube for lifting.

PLATE 1. Motor breaker used to drive coring tube. In the background tripod, hoist and gear-puller legs for extracting tubes from soil.

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PLATE 3. Removing liners containing soil core from coring tube using hand winch.

PLATE 4. Cutting core lying in a half-liner into layers.

studied in a particular experiment (Plate 4). The core sections were transferred to polyethylene bags in which they were stored between 0 and 4°C until required for processing and root measurement. Usually the sections corresponding to a given soil layer from all the cores cut within one sample area were combined to give one composite sample for each layer from each plot. On some occasions cores from beneath rows of a crop were kept separate from cores from beneath spaces between rows to check the horizontal uniformity of root distribution.

Core compaction. The coring tube method of sampling did not cause undue compaction of the samples when the soil was moist or dry. In favourable conditions the level of the core surface inside the tubes when it had been driven in was not more than 1 or 2 cm below that outside, corresponding to 1 or 2% vertical compaction. A further test described in *Rothamsted Report for 1966*, p. 84, in which bulk densities of cores cut with the tube were compared with densities of undisturbed samples showed core bulk densities ranging from 1 to 5% greater than those of undisturbed soil at different depths.

With some soils, especially when wet, cores deform greatly during sampling and the core surface in a tube driven to a depth of 1m may be as much as 25 cm below the soil surface outside. This is probably caused by a combination of the soil ahead of the cutting edge being compressed by the soil already in the tube, the soil within the tube slumping to fill the clearance space allowed within the liners and the soil particles of the core re-arranging themselves under the influence of the vibration so as to occupy a smaller volume. If the core is sectioned after it has been compacted, the amount of roots in a given layer may be overestimated, because a given length of core corresponds to a thicker layer of undisturbed soil. In experiments before 1970 no way of correcting for this error was available. In 1970 a technique was devised in which about 0·5 ml of paint was injected into the soil at known depths with a pointed tubular probe 1·27 cm (0·5 in.) diameter which was unlikely to disturb the soil for more than a few times its own radius around the point of insertion (*Rothamsted Report for 1970*, p. 96). A soil core was then cut over the injection point and cut open to disclose the paint marks. The apparent depths at which the marks were found were used to adjust the sectioning depths of subsequent cores to correct for their compaction.

Sample preparation. Roots were washed from soil samples in washing cans developed from the design of Cahoon and Morton (1961) (Fig. 2). Water is supplied through four tangential jets in the base of each can so that a vortex is set up in the can overflowing through the central hole on to a screen with apertures 0·5 mm square. Roots and organic debris overflow with the water and are retained by the screen, without being continually battered by water jets, as they would be were the whole sample placed on a sieve and washed through. Stones and coarse sand move to the outside of the vortex and remain behind in the can without blocking the screen holes. The material on the screen is washed into water and the roots and organic matter separated from any remaining mineral particles by flotation. Similar processes are used to separate roots from some of the organic debris, but final separation by hand using forceps and pipettes is necessary to produce an adequately clean sample for weighing or chemical analysis.

Root measurement. The lengths of roots from Experiments 2 (one sampling only), 3, 4, 5 and 6 were measured by Newman's (1966) method in which the roots are spread in a uniform single layer in a tray of known area and viewed through a low-power microscope with a hairline in one eyepiece which appears as a line of known length projected on to the image of the roots. The number of intersections between the hairline and the centre lines of roots are counted at about 80 random positions on the root array

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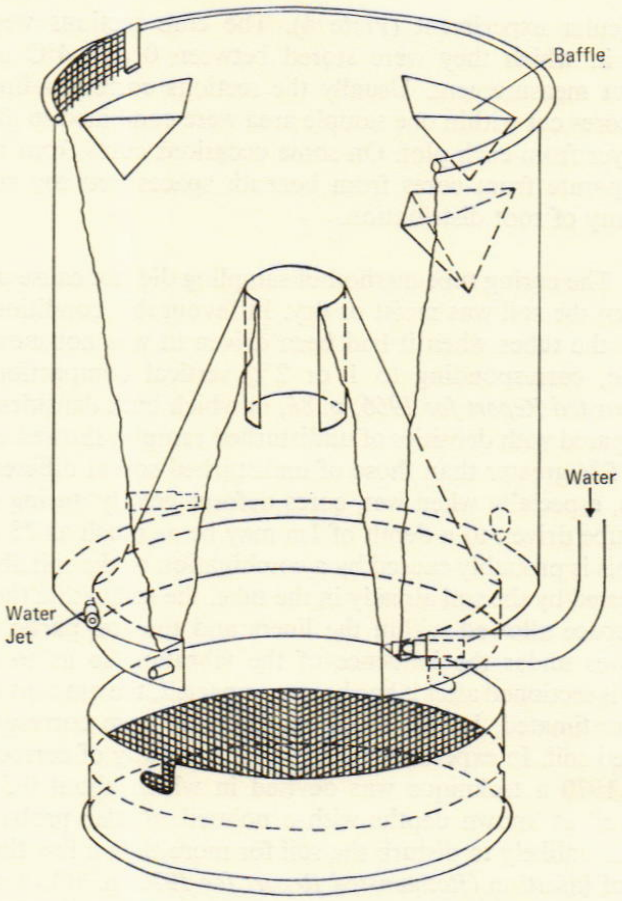

FIG. 2. Can for washing roots (approximately 30 cm diameter).

and converted to length of roots by a simple formula involving the known length of one transect line, the number of transects observed within the area of the tray, the area of the tray and the total number of intersections. The total number of intersections counted sets a limit to the precision of the length estimates, but if the roots are clumped rather than uniformly distributed the precision will be worse than this limit. To ensure adequate precision, at least 400 intersections were routinely counted and as many as 2000 intersections were counted for large samples. To give adequate counts from small samples, the 80 transect positions were distributed within trays of area about 290 cm^2; for larger samples an area of 625 cm^2 was used and for very large samples an area of 1260 cm^2. For the largest samples, subsamples only were measured in this way, both subsample and the remainder being subsequently dried and weighed: the estimate of total length was based on the dry weight determinations.

Root samples were dried at 80–85°C to constant weight. The dried roots were later ground and analysed for major inorganic plant nutrients in some experiments.

Experiment 1

Effect of nitrogen on barley root growth

The results of this experiment have been published (Welbank & Williams, 1968) and therefore essential details only are given here.

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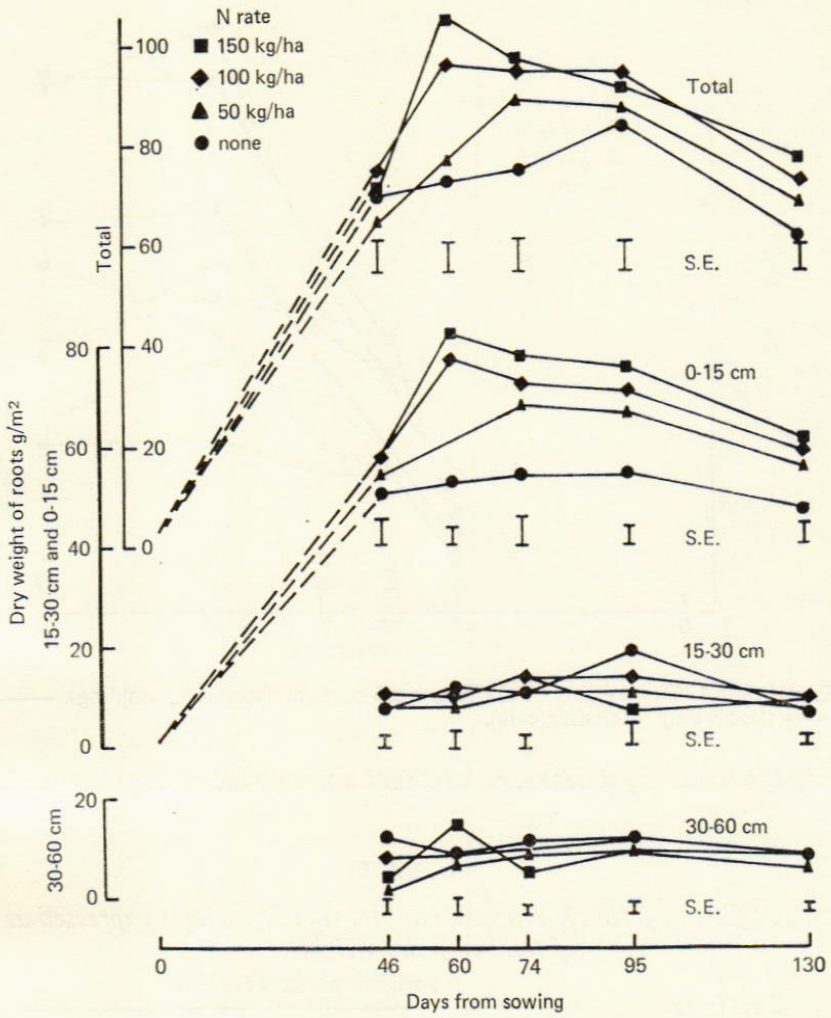

FIG. 3. Experiment 1. Dry weights of roots from different depths in the soil at successive samplings.

Barley (*Hordeum vulgare* L.), var. Maris Badger, was sown on 29 April 1966 at 173 kg/ha with fertilisers supplying 63 kg P_2O_5 and 126 kg K_2O/ha combine-drilled on plots 13 m long × one 12 row drill width (2·14 m) wide. Four nitrogen treatments supplying respectively 0, 50, 100 or 150 kg N/ha as 'Nitro-Chalk 21' were applied at sowing to plots in four randomised blocks. The crop was sampled 46, 60 (when the ears emerged), 74, 95 and 130 (when it was ripe) days after sowing. Dry weights and green areas of tops were measured and dry weights of roots in the soil layers 0–15, 15–30 and 30–60 cm.

Results. Root sampling was not commenced until 46 days after sowing. At that stage, the total dry weight of roots in the soil layers studied had already reached 60–80% of the maximum weights estimated later (Fig. 3), although tops had reached only about 20% of their maximum weight (including grain) or about 50% of the maximum weight of straw (Fig. 4). Root weights reached their maximum 60 or 74 days after sowing and then decreased to values similar to those at the first sampling. Nitrogen fertiliser up to 100 kg/ha increased the growth of tops greatly and the growth of roots slightly, but there was no significant further response to 150 kg/ha. In general, therefore, the ratio

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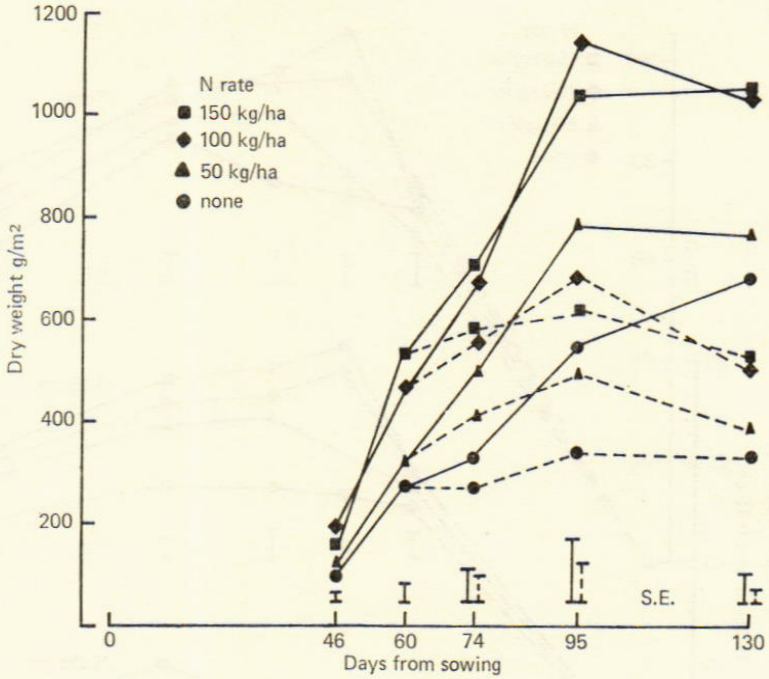

FIG. 4. Experiment 1. Dry weights of above-ground parts at successive samplings. ——— shoots + ears, – – – – – – shoots only (excluding ears).

of root weight to total weight decreased with time and with increasing nitrogen fertilisation (Table 1).

TABLE 1

Experiment 1. Effect of fertiliser nitrogen on total root dry weight expressed as a fraction of total crop dry weight

Days from sowing	Fertiliser nitrogen (kg/ha)				
	0	50	100	150	S.E.
46	0·417	0·362	0·280	0·300	0·010
60	0·208	0·195	0·171	0·169	0·014
74	0·188	0·151	0·124	0·120	0·010
95	0·133	0·101	0·079	0·081	0·011
130	0·081	0·080	0·064	0·067	0·003

As much as 80% of the total weight of roots recovered were from the top 15 cm of the soil (Fig. 3). About 12% was between 15 and 30 cm deep and about 10% between 30 and 60 cm. During the period of sampling (46–130 days after sowing) there were no clear effects either of time or of nitrogen treatment on the quantity of roots growing deeper than 15 cm.

A number of important features of cereal root growth were shown by this experiment. These are (i) the relatively early attainment of maximum size of root system, (ii) the relatively small effect of nitrogen fertiliser on the roots and (iii) the concentration of roots in the upper layers of the soil. It should not be assumed that there was no turnover of root material after flowering (i.e. new roots being produced and old ones or old root material dying), but the techniques used, or indeed any other techniques available for field use, cannot readily detect or measure such a turnover. Nor is it implied that roots growing below 15 cm are not very important to the plant: they may indeed be vital when

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all available water has been extracted from the surface soil layers. There was a suggestion from total roots weights recorded at the first few samplings for the two lowest nitrogen rates that nitrogen fertiliser may have decreased root dry weight at an earlier stage of growth. This was supported by results of later experiments (see Experiments 2 and 4).

Experiment 2

Effects of factorial combinations of nitrogen, phosphorus and potassium on barley root growth

Barley, var. Maris Badger, was sown on 31 March 1967 at 157 kg/ha, in plots 20 m long × 2·14 m (12 rows) wide. Fertiliser treatments were applied at sowing supplying all combinations of N : 0 or 100 kg/ha, P_2O_5 : 0 or 126 kg/ha, and K_2O : 0 or 126 kg/ha in a factorial design of three randomised blocks.

The crop was first sampled on 3 May and thereafter shoots were sampled at intervals of approximately two weeks until 10 July (Sampling 6: ears emerging) with further samples on 31 July and 21 August (ripe crop) (dates given on Fig. 5). Samples were 0·5 m × 8 rows = 0·71 m^2 in area from randomly determined positions within each plot. Plant material was subsampled on a fresh weight basis to estimate dry weights and on a fresh weight or shoot number basis to estimate leaf areas, which were measured by a photo-electric planimeter for early samples and estimated by a rating method (Watson, Thorne & French, 1958) for later ones.

Root dry weights were estimated for Samplings 2, 4 and 6. Four soil cores were taken from each plot and cut into layers at 15, 30 and 60 cm deep. The soil was washed off and the roots and any undecayed plant residues stored in deep freeze (about −20°C) for eventual separation and drying when time was available. Root samples were similarly collected for the remaining sampling occasions, but these were weighed only after prolonged storage in deep freeze, which may have affected dry weights so that less confidence can be placed in their absolute values. In particular, the mean root dry weights from Sampling 5 were less than from either of Samplings 4 or 6, although they may still indicate the relative effects of different treatments. The accuracy of estimates for Sampling 1 is uncertain, but as its results are not obviously inconsistent with those of Samplings 2 and 3 they have been treated as correct. It seems likely that the absolute values for Sampling 3, which were intermediate between values for Samplings 2 and 4, and Samplings 7 and 8, when root growth had probably ceased, were not greatly affected by storage. Lengths of roots from Sampling 3 were estimated by Newman's (1966) coincidence method, for comparison with their dry weights.

Results and discussion. The only clear and consistent effect of treatments on the total dry weight of roots was an increase in the average amount of roots with the higher rate of nitrogen at all samplings from the third onwards (Fig. 5). However, this does not imply that other treatment effects were fortuitous, even though they reached statistical significance on only one occasion. There was an indication that nitrogen decreased the amount of roots at the first sampling on 3 May, although overall the treatment effects did not reach significance at the 5% level on this occasion. Throughout the experiment the PK treatment (i.e. given phosphorus and potassium, but not nitrogen) produced much more roots than any other treatment that did not include nitrogen and at Samplings 1–4 it produced as much as, or more roots than, treatments including nitrogen. The advantage of the PK combination in the presence of nitrogen was less marked. It is not clear why the interaction between the PK treatment and nitrogen should occur and further experiment is required to confirm and explain this phenomenon. The effect of phosphorus was significant at Sampling 4, increasing root dry weight from a mean of

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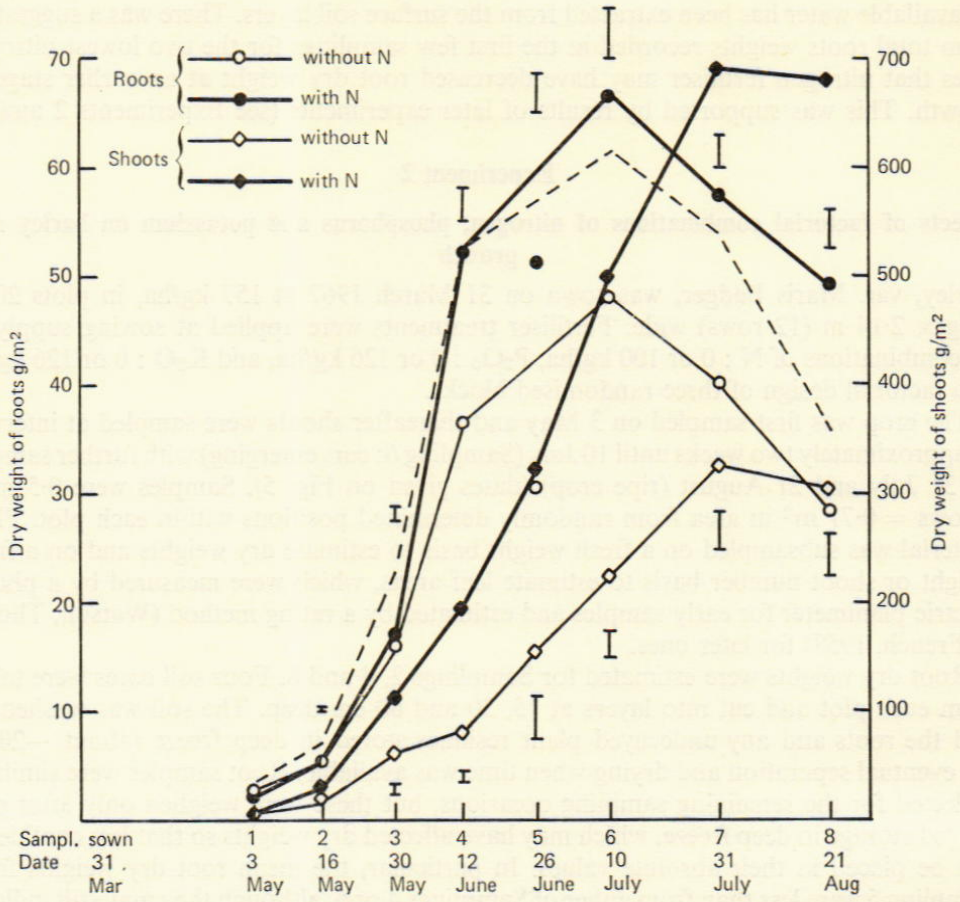

FIG. 5. Experiment 2. Dry weights of total roots and shoots at successive samplings without and with nitrogen fertiliser; means of all phosphorus and potassium treatments. The broken line shows total root dry weights for the PK treatment (also included in the without-nitrogen mean). Root dry weights for Sampling 5 are shown, but not joined to other points because they were probably affected by storage (see text). Standard errors shown for shoots below and for roots above the graphs. Standard errors too small to be shown for early samplings were for roots Sampling 1: 0·2; for shoots Sampling 1: 0·4, Sampling 2: 1·6. Note that the shoot dry weight scale is ten times the root dry weight scale.

37·6 to 51·0 g/m² (±3·1), and the effect of potassium significant at the 5% level at Sampling 6, increasing root dry weight from 49·7 to 64·9 g/m² (±4·6). With the exception cited, the experiment produced no evidence that phosphorus stimulates root growth. Different results might possibly have been obtained from an experiment on soil in which the growth of the crop as a whole responded differently to phosphorus.

Shoot growth was consistently increased by nitrogen throughout the experiment

TABLE 2

Experiment 2. Effects of phosphorus and potassium on total shoot dry weights (g/m²) at Samplings 1, 4, 7 and 8; means of both nitrogen rates

Sampling	Treatment combination: nil	P	K	PK	S.E.
1	7·2	6·5	6·1	8·0	0·53
4	117	150	111	166	15
7	535	454	404	635	47
8	510	430	409	618	54

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(Fig. 5). There was also evidence of an interaction between phosphorus and potassium effects which reached statistical significance at the 5% or 1% levels at Samplings 1, 7 and 8, but which probably occurred throughout: potassium had a negative or nil effect in the absence of phosphorus, but a large positive effect with phosphorus (Table 2). At Sampling 4 phosphorus increased shoot growth from 155 to 233 g/m² (±14·6) when nitrogen was also supplied (significant at 1% level), but by only an insignificant amount (from 73 to 83 g/m²) when nitrogen was omitted.

In general, therefore, the effects of treatments on roots were similar to their effects on shoots, except for the small or negative effect of nitrogen on roots at the early samplings compared with its positive effect on shoot growth. The absence of any clear effect of phosphorus or potassium on roots independently of their effects on crop growth as a whole is shown by the ratios of root dry weight to total dry weight (Fig. 6). Nitrogen, however, consistently depressed the fraction of total dry matter in the roots.

Treatment effects on root dry weight in the top 15 cm of the soil were responsible for most of the differences observed in total root dry weight (Fig. 7). However, at Samplings 2 and 3 nitrogen decreased the dry weight of roots in layers below 15 cm, without significantly affecting the weight in the top 15 cm.

At Sampling 3 an interaction between phosphorus and potassium affected only roots below 15 cm: both phosphorus and potassium alone depressed root dry weight, but this effect was greatly reduced when they were supplied together (Table 3).

TABLE 3

Experiment 2. *Effects of phosphorus and potassium on root dry weights (g/m²) at Sampling 3; means of both nitrogen rates*

	Treatment combination				
Depth (cm)	nil	P	K	PK	S.E.
0–15	13·9	14·0	12·9	17·9	1·4
15–30	2·59	0·70	0·69	1·67	0·55
30–60	0·75	0·18	0·29	0·72	0·17

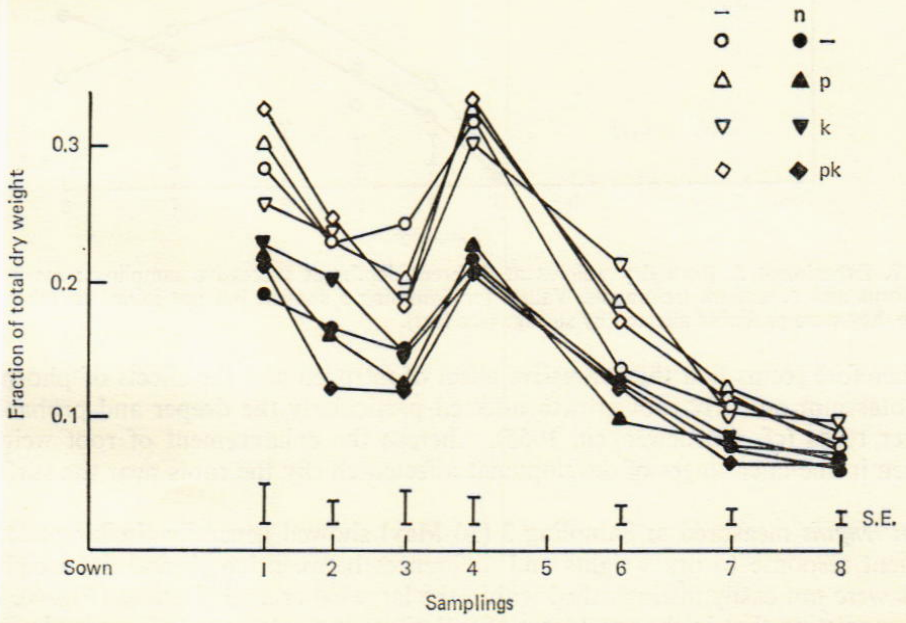

FIG. 6. Experiment 2. Root dry weights at successive samplings expressed as fractions of total dry weights for all treatments. Sampling 5 values omitted.

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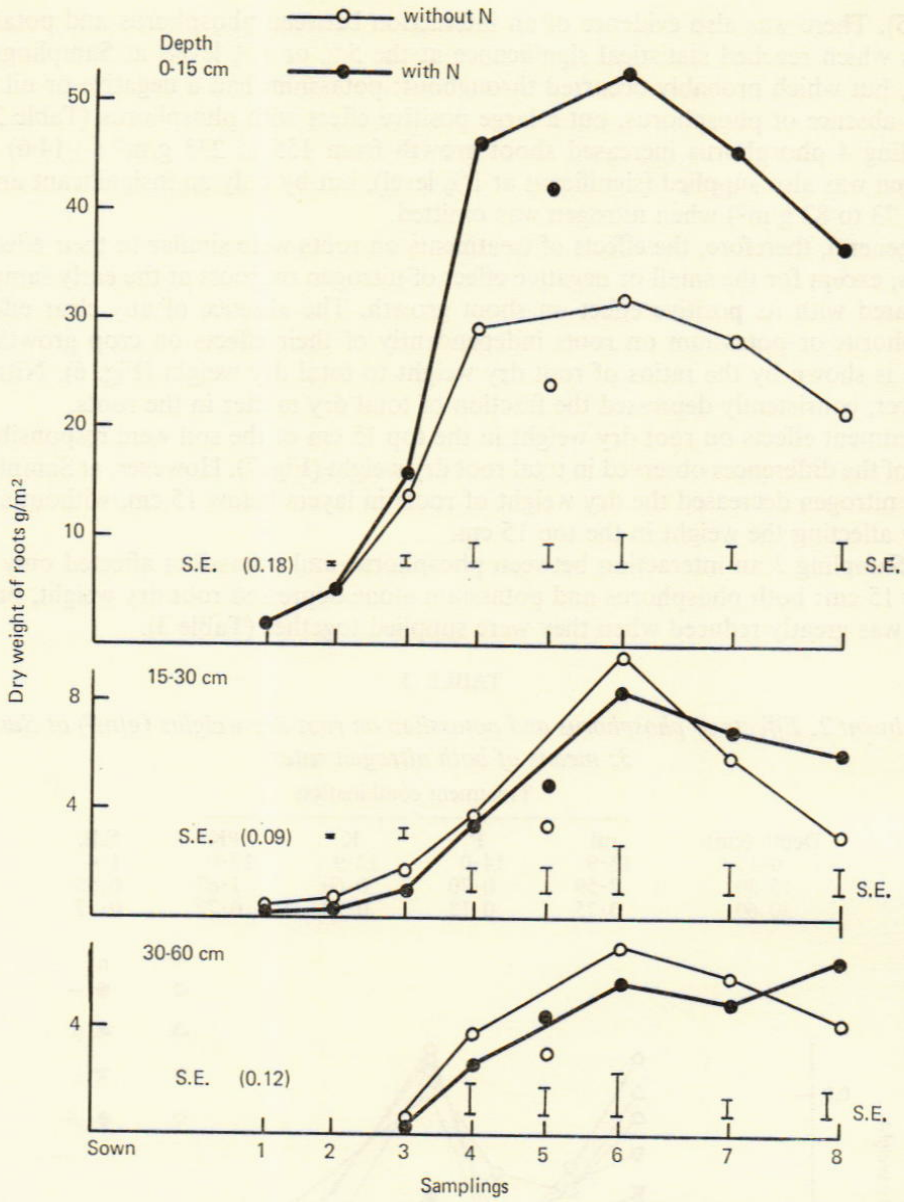

FIG. 7. Experiment 2. Root dry weights at different depths at successive samplings; means of all phosphorus and potassium treatments. Values for Sampling 5 shown, but not joined to other points because they were probably affected by storage (see text).

It therefore seems that the depressive effect of nitrogen and the effects of phosphorus and potassium on early root growth affected particularly the deeper and probably the younger roots (cf. Goedewaagen, 1955), whereas the enhancement of root weight by nitrogen in the later stages of development affected chiefly the roots near the surface.

Root lengths measured at Sampling 3 (30 May) showed generally similar patterns of treatment response to dry weights and differences between length and dry weight responses were not easily distinguished within the large experimental errors (Fig. 8). There was a suggestion that in the top 15 cm of soil nitrogen tended not to increase lengths of roots as it did dry weights. A better indication of differences in response between root

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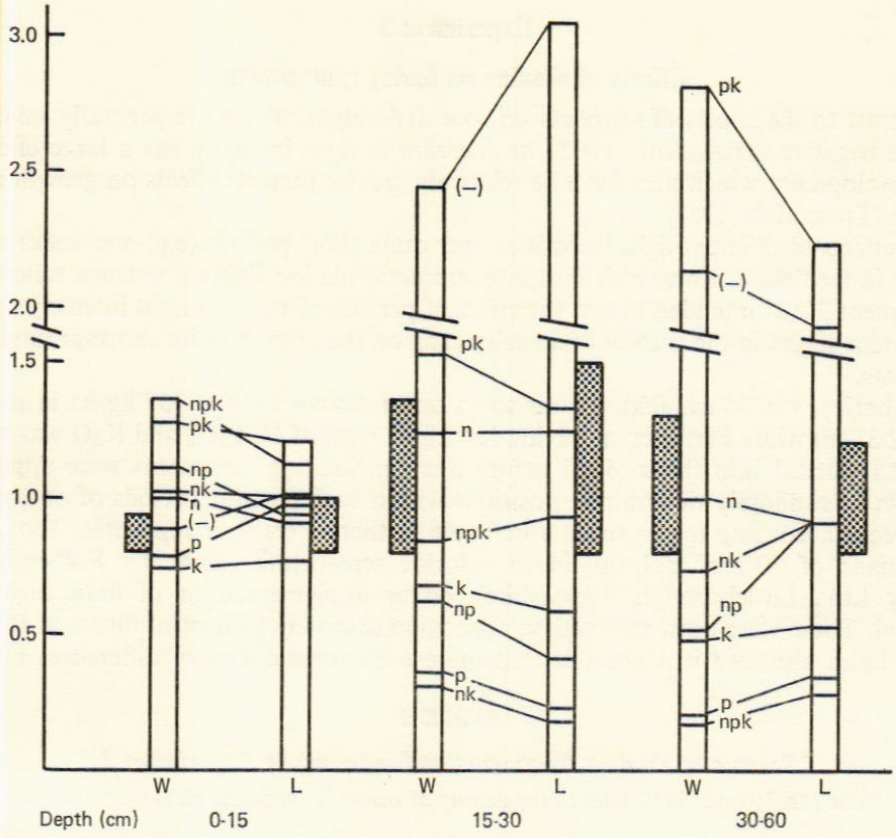

FIG. 8. Experiment 2. Comparison of root dry weights (W) and lengths (L), both expressed as fractions of their mean values at different depths, for each treatment at Sampling 3. Mean values given beneath and standard errors shown adjacent to their respective variates by stippled bars.

lengths and dry weights is given by the specific root length (length of root per unit dry weight). In the top 15 cm of soil both nitrogen and potassium decreased specific root length, but their effects were not cumulative (Table 4). Similar interactions affected roots in deeper layers and it was probably only the larger experimental errors that prevented them appearing as statistically significant. The specific root length was greater in the top 15 cm of soil than in deeper layers, indicating that there were proportionately more fine roots in the top layer, in spite of its containing the thick root bases.

TABLE 4

Experiment 2. Effect of nitrogen and potassium at Sampling 3 on specific root length (length of roots per unit root dry weight, m/g); means of both phosphorus rates

	Treatment combination					
Depth (cm)	nil	N	K	NK	S.E.	Mean
0–15	226	160	186	176	12	187
15–30	197	109	110	88	34	126
30–60	149	129	93	122	27	123

The final grain yields in this experiment were small, perhaps partly because of rather late sowing and because wet weather maintained the soil very wet after the crop had emerged. Without nitrogen fertiliser the mean yield at 85% DM was 1·4 t/ha and with 100 kg N/ha it was 2·8 t/ha (±0·2). The best yield with all three fertilisers was 3·2 t/ha.

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Experiment 3

Effects of shading on barley root growth

In contrast to the effects of nutrients on root dry weight, which are generally small and may be negative (Troughton, 1962), an increase in light intensity has a large effect on root development which may even be relatively greater than its effects on growth above ground (Troughton, 1962).

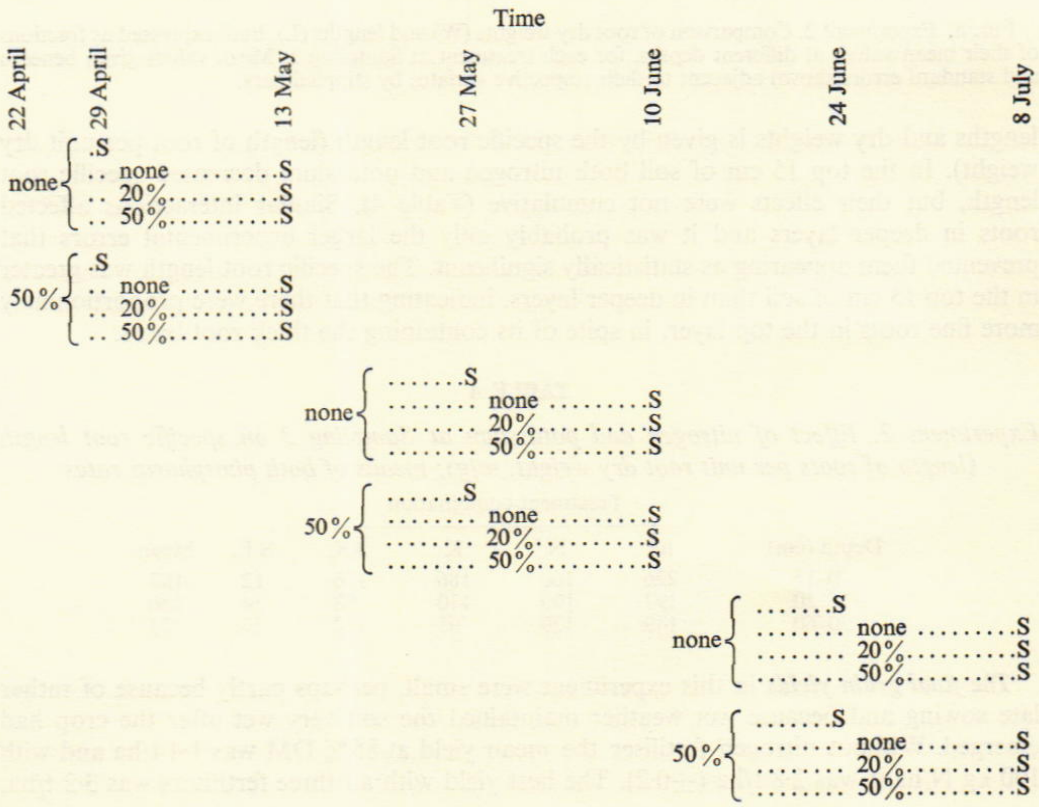
The effects of different light intensities over quite short periods (e.g. one week) can be studied in the field in a way which is quite impracticable for different nutrient treatments. Experiment 3 was intended to test the effect of periods of reduced light intensity applied at different stages in the growth of a barley crop on the growth of its above-ground parts and roots.

The barley, var. Maris Badger, was sown on 11 March 1968 at 157 kg/ha in plots 13 rows (2·31 m) wide. Fertiliser supplying 126 kg/ha each of N, P_2O_5 and K_2O was broadcast and worked into the seedbed before sowing. Shading treatments were applied to subplots at randomly determined positions within each plot for periods of one, two or four weeks according to the scheme in Table 5: there were four replicates. The shades were made of 'Tygan' polyvinylidene chloride screencloth (made by Fothergill and Harvey Ltd., Littleborough, Lancashire), either unpigmented or of dark pigmented material. These were both assumed to approximate closely to neutral filters, at least for visible light, although it is possible that there were some effects of differences between

TABLE 5

Scheme of shading treatments and sampling in Experiment 3

'None', '20%' and '50%' refer to the density of shade. 'S' indicates plots were sampled



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unpigmented and dark material. Transmissions measured with radiometers were: unpigmented, 78% of total or 76% of visible radiation; dark pigmented, 49% of total or 46% of visible radiation. The corresponding degrees of shade will hereafter be referred to by the approximate values of 20% and 50% respectively. The shades were supported on light wooden frameworks 1·8 m square about 0·30 m above crop height and hung down about 0·45 m from the flat top on all sides, so that the bottom edges were about 15 cm below the level of the upper leaves.

The shades extended over 11 rows of crop and samples were cut from an area 0·50 m × 1·60 m including the seven centre rows of the 11 that were shaded. From samples of above-ground parts dry weights and leaf areas were estimated. Four soil cores were cut from within each sample area for root estimation and cut into layers of 0–15, 15–30 and 30–60 cm deep. The total length of root in each sample was estimated by Newman's (1966) coincidence method and the roots then dried and weighed.

Results and discussion. The first period of shading to 50% of full daylight, before the first sampling 49 days after sowing, lasted for only seven days. It decreased dry weight of roots and also of shoots by 25% of unshaded controls (Fig. 9). Later shading periods lasted 14 days. When the crop was shaded to 50% of daylight for the first time during the second period (14 days) its root weight was decreased by about 30%. However, if it had previously been shaded in the first (seven day) period, its root dry weight was decreased by more than a further 50%. Responses to 20% shade were in each case intermediate. The greater percentage responses to shading in the second period following a preliminary seven-day shading treatment were not simply a reflection of a smaller initial root dry weight, because the absolute root weight difference between shaded and unshaded plots was also greater when they had previously been shaded in the seven-day period than when they had not.

During the third period the effects on root weights of shading to 50% daylight for the first time were similar to those in the second period, but shading during the fourth period for the first time had only a small effect on root weights, probably because root growth was by then slowing down. On the other hand, plots which had been shaded in the third period and which were then shaded to 50% daylight in the fourth period had significantly less roots than those unshaded during the fourth period. Shading during the fifth or sixth periods had no significant effect on root dry weights at the end of the shading period concerned, but in plots shaded during the fifth period, differences in root weight developed during the following 14 days, so that by the end of the sixth period they had less roots than plots unshaded during the fifth period.

The effect of shading on root growth (i.e. increase in root dry weight during the shading period) seemed often to be more than proportional to the fractional decrease in light intensity. Thus during the second period 50% shade decreased root growth by more than 70% when the plots had also been shaded during the previous seven days; during the third period it decreased growth of previously unshaded plots by 66% and during the fourth period it decreased growth of plots also shaded in the previous period by 64%. As it is unlikely that photosynthesis would be decreased in proportion to the degree of shading, this suggests that root growth suffered disproportionately, probably to the benefit of shoot growth.

It therefore appears that the response of total root weight to shading increased as the period of shading was prolonged, especially during the stage of rapid root growth. This may have happened because reserves of assimilates were available to maintain root growth during short periods of shading, or because it took some days for the plant to respond to shading by diverting more resources to leaf production.

Shading in the preceding two weeks decreased the amount of roots at the second

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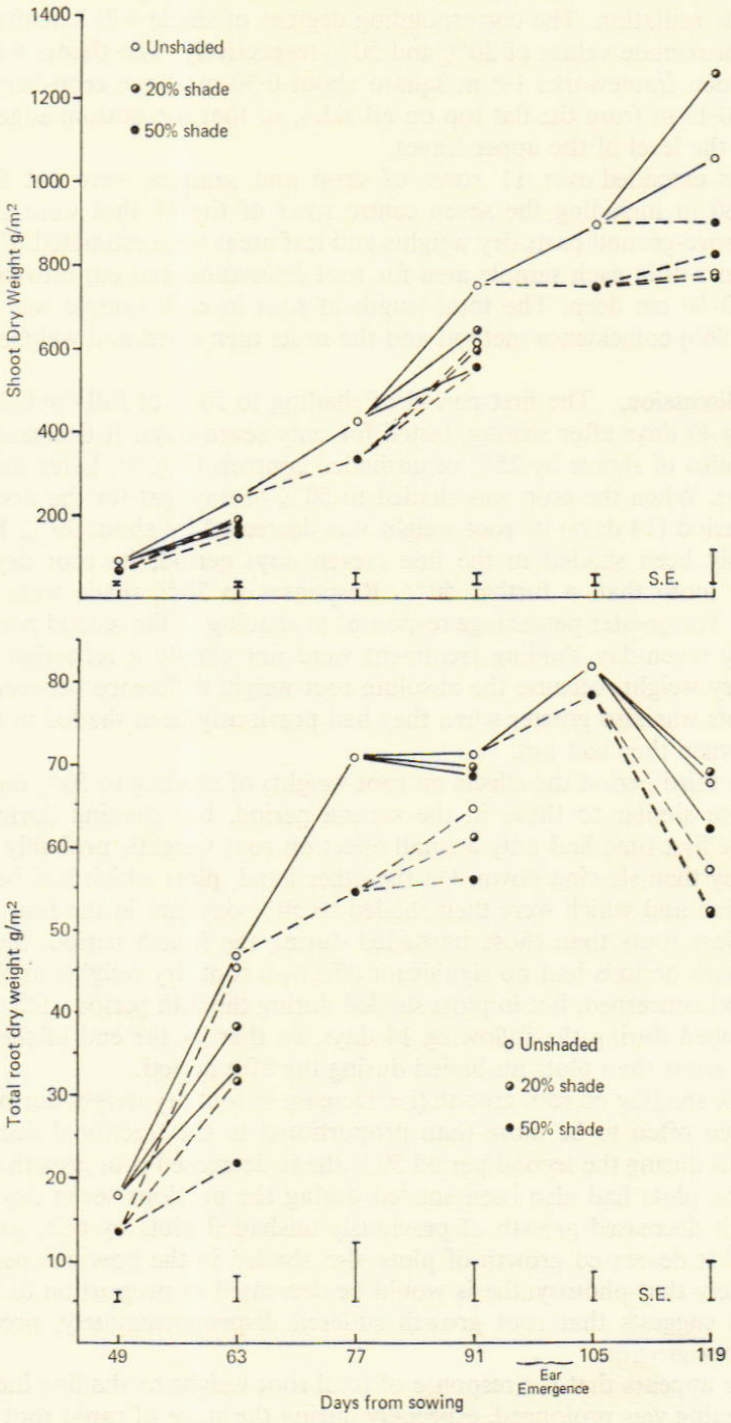

FIG. 9. Experiment 3. Effects of different degrees of shading on dry weights of shoots (above) and total roots (below). Note: shoot dry weight scale is 20 times the root dry weight scale.

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TABLE 6

Experiment 3. Dry weight of roots (g/m^2) at Samplings 2 and 4

The figures in brackets are the % of total recovered roots in each layer

	Sampling 2				
	Unshaded in period 1		Shaded in period 1		
Depth (cm)	Unshaded	50% shade	Unshaded	50% shade	S.E.
0–15	31·0 (67)	27·3 (83)	33·5 (74)	18·6 (85)	1·7
15–30	9·0 (19)	4·9 (13)	7·9 (17)	2·0 (9)	1·2
30–60	6·7 (14)	1·4 (4)	4·1 (9)	1·3 (6)	1·0
	Sampling 4				
	Unshaded in period 3		Shaded in period 3		
Depth (cm)	Unshaded	50% shade	Unshaded	50% shade	S.E.
0–15	41·1 (59)	48·4 (70)	42·9 (66)	39·8 (71)	3·2
15–30	12·7 (19)	15·1 (22)	13·2 (21)	9·2 (17)	1·5
30–60	16·9 (23)	5·1 (8)	8·3 (13)	6·8 (12)	2·6

sampling between 15 and 30 cm deep and between 30 and 60 cm deep (Table 6). At the fourth sampling root weights between 15 and 30 cm were less from plots which had been shaded to 50% daylight during the third period, ending two weeks before sampling; similarly at the sixth sampling, shading during the fifth period decreased weights of roots recovered from 15–30 and 30–60 cm deep. Otherwise effects on growth of deeper roots were not detected at the 5% significance level. The smaller amounts of roots in layers below 15 cm deep usually also represented a smaller fraction of the total roots recovered (Table 6), so shading suppressed deeper root growth proportionately more than growth near the surface. Thus it appeared that during the period of rapid root growth shading decreased the rate of root penetration into deeper layers.

***Root length* (*Table 7*)** was generally affected similarly to root dry weight by treatments. However, in some instances the effects of shading on length seemed less than on weight, so that length per unit dry weight (specific root length) increased with shading. For example, at the first sampling specific root length between 15 and 30 cm was 52 m/g following 50% shade for one week, compared with 47 m/g unshaded (both $\pm 1{\cdot}2$). Similarly root lengths at Sampling 6 were depressed proportionately less than dry weights by shading during Period 5, especially in the deeper soil layers where specific root lengths increased from 135 to $160 \pm 8{\cdot}1$ m/g in the 30–60 cm deep layer.

Shoot growth. The effects of treatments on shoot growth were usually proportionately less than their effects on roots and smaller during a second two-week period of shading than during a first period (Fig. 9). For example, 50% shade applied for the first time during the second period decreased shoot growth by 41%, during the third period by 50% and during the fourth period by 59%. When applied to plants shaded during the previous period it decreased growth in the second period by 30% and in the fourth period by 30%.

Shading effects on leaf area were proportionately even smaller. Fifty per cent shade applied for the first time during the second period decreased leaf area growth by 23%, and during the third period by 25% (thereafter leaf area index declined). When applied to plants previously shaded during the first period, 50% shade during the second period decreased leaf area growth by only 4%.

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TABLE 7

Experiment 3. Length of roots in different soil layers (km/m² of soil surface)

Sample depths (cm)	Degree of shade: Unshaded during previous period 0	Unshaded during previous period 20%	Unshaded during previous period 50%	Shaded during previous period 0	Shaded during previous period 20%	Shaded during previous period 50%	S.E.
			Sampling 2, 13 May				
0–15	4·94	6·22	7·41	8·05	5·93	3·24	1·09
15–30	1·48	0·88	1·16	1·57	1·19	0·45	1·07
30–60	0·64	0·38	0·22	0·41	0·28	0·13	0·79
Total	7·05	7·48	8·79	10·03	7·40	3·82	1·17
			Sampling 4, 10 June				
0–15	5·42	6·30	6·54	6·30	7·01	6·09	0·57
15–30	1·94	2·16	2·12	2·11	1·34	1·68	0·20
30–60	2·38	1·38	0·71	1·13	0·66	0·96	0·36
Total	9·74	9·84	9·48	9·53	9·42	9·05	0·79
			Sampling 6, 8 July				
0–15	10·33	8·01	10·63	11·64	10·68	6·18	1·58
15–30	1·89	1·80	3·01	1·68	1·95	1·52	0·49
30–60	1·54	1·37	1·16	1·08	1·18	1·29	0·14
Total	13·76	11·17	14·79	14·41	13·80	8·99	1·68

Note: Any comparison with results in a previous period should be made with the completely unshaded plots (first column)

These results support the suggestion that shaded plants divert proportionately more of their resources to top growth at the expense of root growth, and that over a period of a few weeks they adapt partially to shade so that top growth is not reduced in proportion to the decrease in light intensity.

Experiment 4

Comparison of root growth of winter wheat, spring wheat, spring oats and spring barley

Winter wheat (*Triticum aestivum* L.), var. Cappelle-Desprez, was sown on 24 October 1968 at 196 kg/ha. Spring wheat, var. Kolibri, spring oats (*Avena sativa* L.), var. Manod, and spring barley, (*Hordeum vulgare* L.), var. Maris Badger, were sown on 27 March 1969 at 202, 157 and 157 kg/ha respectively. Plots of each crop measured 7·6 m long by 2·14 m (12 rows) wide. Fertilisers supplying 25 kg N, 188 kg P_2O_5, 188 kg K_2O and 126 kg MgO per ha were applied to the whole site and worked in before sowing the winter wheat. Nitrogen fertiliser ('Nitro-Chalk 21') supplying 100 kg N/ha was applied to half the plots of each crop on 16 April in a factorial design of three blocks.

The winter wheat was sampled on 31 March and all crops sampled on 5 May, 2 June and 30 June. Each sample area was 0·5 m long and extended over the six centre rows of the plot (1·07 m). From each sample area four soil cores were cut within the crop rows and four between the rows. At Samplings 1 and 2 roots from the two sets of four cores were separately measured. Cores were sectioned at 15, 30, 60 and 100 cm deep. From samples of shoots leaf areas were estimated using an EEL photoelectric area meter on a fresh weight subsample (Samplings 1 and 2) or by rating a subsample of 36 shoots (Samplings 3 and 4). Shoot and root dry weights were measured and lengths of roots estimated by Newman's (1966) method. Final samples of tops only of the ripe crops were cut for yield estimates on 4 (winter wheat, oats and barley) or 15 (spring wheat) August.

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Results and discussion

Roots. The differences in amount of roots between samples from the rows and from the spaces between rows tested at Samplings 1 and 2 were chiefly confined to the top 15 cm of soil (Table 8). It is unlikely that the differences became greater or extended deeper in later samplings. The remainder of the results are given as the means of within and between row samples.

TABLE 8

Experiment 4. Dry weight of roots (g/m² soil surface) from rows and spaces between rows at different depths on 31 March and 5 May; means of N and no N

		31 March		5 May				
Depths (cm)		Winter wheat	S.E.	Winter wheat	Spring wheat	Oats	Barley	S.E.
0–15	Rows	4·5	0·9	21·1	11·0	9·2	7·6	0·8
	Spaces	2·0	0·3	9·5	4·4	2·6	3·0	0·6
15–30	Rows	1·3	0·2	6·3	1·1	0·5	1·0	0·4
	Spaces	1·0	0·3	6·7	0·6	0·4	0·6	0·4
30–60	Rows			7·7				1·1
	Spaces			6·7				0·8

The dry weights of roots produced by the different crops with 100 kg N/ha (Fig. 10) and their lengths (Table 9) are probably more typical of a normally fertilised crop than the controls not given nitrogen fertiliser in spring. On 31 March winter wheat had a root system extending to about 30 cm deep and about 5–8% of its size at ear emergence (near maximum). This advantage over the spring sown crops increased slightly by 5 May and at this stage the spring sown cereals, especially oats and barley, already had a smaller fraction of their total weights in their root systems than winter wheat had at the end of

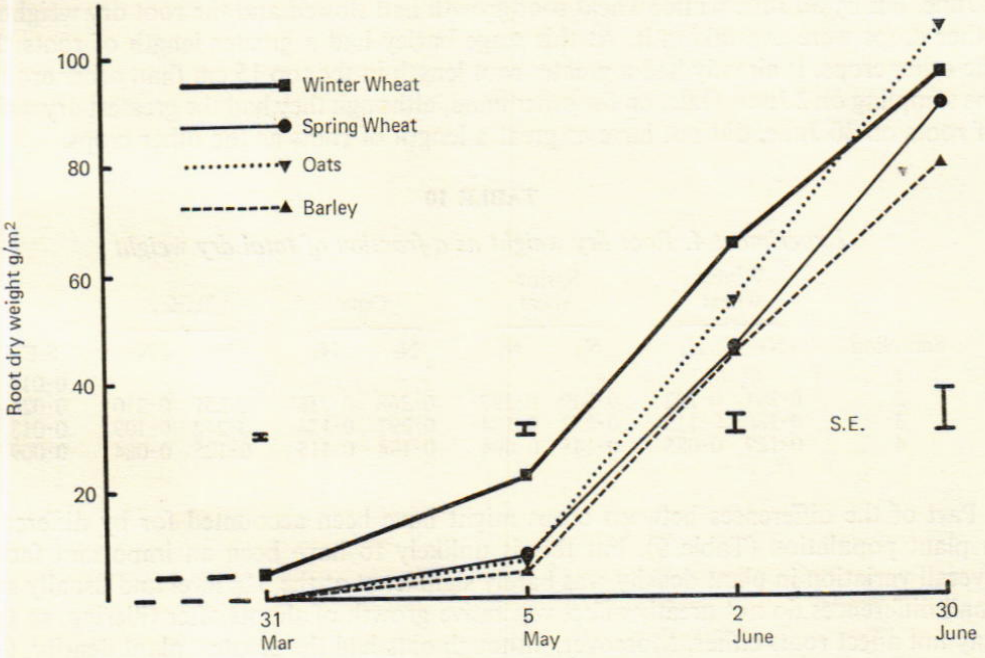

FIG. 10. Experiment 4. Dry weights of roots of different cereals given 100 kg N/ha.

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TABLE 9

Experiment 4. Length of roots (km/m² soil surface) in different soil layers and plant densities (plants/m²) of different cereals given 100 kg N/ha in spring

Depths (cm)	Winter wheat	Spring wheat	Oats	Barley	S.E.
		Sampling 1, 31 March			
0–15	0·66				0·095
15–30	0·25				0·057
Total	0·90				0·067
		Sampling 2, 5 May			
0–15	1·52	1·11	1·07	0·79	0·21
15–30	0·85	0·06	0·07	0·07	0·06
30–60	0·49	0·0	0·0	0·0	0·12
Total	2·86	1·18	1·14	0·86	0·28
		Sampling 3, 2 June			
0–15	4·5	4·3	4·2	5·3	0·55
15–30	1·4	1·1	1·4	1·3	0·22
30–60	2·0	0·8	0·6	1·2	0·31
Total	7·9	6·2	6·2	7·7	0·51
		Sampling 4, 30 June			
0–15	4·9	4·9	5·1	6·3	0·68
15–30	2·1	1·7	1·7	1·9	0·28
30–60	2·6	3·4	3·1	2·4	0·21
60–100	2·2	1·3	1·5	2·0	0·30
Total	11·8	11·3	11·3	12·6	0•87
		Plant densities at seedling emergence			
	256	283	319	274	20

the winter (Table 10), i.e. they diverted less of their current assimilates into root production during early growth. Winter wheat had the greatest root dry weight at least until 2 June, but by 30 June winter wheat root growth had slowed and the root dry weights of other crops were overtaking it. At this stage barley had a greater length of roots than the other crops. It already had a greater root length in the top 15 cm than other crops at the sampling on 2 June. Oats, on the other hand, although they had the greatest dry weight of roots on 30 June, did not have as great a length of roots as the other crops.

TABLE 10

Experiment 4. Root dry weight as a fraction of total dry weight

	Winter wheat		Spring wheat		Oats		Barley		
Sampling	N_0	N_1	N_0	N_1	N_0	N_1	N_0	N_1	S.E.
1	0·369								0·014
2	0·381	0·222	0·349	0·297	0·268	0·218	0·251	0·210	0·024
3	0·188	0·115	0·252	0·134	0·297	0·158	0·242	0·109	0·018
4	0·129	0·085	0·145	0·094	0·184	0·115	0·125	0·084	0·009

Part of the differences between crops might have been accounted for by differences in plant population (Table 9), but this is unlikely to have been an important factor. Overall variation in plant density was barely significant at the 5% level and usually such small differences do not greatly affect vegetative growth of shoots after tillering, so they may not affect roots either. Moreover, although oats had the greatest plant density, they did not have the greatest weight or length of roots when they were first sampled in May.

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Plots given no spring nitrogen usually had more roots at the earlier samplings than those given 100 kg/ha (Fig. 11). Later, the overall increase in the size of the plants given spring nitrogen resulted in root systems as large or larger than the controls, which, however, still had root systems comprising a larger fraction of the total dry weight than the nitrogen-treated plants (Table 10). At Sampling 2 nitrogen decreased the amount of roots in the top 15 cm soil layer: it decreased length by 0·74 km/m² soil surface (about 30%) in winter wheat and by 0·65 km (about 45%) in barley. At Sampling 3 effects of

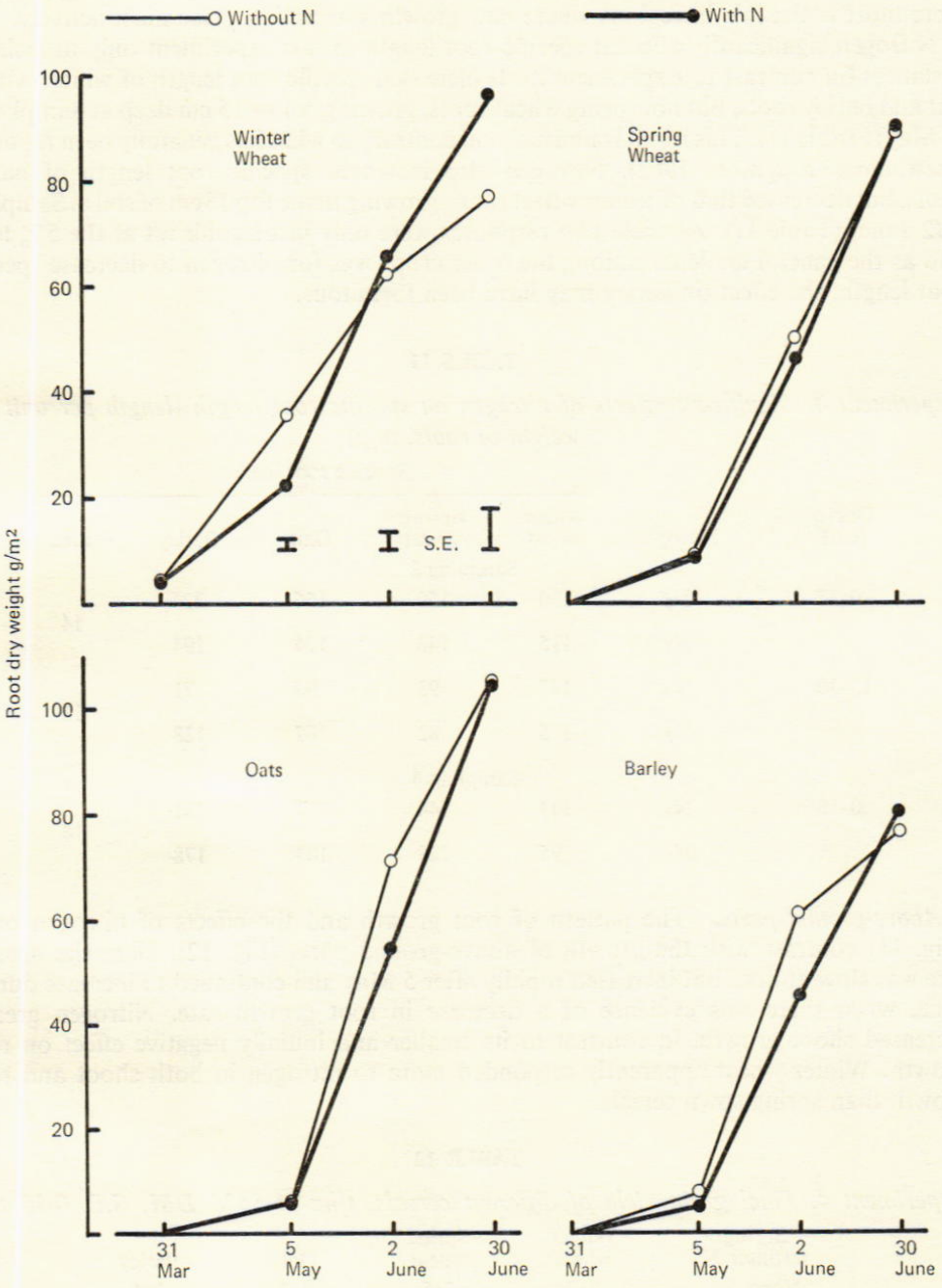

FIG. 11. Experiment 4. Effects of nitrogen fertiliser (100 kg N/ha) on roots of different cereals.

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nitrogen were most significant at 15–30 cm deep, where root length of barley was decreased by 0·89 km/m² soil surface (about 40%) and that of other spring sown cereals by smaller amounts. Its effects on spring wheat and barley roots in the 30–60 cm deep soil layer were almost as great, although they did not reach significance at the 5% level. By Sampling 4, although nitrogen decreased the length of oat roots in the 15–30 cm deep layer by 1·43 km/m² and spring wheat roots by a lesser amount, it increased the length of barley roots in the top 15 cm by 2·07 km/m² and of roots of all crops in the 60–100 cm deep layer by an average of 0·56 km/m² (about 47%). Thus the nitrogen effects were most noticeable in regions where new growth was taking place most actively.

Nitrogen significantly affected specific root length in this experiment only in isolated instances (in contrast to Experiment 2). It increased specific root length of winter wheat, oat and barley roots, but not spring wheat roots, growing below 15 cm deep at Sampling 2 (5 May) (Table 11). This result is unusual and contrary to what has generally been reported elsewhere (Troughton, 1962). Nitrogen also increased specific root length of barley roots, but decreased that of winter wheat roots, growing in the top 15 cm of soil at Sampling 4 (2 June) (Table 11). As these two responses were only just significant at the 5% level and as the general tendency among the other crops was for nitrogen to decrease specific root length, the effect on barley may have been fortuitous.

TABLE 11

Experiment 4. Significant effects of nitrogen on specific root length (length per unit dry weight of roots, m/g)

Depth (cm)	Nitrogen	Specific root lengths: Winter wheat	Spring wheat	Oats	Barley	S.E.
		Sampling 2				
0–15	N_0	130	150	166	224	14
	N_1	115	148	174	194	
15–30	N_0	137	93	90	71	10
	N_1	175	82	167	128	
		Sampling 4				
0–15	N_0	143	144	117	131	14
	N_1	95	128	103	178	

Above-ground parts. The pattern of root growth and the effects of nitrogen on it (Fig. 11) contrast with the growth of above-ground parts (Fig. 12). Here the growth rate was slow at first, but increased rapidly after 5 May and continued to increase during June, when there was evidence of a decrease in root growth rate. Nitrogen greatly increased shoot growth, in contrast to its smaller and initially negative effect on root growth. Winter wheat apparently responded more to nitrogen in both shoot and root growth than spring sown cereals.

TABLE 12

Experiment 4. Final grain yield of different cereals, t/ha at 85% DM, S.E. 0·18 t/ha

Spring fertiliser N	Winter wheat	Spring wheat	Oats	Barley
None	2·2	3·5	3·3	3·4
100 kg/ha	5·4	4·3	4·8	4·6

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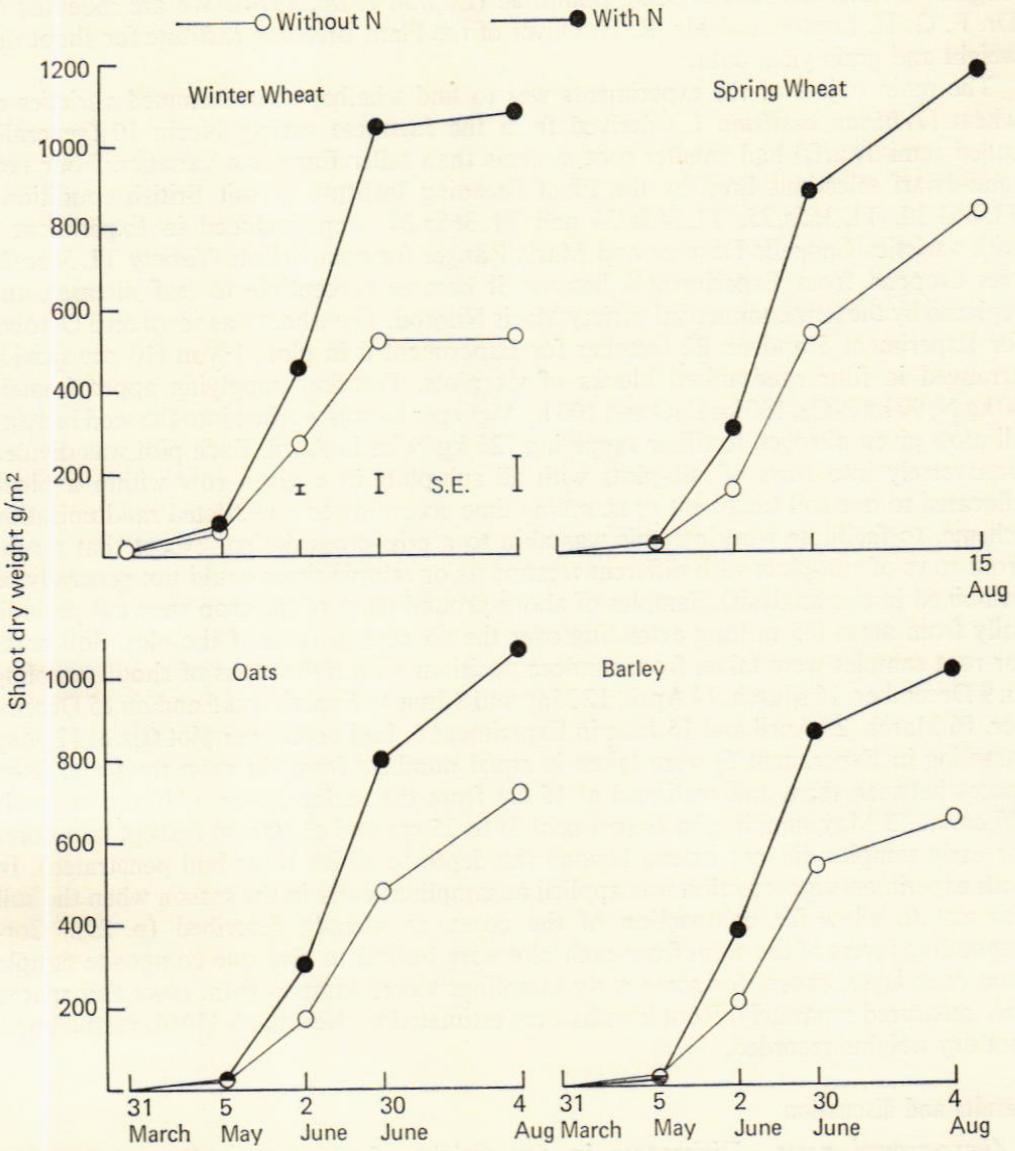

FIG. 12. Experiment 4. Effects of nitrogen fertiliser (100 kg N/ha) on shoots of different cereals.

Final grain yields of plots given spring nitrogen (Table 12) were as good as or greater than normally expected from this land.

Experiments 5 and 6

Comparison of growth of shoots and roots of normal and semi-dwarf winter wheat varieties

Two experiments were done in 1969/70 and 1970/71 in collaboration with staff of the Plant Breeding Institute, Cambridge, who measured top growth and yield, and of the Agricultural Research Council's Letcombe Laboratory, who studied the distribution of roots in the soil and their activity in absorbing nutrients by radioactive tracer techniques. The present account deals only with results for dry weights of roots and shoots and root

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lengths; a fuller account is being published (Lupton *et al.*, 1974). We are indebted to Dr. F. G. H. Lupton and Mr. R. H. Oliver of the Plant Breeding Institute for shoot dry weight and grain yield data.

The main object of the experiments was to find whether short-stemmed varieties of wheat (*Triticum aestivum* L.) derived from the Japanese variety Norin 10 (generally called semi-dwarfs) had smaller root systems than taller European varieties. Four new semi-dwarf selections bred by the Plant Breeding Institute to suit British conditions, TL 363/30, TL 365a/25, TL 365a/34 and TL 365a/37, were included in Experiment 5 with varieties Cappelle-Desprez and Maris Ranger for comparison. Variety TL 365a/25 was dropped from Experiment 6 because it became susceptible to leaf diseases, and replaced by the new commercial variety Maris Nimrod. The wheat was sown on 3 October for Experiment 5 and on 22 October for Experiment 6 in plots 1·8 m (10 rows) wide arranged in four randomised blocks of six plots. Fertiliser supplying approximately 40 kg N, 90 kg P_2O_5, 180 kg K_2O and 100 kg MgO per ha was worked into the seed bed and all plots given nitrogen fertiliser supplying 126 kg N/ha in April. Each plot was divided transversely into rows of sub-plots with all sub-plots in a given row within a block allocated to one soil treatment or sampling time according to a restricted randomisation scheme, to facilitate working (this was akin to a criss-cross design, except that results from rows of sub-plots with different treatments or sample times could not generally be combined in one analysis). Samples of above-ground parts of the crop were cut periodically from areas 0·5 m long extending over the six central rows of the plot. Soil cores for root samples were taken from random positions within the areas of shoot sampling on 9 December, 16 March, 14 April, 12 May and 8 June in Experiment 5 and on 15 December, 16 March, 28 April and 15 June in Experiment 6. Eight cores per plot (six at 12 May sampling in Experiment 5) were taken in equal numbers from the crop rows and from spaces between them and sectioned at 15 cm from the surface, then at 10 cm intervals (20 cm at 12 May sampling in Experiment 5) to 75 cm and at 100 cm (except that cores for early samples did not extend beyond the depth to which roots had penetrated). In both experiments a correction was applied at samplings early in the season when the soil was wet to allow for compaction of the cores, as already described (p. 29). Corresponding layers of the cores from each plot were bulked to give one composite sample from each layer, except for some early samplings where samples from rows and spaces were measured separately. Root lengths were estimated by Newman's (1966) method and root dry weights recorded.

Results and discussion

Above-ground parts. Differences in dry weight of above-ground parts between varieties were small until the time of the last root sampling in each experiment, about the time of flowering (Fig. 13). In Experiment 5, larger differences, although still only 15–20% of the means, developed after flowering; semi-dwarfs then tended to produce more grain and have less straw than taller varieties. In Experiment 6 TL 365a/37 had smaller shoot weights than other varieties after May, but differences between varieties were otherwise neither statistically significant nor consistent between samplings.

The grain yields (Table 13) in Experiment 5 ranged from good (TL 365a/25) to small

TABLE 13

Experiments 5 and 6. Grain yields, t/ha at 85% DM

	Cappelle-Desprez	Maris Ranger	Maris Nimrod	TL 363/30	TL 365a/25	TL 365a/34	TL 365a/37	S.E.
Experiment 5	5·1	4·4	—	5·6	6·4	4·7	4·9	0·34
Experiment 6	5·9	5·6	6·0	7·3	—	7·2	6·4	0·31

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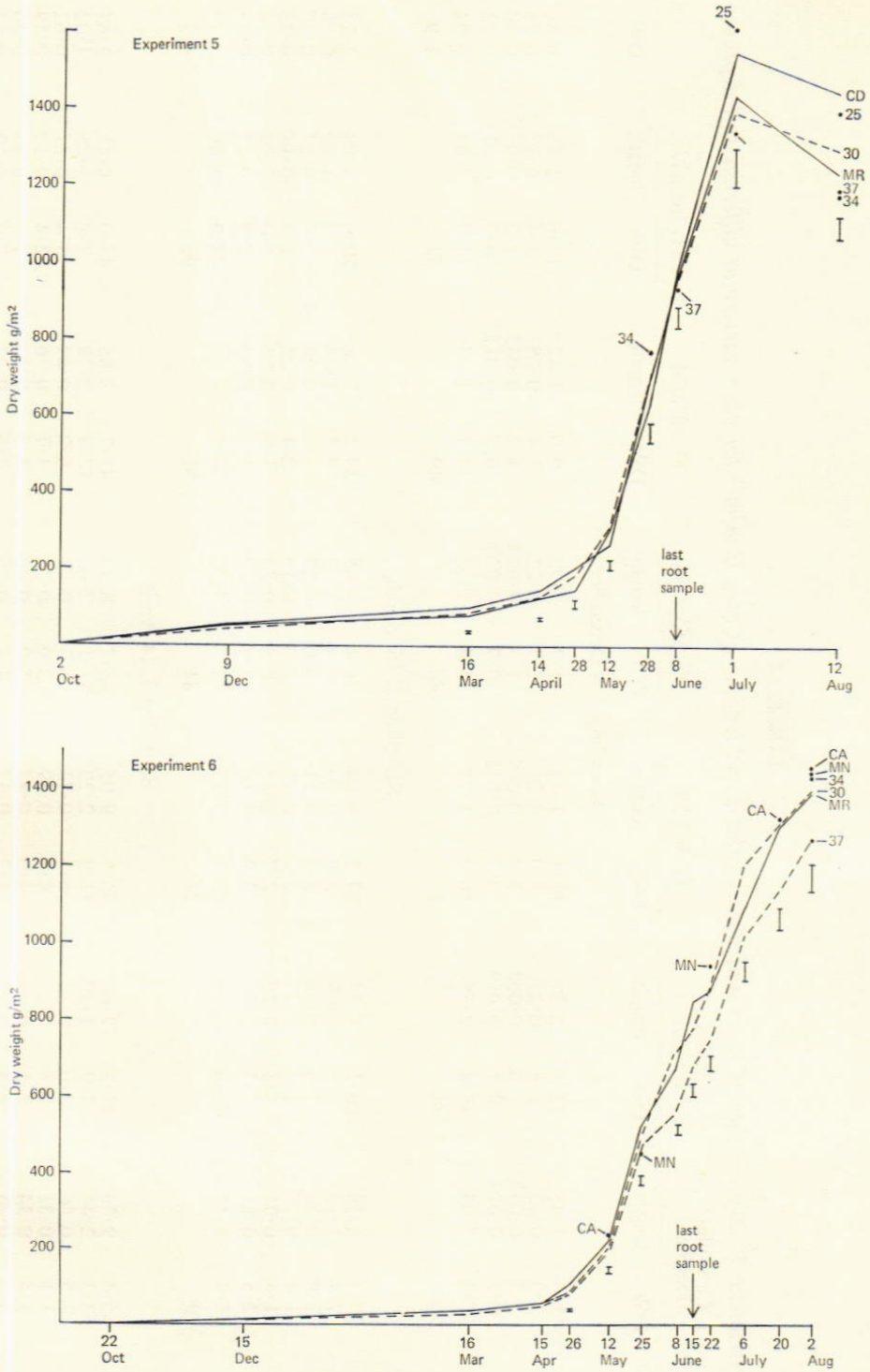

FIG. 13. Dry weights of above-ground parts of selected varieties in Experiment 5 (above) and 6 (below). Semi-dwarf varieties shown by broken lines, taller varieties by solid lines. CD: Cappelle Desprez, MN: Maris Nimrod, MR: Maris Ranger; semi dwarfs TL 363/30, TL 365a/25, TL 365a/34 and TL 365a/37 indicated by terminal code number. For Experiment 5 only Cappelle-Desprez, Maris Ranger and TL 363/30 and for Experiment 6 only Maris Ranger, TL 363/30 and TL 363/37 are plotted in full; where weights of other varieties lie outside these ranges they are also indicated.

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TABLE 14

Experiment 5. Dry weights of roots and shoots (g/m^2) and lengths of root (km/m^2) for each variety at different soil depths

Variety	Cappelle-Desprez		Maris Ranger		TL 363/30		TL 365a/25		TL 365a/34		TL 365/a37		S.E.	
Depth (cm)	DW	length	DW	length	DW	length	DW	length	DW	length	DW	length	DW	length
Sampling 1, 9 December														
Roots														
0–15	11·3	1·75	12·1	2·27	11·1	1·44	11·7	1·72	9·9	1·42	10·6	1·73	0·80	0·13
15–25	2·3	0·23	1·8	0·21	2·0	0·21	2·7	0·23	2·4	0·26	2·4	0·23	0·26	0·04
25–35	1·5	0·057	1·0	0·052	1·8	0·068	1·3	0·050	1·2	0·053	1·2	0·051	0·30	0·016
35–45	0·5	0·019	0·4	0·019	0·7	0·033	0·9	0·020	0·5	0·017	0·7	0·023	0·22	0·009
Total	15·7	2·05	15·4	2·55	16·0	1·75	16·4	2·02	14·1	1·75	14·9	2·04	0·94	0·13
Shoots	50		54		42		46		49		53		2·9	
Sampling 2, 16 March														
Roots														
0–15	30·7	6·36	28·1	5·75	29·2	6·04	31·1	6·05	39·4	7·28	29·6	5·88	2·78	0·40
15–25	7·4	1·13	6·3	1·08	5·9	0·80	6·4	1·02	8·4	1·04	6·7	1·00	0·70	0·14
25–35	2·9	0·24	2·6	0·26	3·5	0·31	3·0	0·27	3·1	0·28	2·8	0·28	0·37	0·05
35–45	1·4	0·15	1·4	0·13	2·5	0·21	2·0	0·19	2·4	0·22	1·9	0·18	0·35	0·03
45–55	1·4	0·06	1·5	0·10	2·7	0·23	2·8	0·20	1·8	0·14	2·0	0·09	0·38	0·04
55–65	2·5	0·21	1·7	0·08	3·9	0·18	3·4	0·20	1·7	0·09	2·9	0·23	0·79	0·07
Total	46·4	8·12	41·6	7·39	47·7	7·77	48·7	7·92	56·8	9·06	45·9	7·66	3·87	0·50
Shoots	79		98		84		81		91		91		6·3	
Sampling 3, 14 April														
Roots														
0–15	46·4	9·76	42·3	7·67	46·1	9·05	45·7	8·72	41·7	8·85	45·9	8·41	2·67	0·43
15–25	12·3	2·44	7·9	1·50	11·3	2·22	11·1	2·02	12·7	2·28	7·8	1·25	1·02	0·26
25–35	4·6	0·66	3·6	0·34	6·3	0·73	6·3	0·41	6·2	0·69	3·4	0·27	0·62	0·10
35–45	3·1	0·31	2·8	0·28	4·8	0·59	3·9	0·32	3·7	0·36	2·4	0·18	0·49	0·06
45–55	3·4	0·34	2·1	0·25	4·2	0·45	3·9	0·40	4·3	0·33	1·9	0·15	0·56	0·05
55–65	3·2	0·23	1·8	0·13	4·2	0·37	4·2	0·36	4·6	0·37	2·8	0·19	0·54	0·04
65–75	2·6	0·27	1·1	0·08	3·1	0·26	3·0	0·27	3·6	0·31	2·7	0·22	0·73	0·07
75–100	2·7	0·32	0·6	0·37	3·7	0·31	2·2	0·22	3·7	0·35	1·4	0·11	1·03	0·16
Total	78·3	14·3	62·3	10·6	83·8	14·0	79·5	12·7	80·7	13·5	68·3	10·8	3·40	0·81
Shoots	124		143		128		133		143		124		8·0	

Sampling 4, 12 May														
Roots														
0–15	65·8	9·63	58·4	9·33	68·8	—	69·3	—	69·5	—	66·7	—	5·67	0·83
15–35	14·8	3·13	14·7	3·12	18·6	—	11·8	—	18·0	—	12·9	—	1·43	0·31
35–55	6·5	1·18	7·7	1·15	9·5	—	7·2	—	6·8	—	7·8	—	1·66	0·20
55–75	5·1	0·57	6·5	0·67	7·0	—	6·3	—	7·7	—	6·0	—	1·56	0·08
75–100	4·2	0·42	3·6	0·38	6·2	—	4·4	—	4·0	—	3·6	—	1·29	0·11
Total	96·5	14·9	90·9	14·4	110·1	—	99·1	—	106·0	—	97·1	—	7·41	1·08
Shoots	304		264		313		274		319		279		25·6	
Sampling 5, 8 June														
Roots														
0–15	67·1	11·9	64·3	12·1	71·8	13·7	83·4	14·7	78·8	12·6	57·1	10·6	4·85	1·05
15–25	18·2	3·88	16·4	3·11	17·3	3·69	18·2	3·70	20·6	3·55	17·8	3·48	1·75	0·39
25–35	6·9	1·00	6·8	1·04	7·7	1·30	7·6	0·95	7·1	0·87	7·9	1·00	0·84	0·15
35–45	5·2	0·89	4·8	0·77	7·4	1·11	5·3	0·82	5·5	0·75	6·0	0·85	0·75	0·13
45–55	3·1	0·41	3·4	0·46	4·6	0·57	5·5	0·61	3·6	0·44	4·9	0·61	0·51	0·08
55–65	3·7	0·34	4·1	0·51	3·8	0·37	6·4	0·60	4·8	0·45	4·7	0·41	0·75	0·07
65–75	2·4	0·30	3·1	0·31	4·2	0·42	5·6	0·49	4·4	0·41	4·5	0·44	0·64	0·06
75–100	4·5	0·55	7·5	0·86	7·8	0·90	9·6	0·80	10·6	1·05	10·0	1·03	1·91	0·16
Total	111·3	19·3	110·4	19·2	124·8	22·1	141·5	22·7	135·5	20·1	112·9	18·4	7·96	1·37
Shoots	988		971		960		870		952		934		53·7	

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TABLE 15 *Experiment 6. Dry weights of roots and shoots (g/m²) and lengths of root (km/m²) for each variety at different soil depths*

Variety	Cappelle-Desprez		Maris Nimrod		Maris Ranger		TL 363/30		TL 365a/34		TL 365a/37		S.E.	
Depth (cm)	DW	length	DW	length	DW	length	DW	length	DW	length	DW	length	DW	length
Sampling 1, 15 December														
Roots														
0–15	4·1	0·81	3·0	0·60	3·6	1·00	3·9	0·87	2·9	0·70	3·1	0·67	0·45	0·11
15–25	1·1	0·12	0·9	0·14	1·2	0·16	1·2	0·13	1·0	0·41	0·9	0·11	0·08	0·013
25–35	0·6	0·039	0·5	0·029	0·4	0·028	0·4	0·023	0·3	0·019	0·4	0·026	0·07	0·005
35–45	0·04	0·003	0·05	0·004	0·06	0·005	0·06	0·004	0·02	0·001	0·02	0·002	0·03	0·003
Total	5·8	0·98	4·4	0·77	5·3	1·19	5·6	1·03	4·3	0·87	4·4	0·81	0·47	0·11
Shoots	9·1		9·1		9·2		8·4		8·1		8·4		0·53	
Sampling 2, 16 March														
Roots														
0–15	24·1	5·95	18·3	5·87	25·9	6·62	21·9	5·57	24·2	6·16	17·4	4·19	0·80	0·30
15–25	6·1	1·53	5·7	1·44	7·9	1·93	6·1	1·48	8·2	1·65	4·6	1·05	0·80	0·17
25–35	1·9	0·20	1·4	0·13	2·0	0·24	1·8	0·14	1·9	0·20	1·6	0·12	0·33	0·050
35–45	1·1	0·066	0·7	0·070	1·2	0·118	1·3	0·106	1·1	0·067	0·7	0·049	0·28	0·029
45–55	1·3	0·081	0·8	0·031	0·9	0·112	1·2	0·082	0·7	0·029	0·7	0·044	0·18	0·027
55–65	0·6	0·036	0·4	0·022	1·2	0·108	0·9	0·044	0·3	0·019	0·5	0·048	0·26	0·028
Total	35·2	7·86	27·2	7·56	39·2	9·12	33·3	7·42	36·3	8·12	25·7	5·51	1·75	0·42
Shoots	27		26		35		29		28		25		1·5	
Sampling 3, 26 April														
Roots														
0–15	41·5	9·43	33·3	7·99	43·0	8·68	40·8	7·94	40·2	8·66	36·1	8·08	2·51	0·61
15–25	7·9	1·74	6·7	1·40	10·9	1·97	7·0	1·30	8·3	1·54	6·7	1·66	1·54	0·31
25–35	2·1	0·18	1·7	0·14	3·7	0·45	2·8	0·23	2·5	0·17	2·3	0·14	0·33	0·05
35–45	2·8	0·28	1·6	0·14	2·8	0·21	1·8	0·14	2·6	0·21	1·5	0·14	0·64	0·06
45–55	2·6	0·23	1·4	0·17	2·2	0·18	1·8	0·16	2·0	0·16	2·1	0·23	0·70	0·06
55–65	1·4	0·11	1·0	0·08	1·7	0·13	1·4	0·13	1·2	0·09	3·0	0·27	0·84	0·07
65–75	1·2	0·07	0·8	0·06	1·4	0·10	1·4	0·08	0·6	0·05	1·0	0·07	0·41	0·04
75–100	0·6	0·04	0·8	0·06	1·4	0·09	1·2	0·06	0·2	0·01	0·7	0·05	0·42	0·03
Total	60·1	12·08	47·5	10·04	67·1	11·82	58·1	10·03	57·6	10·89	53·5	10·63	5·01	0·68
Shoots	83		70		105		83		75		80		6·1	
Sampling 4, 8 June														
Roots														
0–15	80·7	11·3	88·4	9·2	82·2	11·9	84·7	11·6	112·3	11·4	85·0	9·9	9·73	1·0
15–25	12·7	2·50	12·7	2·68	13·9	3·01	14·5	2·93	15·8	2·90	11·7	2·45	1·52	0·40
25–35	4·8	0·43	3·6	0·43	5·0	0·53	4·3	0·55	5·7	0·43	4·1	0·44	0·62	0·08
35–45	4·1	0·51	4·3	0·51	3·5	0·43	4·1	0·51	3·7	0·40	4·8	0·51	0·64	0·07
45–55	3·8	0·50	4·1	0·54	4·2	0·50	4·5	0·58	3·8	0·45	4·0	0·46	0·73	0·10
55–65	3·5	0·38	3·6	0·48	4·2	0·43	4·2	0·43	2·7	0·33	3·1	0·32	0·78	0·07
65–75	3·5	0·46	2·4	0·29	3·6	0·40	3·2	0·38	2·7	0·33	3·0	0·34	1·00	0·11
75–100	5·9	0·66	3·2	0·34	6·4	0·68	5·3	0·50	2·4	0·31	5·5	0·54	1·98	0·18
Total	119·1	16·7	122·4	14·4	123·0	17·9	124·8	17·5	149·7	16·5	121·2	15·0	10·75	0·97
Shoots	641		688		669		709		614		556		25·0	

(Maris Ranger), though not unusually so for the type of land. In Experiment 6 yields were larger than in Experiment 5; all were good for this land and the best (TL 363/30) exceptionally so.

Roots. In both experiments all varieties had similar amounts of roots and few differences were significant at the 5% level (Tables 14, 15 and Fig. 14). In Experiment 5 root dry weights on 9 December had already reached more than one-tenth of their June weights, which were probably close to their maxima because roots of cereals appear to grow little after flowering (Experiments 1 and 2 above and Troughton, 1962). They continued to grow at about the same average rate during the winter, then from mid-March grew at a faster rate until June (Fig. 14). Roots extended below 35 cm deep on 9 December, below 55 cm on 16 March and below 1 m on 12 May (Fig. 15) (consequently a small fraction of the total roots were probably not recovered in the 8 June samples).

In Experiment 6 root dry weights on 15 December were less than 5% of their June weights because of later sowing and cooler autumn weather. Roots grew at almost the

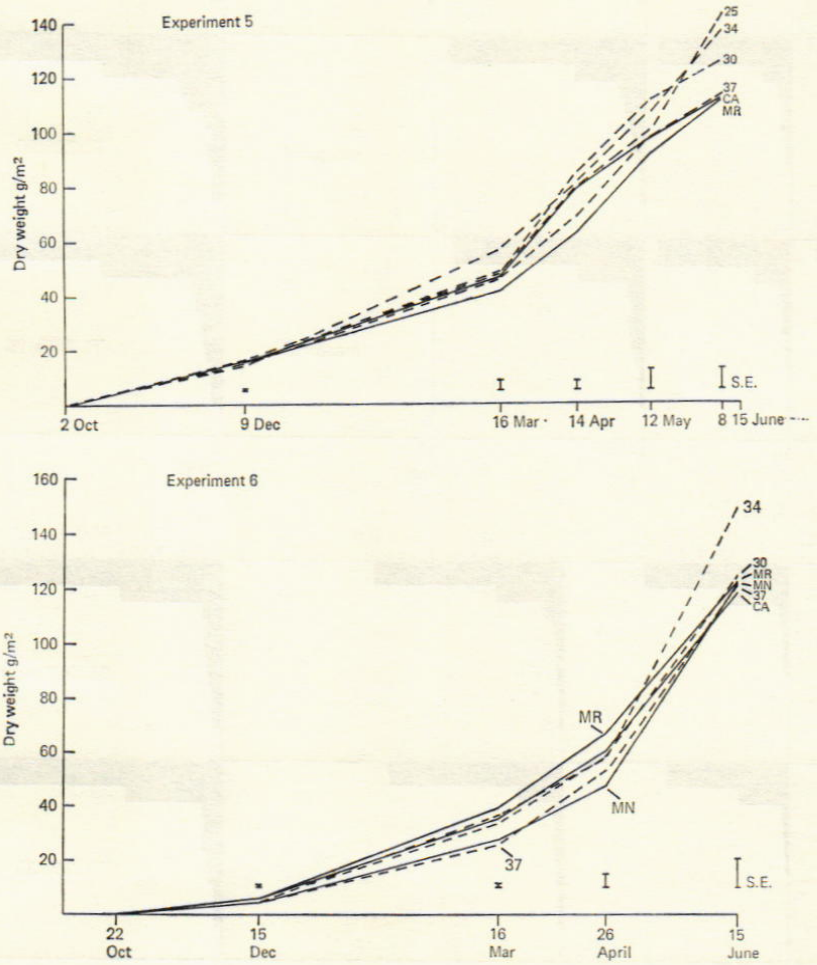

FIG. 14. Total dry weights of roots in Experiments 5 (above) and 6 (below). Semi-dwarf varieties shown by broken lines and taller varieties by solid lines. CD: Cappelle-Desprez, MN: Maris Nimrod, MR: Maris Ranger; semi-dwarfs TL 363/30, TL 365a/25, TL 365a/34 and TL 365a/37 indicated by terminal code number.

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same rate during the winter as in Experiment 5, however, and after mid-March grew faster than in the previous year so that the weights in June were very similar to those in Experiment 5 (Fig. 14). Although smaller amounts of roots were produced in autumn and winter in Experiment 6, they penetrated to about the same depth at each sampling as in Experiment 5 (Tables 14, 15 and Fig. 15).

At early samplings in both experiments there were more roots in the top 15 cm of soil beneath the crop rows than between them (Table 16). However, except for the sample on 15 December in Experiment 6 when the crop had grown little and when there were

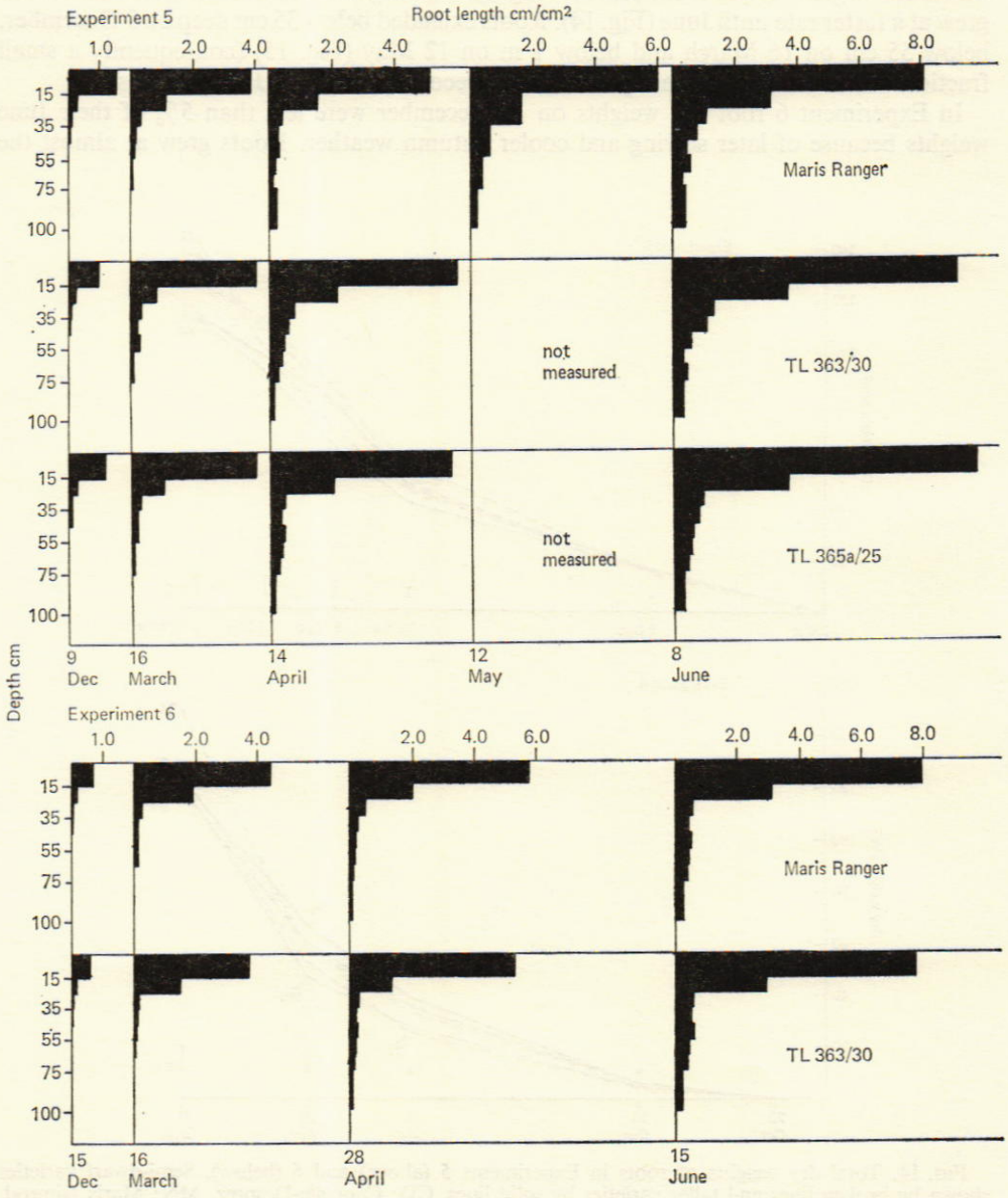

FIG. 15. Distribution of root length with depth for selected varieties in Experiments 5 (above) and 6 (below).

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significantly less roots between the rows at all depths, there was little evidence of differences between rows and spaces in horizontal distribution of roots below 15 cm deep. Moreover in samples on 16 March, when length of roots beneath rows and beneath inter-row spaces were separately determined, there was evidence in Experiment 5 and to a lesser extent in Experiment 6 that the differences in horizontal distribution of root length in the top 15 cm of soil were smaller than for dry weight distribution. This is consistent with the large contribution to dry weight beneath the rows, but not to length, expected from the thickened bases of adventitious crown roots.

TABLE 16

Experiments 5 and 6. Mean dry weights of roots (g/m^2) and root lengths (km/m^2) where separately measured, from beneath crop rows (R) and spaces between rows (S). Standard errors in brackets

(Weights and lengths are given per unit area of soil beneath the rows or in the spaces between rows respectively, i.e. the total weight or length per unit plot area is the mean of the row and space values, not the sum)

Experiment 5

	Sampling 1, 9 December		Sampling 2, 16 March				Sampling 3, 14 April	
	Weight		Weight		Length		Weight	
Depth (cm)	R	S	R	S	R	S	R	S
0–15	15·0 (0·52)	7·3 (0·32)	38·5 (1·68)	24·2 (0·78)	6·61 (0·22)	5·85 (0·22)	54·8 (1·77)	34·6 (0·82)
15–25	2·5 (0·15)	2·1 (0·14)	7·0 (0·39)	6·7 (0·39)	1·09 (0·09)	0·93 (0·06)	11·1 (0·50)	10·0 (0·57)
25–35	1·5 (0·11)	1·2 (0·16)	3·3 (0·24)	2·7 (0·16)	0·29 (0·03)	0·26 (0·03)	5·4 (0·35)	4·4 (0·35)
35–45	0·6 (0·10)	0·7 (0·13)	2·0 (0·19)	2·0 (0·20)	0·19 (0·02)	0·17 (0·02)	not separated	
45–55			2·3 (0·26)	1·7 (0·15)	0·17 (0·03)	0·10 (0·01)		
55–65			3·0 (0·45)	2·4 (0·30)	0·19 (0·04)	0·14 (0·03)		
Total	19·6 (0·62)	11·3 (0·46)	56·0 (1·94)	39·7 (1·41)	8·54 (0·023)	7·45 (0·29)	71·2 (1·76)	49·0 (1·17

Experiment 6

	Sampling 1, 15 December				Sampling 2, 16 March			
	Weight		Length		Weight		Length	
Depth (cm)	R	S	R	S	R	S	R	S
0–15	4·67 (0·34)	2·21 (0·11)	1·00 (0·081)	0·55 (0·027)	23·6 (0·58)	20·4 (0·62)	5·97 (0·199)	5·49 (0·156)
15–25	1·28 (0·05)	0·82 (0·06)	0·18 (0·008)	0·09 (0·008)	7·0 (0·43)	5·9 (0·35)	1·61 (0·080)	1·41 (0·076)
25–35	0·56 (0·05)	0·31 (0·04)	0·04 (0·004)	0·02 (0·003)	2·1 (0·18)	1·5 (0·14)	0·20 (0·028)	0·14 (0·017)
35–45	0·57 (0·02)	0·31 (0·01)	0·004 (0·001)	0·003 (0·001)	0·9 (0·17)	1·1 (0·16)	0·09 (0·019)	0·07 (0·011)
45–55					0·9 (0·18)	1·0 (0·11)	0·08 (0·021)	0·05 (0·007)
55–65					0·7 (0·19)	0·6 (0·13)	0·06 (0·023)	0·03 (0·007)
Total	6·57 (0·37)	3·37 (0·13)	1·22 (0·084)	0·66 (0·028)	35·2 (1·16)	30·4 (0·93)	8·01 (0·217)	7·19 (0·215)

Consideration of root length did not show any striking differences compared to root dry weight. Where the relative growth rate or distribution of length differed from those of dry weight the differences can be seen most clearly by examining the specific root lengths (length per unit dry weight of roots) (Table 17). The length corresponding to a given weight of roots tended to increase during the winter, when presumably few assimilates were available, and was greater at this stage in Experiment 6 when little growth was made in autumn than in Experiment 5 when the crop was well grown at the beginning of winter. During spring and early summer specific root length decreased as the supply of assimilates increased, and was eventually less in Experiment 6 than in Experiment 5. Specific root length was usually much less in layers below 25 cm than above, indicating the large numbers of fine roots in the top soil, and there was a tendency towards smaller values in deeper layers. The sharp decrease in specific root length below 35 cm at Sampling 3 of Experiment 5 may reflect the advance of thicker adventitious (crown) roots into these layers.

Although differences between varieties in amount of roots did not usually persist throughout the season, some differences reached significance at the 5% level at particular samplings. In Experiment 5, TL 365a/37 and Maris Ranger had less roots than other varieties below the top 15 cm of soil on 14 April (in Maris Ranger this may have resulted

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TABLE 17

Experiments 5 and 6. Mean specific root length (length per unit dry weight, m/g) at each depth

Experiment 5

Depth (cm)	Sampling 1 9 December	Sampling 2 16 March	Sampling 3 14 April	Sampling 4 12 May*	Sampling 5 8 June
0–15	155	199	198	151	182
15–25	101	148	187		197
25–35	40	92	105	211	140
35–45	33	92	49		153
45–55		67	52	169	124
55–65		62	44		99
65–75				108	102
75–100				107	108
0–bottom	132	168	168	158	167

Experiment 6

	Sampling 1 15 December	Sampling 2 16 March	Sampling 3 28 April	Sampling 4 15 June
0–15	226	262	217	127
15–25	128	242	200	202
25–35	62	91	82	104
35–45	84	74	84	118
45–55		62	89	124
55–65		69	77	114
65–75			62	125
75–100			71	116
0–bottom	189	233	192	131

* Mean of Cappelle-Desprez and Maris Ranger only

from bad winter mildew infection). Fig. 15 illustrates the difference in density of roots between Maris Ranger and two other varieties; such behaviour might have adverse consequences in a dry spring. On 12 May TL 363/30 and TL 365a/34 had more roots than other varieties between 15 and 35 cm deep and on 8 June TL 365a/25 and 34 had more roots in the top 15 cm of soil (Table 14). In Experiment 6, Maris Ranger had more and Maris Nimrod and TL 365a/37 less weight of roots than other varieties on 16 March, although Maris Nimrod did not have a shorter length of roots (Table 15). By 28 April Maris Ranger had more roots and Maris Nimrod less than other varieties between 25 and 35 cm deep. In general, however, there was no evidence that semi-dwarf varieties had less well developed root systems than taller varieties.

Comparison of different experiments

In the course of the six experiments, barley was grown in the first four years and winter wheat in the last three. Each experiment included at least one treatment in which the crop was grown under conditions approximating to normal agricultural practice (i.e. without shading) and given an adequate supply of the main plant nutrients. It is therefore possible to compare growth of barley or wheat with roughly similar fertiliser treatments in different years and obtain some idea of the range of variation that may be caused by different growing conditions, expecially on root growth.

The following treatments from each experiment are included in the comparisons:

Experiment 1: barley, Maris Badger, given 100 kg N/ha
Experiment 2: barley, Maris Badger, given P, K and 100 kg N/ha
Experiment 3: unshaded barley, Maris Badger, given 126 kg N/ha

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Experiment 4: barley, Maris Badger, and winter wheat, Cappelle-Desprez, given 25 kg N/ha in autumn and 100 kg N/ha in spring

Experiments 5 and 6: winter wheat, Cappelle-Desprez, given 40 kg N/ha in autumn and 126 kg N/ha in spring.

Differences in nitrogen fertiliser rates applied to barley in the above list are probably not important (cf. results of Experiment 1). Winter wheat continues to respond to

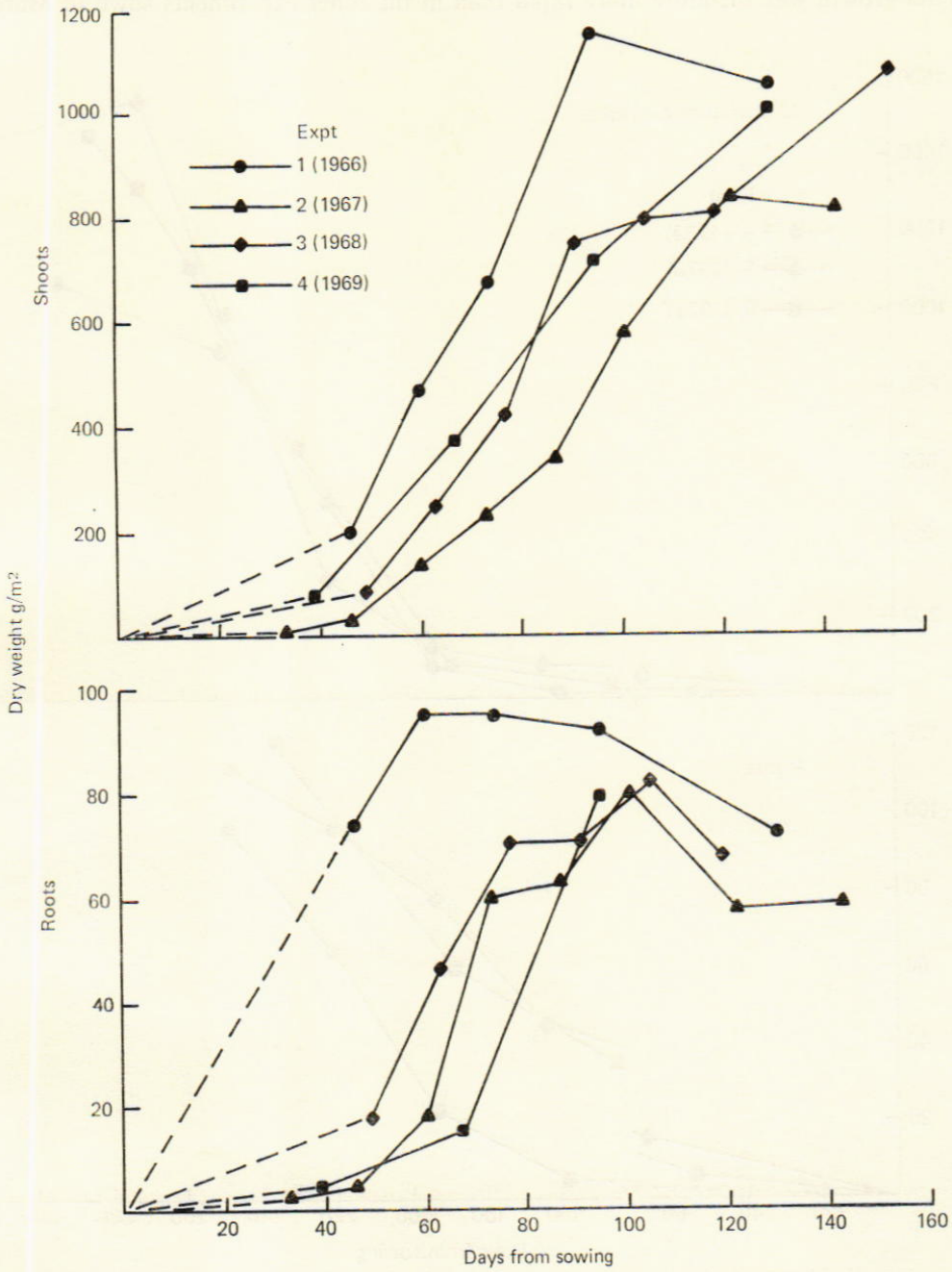

FIG. 16. Dry weights of shoots (above) and roots (below) of barley, given nitrogen fertiliser, in Experiments 1–4 inclusive.

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nitrogen at higher rates of application than does barley so the differences in rates above may have contributed to differences in its growth in different experiments.

Barley. The amounts of barley roots, measured as dry weight, in Experiments 2, 3 and 4 all reached very similar maximum values (presumed in Experiment 4) at approximately 100 days after sowing in each case (Fig. 16). The much quicker attainment of maximum root weight in Experiment 1 probably occurred because it was sown on 29 April and ni tial growth was therefore more rapid than in the other experiments sown in March,

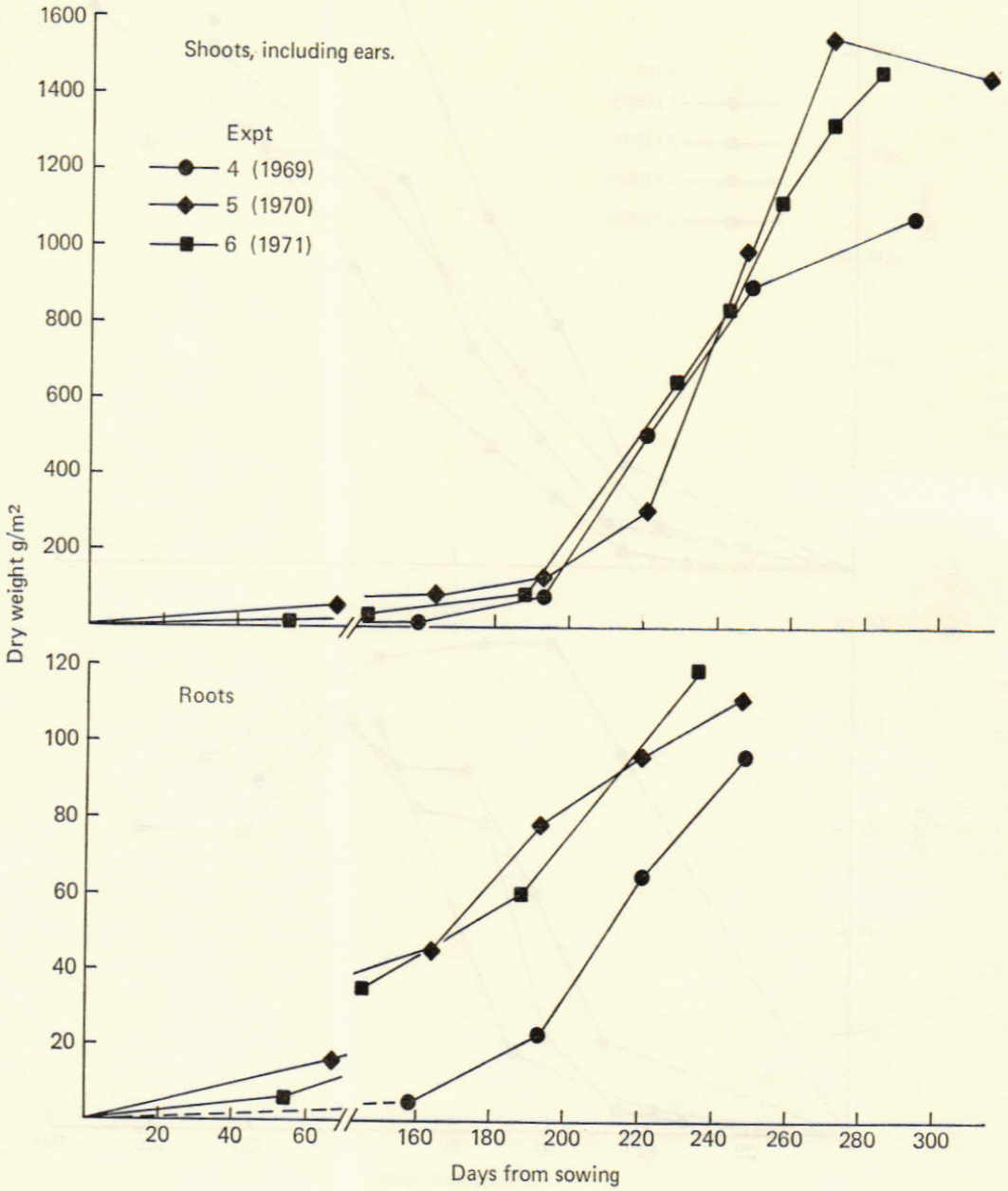

FIG. 17. Dry weights of shoots (above) and roots (below) of winter wheat, var. Cappelle-Desprez, given nitrogen fertiliser, in Experiments 4, 5 and 6.

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but in fact the maximum occurred in Experiment 1 at very much the same time, about 1 July, as in the other experiments. The course of root development in the three following experiments sown at a more normal time varied considerably from year to year. For example, barley in Experiment 3 had roughly twice as much roots as in Experiment 4 at any time up to about 75 days after sowing, in spite of being sown 16 days earlier, which might have been expected to result in slower initial growth. The soil conditions for sowing Experiment 3 were very good, whereas they were rather wet when Experiment 4 was sown, while sowing of Experiment 2 was followed by a very rainy spell which maintained the soil saturated for long periods. These differences may partly have accounted for differences in growth.

The differences in shoot growth between years were not always similar to the differences in root growth (Fig. 16). The development of the shoots after sowing in Experiment 1 was not much faster than in the other experiments. Whereas root development in Experiment 4 was apparently slower during the middle period of vegetative growth than in Experiments 2 and 3, shoot growth at this stage was more rapid. Perhaps, therefore, the retardation of root growth was partly caused by climatic conditions favourable to shoot development leaving little assimilates available for the root system. However, the final shoot dry weight attained was similar in Experiments 3 and 4 and also in Experiment 1.

The differences between root and shoot behaviour in different years mean that there were wide variations in the fraction of total weight represented by roots, e.g. between 39 and 49 days after sowing: from 0·28 in Experiment 1 or 0·21 in Experiment 4 to 0·12 in Experiment 2; between 60 and 70 days after sowing: from 0·17 in Experiment 1 or 0·16 in Experiment 3 to 0·11 in Experiment 4. More detailed study is needed to interpret such differences in root : shoot relationships between years.

Winter wheat. When adjusted to allow for the earlier sowing date of Experiment 5 by plotting dry weights against number of days from sowing, the growth of roots in spring was very similar in both Experiments 5 and 6 (Fig. 17). Although the adjustment did not eliminate the difference in autumn growth, it did not become absolutely greater and was relatively unimportant for root development in the following season. Roots in Experiment 4 had made little growth by March (158 days from sowing), but their rate of growth thereafter was similar to, or a little faster than, growth in Experiments 5 and 6. In this comparison, therefore, it was chiefly the much smaller root systems developed in autumn and winter that accounted for the final differences in root dry weights.

Shoot growth in all three experiments was very similar between the latter half of April (190 days) and flowering (about 250 days), when the time scales had been adjusted for the differences in sowing date (Fig. 17). Although there were obvious differences in the size of the shoots in December (50–70 days) and March (145–165 days), they seemed not to have any important effect for later vegetative growth. The smaller increase in dry weight after flowering in Experiment 4 than in Experiments 5 and 6 may have resulted from the smaller amount of fertiliser nitrogen supplied in this experiment.

General discussion

Methods. We shall not consider here methods that involve separation of root systems more or less intact from the soil, such as the pin-board technique. They may be very useful for visual examination of root distribution, and were used for this purpose in some of our experiments, but their high labour requirement makes them unsuited to quantitive root studies in the field.

Root samples have previously been obtained by soil coring using several different

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types of apparatus (Boehle *et al.*, 1963; Fehrenbacher & Alexander, 1955; Kawatake *et al.*, 1964; Kmoch, 1960; Williams & Baker, 1957). The advantages of the equipment described in this paper are that it enables core sampling to be done reasonably quickly and it is portable. The first makes possible repeated sampling of an experiment needed for measurement of root growth. The second makes it possible to sample microplot areas within experimental plots without serious damage to the surrounding crop. Without the development of much more elaborate equipment great improvements to the sampling process itself seem unlikely in the near future. Its chief limitation is that it becomes increasingly difficult to use for depths greater than 1 m because of the need to place the hammer on top of a tube standing more than this height above the ground before driving it in. It is also somewhat restricted by difficult soil conditions, i.e. very hard, dry or stony soil, although the coring tubes have a surprising ability to produce satisfactory samples in soil with stones of soft or brittle materials such as sandstone or flint. However, this limitation also largely affects other quantitative methods for studying roots.

The sampling process for studying roots by direct measurement, therefore, presents no undue difficulties. The overall labour requirements in the field are probably no greater than are needed for other methods of investigation. The principal difficulties outstanding are separating roots from undecomposed plant residues and to a lesser extent the rather tedious counting involved in visual estimation of length by Newman's (1966) method. No satisfactory alternative to sorting by hand has been found for the first problem, although this can be aided by partial separation in a liquid cyclone. Trials of electronically controlled sorters dependent on photoelectric detection of particles have not yet been successful and it seems likely that expensive equipment would need to be developed to solve the problem by this technique.

It is expected that length estimation will be greatly facilitated in future by using an image analysing computer ('Quantimet 720' made by Image Analysing Computers Ltd., Melbourn, Royston, Herts.) to give direct readings of the length of roots arranged in trays as for Newman's method and recorded on 35 mm film negatives. A successful photomechanical machine for the same purpose has been devised by Dr. H. R. Rowse at the National Vegetable Research Station (Winter, 1972).

The approach to root sampling and measurement we have used is basically straightforward and unsophisticated, but it has proved effective in obtaining important data on growth of root systems not previously available. It has, indeed, several advantages over the less direct methods of measurement. It permits many physical attributes of the roots to be measured on the same samples, for example weight, volume, length, mean diameter. It also permits the roots to be analysed chemically to determine their total mineral content if required, although some elements, such as potassium, may be partly lost during root washing. Other methods of root estimation usually determine only a single parameter, and because they are indirect, may introduce errors of calibration into the root measurements. However, they too may have advantages over the direct method for particular purposes.

Labelling the root system with a radioactive isotope by injecting it into the base of the shoots of the plant and relying on the translocation system of the plant to distribute it uniformly through the root system is one such method. The radioactivity is usually measured in soil samples without needing to separate out the roots. It indicates the proportion of the total roots in each soil layer, but can give absolute amounts only by calibration against direct measurements of roots extracted from soil. The method was first described by Racz, Rennie & Hutcheon (1964) who used ^{32}P to label wheat roots. It was used in Experiments 5 and 6 of this paper (Lupton *et al.*, 1974) with ^{86}Rb as the tracer, which has the advantage of emitting gamma radiation that can be detected through a considerable thickness of soil sample, although it requires rather specialised and

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expensive counting equipment for its use. The radioactive injection method has the important advantage of indicating the distribution of living roots (i.e. those to which translocation is going on) (Ellis & Barnes, 1973), whereas living roots cannot readily be distinguished from non-living in samples separated from soil. For some purposes, however, this is not important, e.g. during early growth of an annual crop little root death is likely to occur; in considering the contribution of roots to total dry matter production of the plant it is irrelevant whether they are alive or not; in considering the volume of soil that has been explored by roots it may not be important that roots have died since they exhausted a nutrient from soil through which they have grown.

Roots labelled with radioactive isotopes in the manner described may be detected *in situ* by driving an autoradiograph-film holder into the soil so that it cuts the roots, whose positions then appear after a suitable exposure time as dark spots on the film (Baldwin, Tinker & Marriott, 1971). The length of roots per unit soil volume can easily be calculated from the density of spots and this technique also permits study of the micro-distribution of roots in the soil, i.e. the degree of regularity of distribution or clumping, which cannot be done by root extraction methods. Baldwin and Tinker (1972) have developed this method to study interpenetrating root systems separately and in relation to each other by injecting different plants with isotopes emitting radiation of different energies. Root extraction methods cannot be used to measure interpenetrating roots directly, except perhaps rarely when they are of different colour or morphology.

Root distribution has been inferred from the extraction by the plant of substances in the soil. An isotope (e.g. ^{32}P) may be injected into the soil at a known depth and its appearance in the shoots of a plant taken to indicate root penetration to that depth, or the amount taken up over a period related to the amount of roots at that depth (Hall *et al.*, 1953; Newbould, Taylor & Howse, 1971). Such measurements are more closely related to the effectiveness of the root system at the particular depth in absorbing the isotope supplied. The amount of roots present is only one component of this. The technique was used to indicate root activity in absorbing ^{32}P in Experiment 5 and 6 of the present paper (Lupton *et al.*, 1974). Similarly, the loss of soil moisture from different depths under a crop, measured with a neutron soil moisture probe, has been used as an indicator of root penetration to each depth (Long & French, 1967; Draycott & Durrant, 1971). The rate of loss may show the activity of the roots in absorbing water if corrections can be made for water flow through the soil and for changes in water potential with water content. Clearly, however, observations of this sort do not replace measurement of the roots themselves by direct or indirect means, but are complementary to them. They measure the total activity of the roots; measurement of the roots shows whether differences in activity can be accounted for by differences in amount of roots or, by inference, whether the activity of unit amount of roots varies.

The results of these experiments not only can help to interpret the responses of cereal crops to the treatments and conditions under which they are grown, but also provide basic data on the amount and distribution of roots at different stages of growth for use in theoretical work on the supply of nutrients and water to the plant, especially their movement through the soil and through the roots themselves.

Nutrition and light intensity. Experiments 1, 2 and 4 all showed that nitrogen fertiliser produced larger plants with relatively smaller root systems (although after the first few weeks absolutely larger) than did no fertiliser. In Experiments 2 and 4 nitrogen generally depressed root growth in the deeper soil layers more than in the surface layer (cf. Goedewaagen, 1955), but the significantly smaller amount of roots in the top 15 cm of soil which also occurred at Sampling 2 on 5 May in Experiment 4 suggests that nitrogen

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affected especially parts of the root system that were young and most actively growing. It did not appear that phosphorus or potassium significantly affected root growth independently of their effects on the plants as a whole, which were in any case small relative to the effects of nitrogen. It is interesting that the roots themselves seem not to have been adversely affected by lack of nitrogen, perhaps because their demand for it is less than that of the leaves and they are nearer to the source of supply. On the other hand the large effects of shading on root growth indicate that roots depend very much on the supply of carbohydrate from the shoots. This is supported by the effects on roots of higher rates of nitrogen fertiliser, which by stimulating growth of shoots, presumably cause a relative decrease in the carbohydrate available for root production.

Results of these field experiments therefore agree with conclusions about the carbohydrate economy of roots in relation to shoots drawn from solution culture and other experiments elsewhere. Similarly the effect of nitrogen in decreasing specific root length, implying that it produced thicker roots, agrees with results of earlier experiments in solution culture or pots of soil (Troughton, 1962). Insofar as phosphorus and potassium significantly increased root dry weights in isolated instances in Experiment 2, their effects also agree with earlier results (Troughton, 1962) and the decrease in specific root length (i.e. thicker roots) with potassium fertiliser found at Sampling 3 supports the observations of Brenchley and Jackson (1921) on barley growing in pots of soil. However, there is doubtful value in pressing further the comparison between the general lack of significant effects of phosphorus and potassium on root : shoot relations in our experiment and the considerable range of effects found by others. More experiments are desirable to study the effects of these two nutrients in greater detail than was possible in the single experiment done so far, in which their factorial combination with nitrogen limited factor levels to two and prevented much replication.

Different crops and varieties. It is notable that root production was similar in all the main cereal crops tested in Experiment 4, and perhaps especially that winter wheat did not ultimately have more roots than spring sown crops. Similarly different varieties of winter wheat tested in Experiments 5 and 6 did not differ greatly in amount or distribution of their roots, although they were selected for widely different shoot habits.

To the extent that different crops have similar amounts of roots, root density cannot account for the differences in susceptibility of different cereals to deficiency of particular nutrients, e.g. phosphorus and potassium. On the Woburn Reference Plots on a nearby site, for example, both grain and straw yield of barley responded well to potassium fertiliser, whereas oats did not (Widdowson & Penny, 1967, 1972). Similarly on the Rothamsted Reference Plots wheat responded more to potassium fertiliser than did barley (Widdowson & Penny, 1973). Here wheat usually extracted more potassium from soil to which no potassium fertiliser had been added than did barley, so it is more likely that the needs of wheat were greater than that it was less able to extract potassium from the soil. With kale, however, the amount of potassium extracted from the soil was much greater than for cereals and sufficient to prevent the crop suffering from potassium deficiency. It would therefore be interesting to have measurements of its root growth to see whether they could account for the difference in its response to potassium.

Further problems. Measurements of root systems of crops other than cereals are an obvious possibility for future work aimed at answering questions such as this. Certain crops, e.g. potatoes, sugar beet and to a lesser extent beans and kale, pose problems of sampling and interpretation because their root distribution in horizontal planes cannot be considered uniform. It is necessary to take samples representing all positions relative

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to the crop rows and plants within the rows and it may be necessary to consider separately root densities in the soil volume corresponding to each position.

The relations between size and growth rate of root systems and uptake of nutrients and water are likely to be another fruitful field of investigation. Uptake rates may depend on the amount of root present or on the rate at which new roots are produced, or they may be controlled by plant demand. Little has been done in the field to test the application of theoretical and laboratory work to practical situations. Some data relevant to these questions were obtained for Experiments 5 and 6 and will be published elsewhere; similar studies on results from Experiment 4 are contemplated.

There remain many effects of the environment on roots to be investigated. Water is one factor that we have not yet studied. Both soil and air temperatures may be expected to affect roots, but the study of these factors in the field is likely to depend on correlations with growth over a period of many years; subsequently confirmation will be required in controlled environments.

Perhaps the most topical factor is the structure and physical condition of the soil itself. All the experiments described were done on a light sandy loam without marked structure and precautions were taken to avoid effects of compaction. Other types of soil could greatly affect the results obtained in experiments similar to ours. Generally roots cannot penetrate compacted or cemented soil or soil aggregates with bulk densities much greater than 1·5 (clays) or 1·7 (sands) g/cm^3 or with pores smaller than about 0·02 mm diameter, unless the soil strength is small (e.g. because it is wet) (Veihmeyer & Hendrickson, 1948; Wiersum, 1957; Zimmerman & Kardos, 1961; Barley, 1963; Voorhees *et al.*, 1971); nor will they grow where oxygen tensions are less than about 0·01 atmospheres, e.g. because of waterlogging (Greenwood, 1969). Several investigations have shown qualitatively the effect of factors such as structure and compaction on roots of field crops (Goedewaagen *et al.*, 1955; Fehrenbacher & Snider, 1954; Fehrenbacher & Rust, 1956; De Roo, 1969) and a few quantitative measurements have been made. Kmoch (1961) investigated the distribution with depth of cereal roots in eight typical soils near Cologne and the Eifel. Vetter & Scharafat (1964) measured root distribution with depth of many species in para-brown-earths, podsol and old marsh soil. Fehrenbacher, Ray & Edwards (1965) investigated qualitatively and quantitatively the rooting of corn and alfalfa in Illinois shale soils. Lupton *et al.* (1974) describe a possible effect of a compact soil zone on root absorption of phosphate. We have made limited observations on roots of winter wheat and barley growing on Rothamsted, Broom's Barn and Saxmundham farms, the soils of which differ greatly from that of Stackyard Field at Woburn. Generally, however, little has been done to study quantitatively the effects of soil physical factors on root development or function or to follow these effects throughout the growth of crops. Like temperature, soil type is not readily amenable to study by normal replicated experiments. Nevertheless, soils producing large effects on growth of crops as a whole are likely to exert their effects at least in part on root growth. What is important is whether the effects of soil on root growth significantly affect root function. Without detailed quantitative studies of root growth and function we cannot say how important the effects on roots are in determining production of economic crop yield.

Summary

The soil coring method used at Rothamsted to sample roots of field crops is described in detail, together with methods for cleaning and measuring roots.

Six experiments on cereal crops growing on sandy loam studied the effects on root growth of nitrogen, phosphorus and potassium fertilisers and shading and compared root growth of different cereal crops and different varieties of winter wheat. When

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sampling was continued to crop ripeness, maximum root dry weights were found about ear emergence. As much as 80% of roots recovered at that stage were in the top 15 cm of soil.

Nitrogen fertiliser produced smaller root systems in the early spring, affecting particularly younger and more actively growing parts of the root system and tending to produce roots which were shorter relative to their dry weight. Later, although it produced absolutely larger root systems, it increased root growth much less than shoot growth and depressed the size of the root system relative to the plant as a whole. Phosphorus and potassium fertilisers produced small increases in growth of the plants as a whole, but did not generally affect roots independently of the rest of the plant.

Shade decreasing the incident light by 20 or 50% was applied to barley for one-, two- or four-week periods between the four-leaf stage and the early grain growth period. Shading decreased root growth somewhat more than proportionally to the degree of shade, and shoot growth somewhat less, when it was applied while the roots were growing most actively, but it did not have as much effect on roots when their growth slowed about the time of flowering. Roots deeper than 15 cm were affected more than roots near the surface.

The results suggest that shortage of carbohydrate caused by reduced light intensity affects root growth more than shoot growth; stimulation of shoot growth by nitrogen fertiliser may similarly restrict carbohydrate supply to roots and hence their growth.

Winter wheat had 5–6% of its maximum (presumed) root dry weight by the end of March in one experiment and as much as 30–40% in others. It had a greater dry weight and length of roots during the early spring than spring-sown wheat, oats or barley, but by ear emergence and flowering oats had a greater weight and barley a greater length. As early as five weeks after sowing, spring sown cereals had smaller fractions of their total weight represented by roots than winter wheat.

Different winter wheat varieties, including Cappelle-Desprez, Maris Nimrod, Maris Ranger and new semi-dwarf varieties, differed little in dry weights or lengths of their roots. However, some varieties had less roots than others at depths greater than 30 cm in spring.

Compared with other methods available for investigating root systems, the sampling methods used permit measurement of weight, length and other physical attributes of roots and their chemical composition if required. Other methods can be used to detect living roots or to study the distribution of root activity.

Acknowledgements

We thank J. H. A. Dunwoody and the Statistics Department for analysis of the results of our experiments and the many members of the Botany Department who assisted with sampling and patiently cleaned and measured the samples.

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