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Report for 1968 - Part 1

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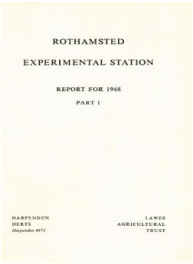
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Botany Department

D. J. Watson

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BOTANY DEPARTMENT

D. J. WATSON

Our work is mainly concerned with how the growth of crops depends on the form and properties of individual plants and the structure of the plant population, how these depend on the environment and husbandry procedures, and how they can be changed in ways that may increase the production of useful parts of the crop, that is, the economic yield. We also study in a similar way the weeds that grow in agricultural environments, but with the opposite aim of using knowledge of the properties and behaviour of weed species to discourage their growth and increase the effects of herbicides, and so lessen losses of crop yield caused by competition from weeds.

Physiology of crop growth and yield

Growth in controlled environments. Construction of the new controlled environment building which began in December 1966 was completed, and the permanent machinery and equipment installed by May 1968. Seven of the complement of nine Saxcil cabinets were delivered and were operational by December. Testing and commissioning of the large growth rooms was delayed by faults in construction or in operation of components, and by inevitable small changes in design, so the rooms had not been handed over for our use by the end of the year. Nevertheless, members of the department, especially G. N. Thorne and M. A. Ford, spent much not immediately productive time in discussions with architects, engineers and contractors, in becoming familiar with the operation of the equipment, checking that it meets our requirements and installing ancillary apparatus.

Meanwhile, some technical problems involved in growing plants in controlled environments were studied. For example, if experiments in growth rooms or cabinets are to be relevant to mature field crops, the plants grown in pots must be comparable in size and other respects to those in heavy field crops. Sugar beet grown previously in pots were usually smaller than in the field, and their leaf area decreased after mid-August, much earlier than in the field. By using large pots, containing 9 or 13 litres of Rothamsted soil, and fertiliser dressings up to 16 g of each of NH_4NO_3 and K_2HPO_4 per pot, plants with 300 g total dry weight, 200 g root dry weight and maximum leaf area of 70 dm^2 were grown. These values resemble those of plants in a field crop with a population of 30000/acre, a maximum leaf area index of 5 and a root yield of 20 tons/acre. (Thorne and Ford)

In growing cereals in growth rooms or glasshouses, infection with mildew is a serious problem that has not been solved by the mildew-resistant varieties yet produced. It is also troublesome in experiments with grasses. Two new fungicides, 'PP 149' and 'PP 781', produced by Plant Protection Ltd. for control of mildews, were therefore tested in comparison with lime sulphur as sprays given on three occasions in May, June and

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July to barley (Proctor), spring wheat (Jufy I), blackgrass (*Alopecurus myosuroides*), wild oats (*Avena fatua*), and couch grass (*Agropyron repens*) grown from rhizome pieces of clonal material, in a glasshouse where the conditions favoured mildew infection. 'PP 149' added to the soil before sowing was also tested. Untreated plants of all species except blackgrass and couch grass were heavily infected. In general, plants sprayed with 'PP 149' had least mildew; spraying with 'PP 149' nearly doubled the grain yield of barley and more than trebled that of wheat. For barley, but not wheat, giving 'PP 149' to the soil was more effective than the spray. Mildew on wild oats was also well controlled by spraying with 'PP 149'; results with blackgrass and couch grass were also encouraging, but the irregular infection made assessment difficult. (Ford, Thurston and Williams)

Effect of atmospheric humidity on growth. Three previous experiments in growth rooms testing the effects of differences in atmospheric humidity on growth gave inconsistent results (*Rothamsted Report for 1963*, p. 79, *for 1964*, p. 105 and *for 1965*, p. 98). With day/night temperatures of 20/15° C, dry weight and especially leaf area of several species were increased when both day and night humidity were increased, but the effects were less when only day humidity was increased. Large effects of humidity were also obtained with a day temperature of 25° C, and when treatments started several weeks after sowing. Two more experiments were done with wheat and sugar beet to test the effects of (*a*) increasing humidity during the day, night or both at 20/15° and (*b*) differences in day humidity at 25/15° C. All other conditions were identical in the two experiments. In each experiment half the plants were sown in growth rooms with the different humidities, and half were grown in the glasshouse for several weeks and then transferred to the growth rooms for 3 weeks. The relative humidities were: wet day (20° C) 86%, dry day (20° C) 57%, wet night (15° C) 87%, dry night (15° C) 48%; wet, medium and dry days (25° C) 85%, 68% and 45% respectively. The differences between wet and dry conditions at 20° C and 15° C and between wet or dry and medium conditions at 25° C all represented a uniform difference in vapour pressure deficit of about 7 mb. The plants were grown in soil that was watered with a wick and was always moist.

Dry weight and leaf area of both species were increased by increase in day humidity at 20° and 25° C and were unaffected by night humidity. When treatment started several weeks after sowing, the effects were less than when the humidity differences were imposed from sowing. When applied continuously, the increase in humidity between dry and wet conditions at 20° C or between dry and medium conditions at 25° C increased plant dry weight by 28–39% and leaf area by 24–41% after three weeks. After six weeks the percentage effects were usually slightly less. The further increase in humidity from medium to wet at 25° C sometimes increased dry weight and leaf area significantly, but the effects were inconsistent, ranging from 4 to 62%. As night humidity had no effect and differences in day humidity had less effect when treatments started several weeks after sowing than when applied continuously, the discrepancies

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between previous experiments must have other explanations. (Thorne and Ford)

Photosynthesis and translocation of semi-dwarf wheats. The semi-dwarf wheats from Mexico grown in 1967 had larger harvest indices (ratios of grain : total dry weight at harvest) and grain : leaf ratios than Jufy I and Kloka (*Rothamsted Report for 1967*, p. 93), possibly because a larger fraction of the products of post-anthesis photosynthesis moved from the shoot to the grain. To test this hypothesis a pot experiment was done in the glasshouse comparing Jufy I and Kloka spring wheats with the semi-dwarf varieties Sonora 64 and Mexico 120.

The dry weight of ears per plant was similar for Jufy I, Kloka and Mexico 120 at 5, 12 and 26 days after anthesis and at maturity (75–80 days); the dry weight of Sonora 64 ears was always less than of the other varieties. The ears of all varieties grew at similar rates. Leaf areas and shoot weights of the semi-dwarf varieties were about half those of Jufy I and Kloka. Shoots of all varieties increased in weight between 5 and 26 days after anthesis and then decreased. The increase was much greater with Jufy I and Kloka than with the semi-dwarf varieties, indicating that more of the current assimilate moved to the ear of the semi-dwarfs. Translocation in the four varieties was also compared by allowing flag leaves to photosynthesise in air containing $^{14}CO_2$ at 5, 12 and 26 days after anthesis and estimating the ^{14}C content of ears and other parts of the treated shoots 24 hours later and at maturity. The leaf below the flag leaf was also treated at 5 and 12 days. The ^{14}C estimations are not yet complete.

Rates of photosynthesis of flag leaves and ears were measured with an infra-red gas analyser in a controlled environment (at 20° C with 11 cal/dm^2/min visible radiation) about 12 days after anthesis. The varieties did not differ in the rate of photosynthesis per dm^2 of flag leaf, so as Jufy I and Kloka had large flag leaves and Mexico 120 very small ones, flag leaves of Jufy I and Kloka absorbed CO_2 fastest and Mexico 120 slowest. The awned ears of Sonora 64 and Mexico 120 absorbed CO_2 slightly faster than the awnless ears of Kloka, but this did not compensate for the slower uptake by the flag leaf of the semi-dwarf varieties, so total CO_2 uptake by flag leaf plus ear was greatest for Kloka (11·9 mg/h), intermediate for Sonora 64 (8·3 mg/h) and least for Mexico 120 (5·7 mg/h). Photosynthesis of Jufy I ears was not measured.

These results suggest that the success of the semi-dwarf wheats in producing large grain yields, in spite of their small leaf area, depends not on greater photosynthetic efficiency of the leaves, but on the transfer of a larger fraction of the products of photosynthesis to the grain. (Thorne and Ford)

Root growth of field crops. No major innovation was made in our methods of taking the soil cores (5·9) from which roots are separated from soil and other organic matter by washing. Root length is now measured routinely by Newman's method (*J. appl. Ecol.* (1966), **3**, 139–145). After roots are separated from the soil, they are stored for various periods before being measured, dried and weighed. Measurements were made of the dry

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weight losses from roots in different post-sampling procedures, including storage at room temperature, at 4° C or at −15° C, formalin treatment, and air drying. Wheat or kale roots from plants grown for about 6 weeks in aerated nutrient solution were cut off and rinsed for 30 seconds in distilled water before use in the tests. Moist roots stored for 3 days at room temperature, or for 21 days at about 4° C, lost significantly more dry weight than roots dried immediately, but roots frozen at −15° C or stored for 7 days at 4° C did not. Deep frozen, air-dried or formalin-treated roots lost dry matter when later washed in water, and roots may have lost some when washed without storage. The best procedure is to complete all washing immediately after harvest, and if roots must then be stored, it should be in a refrigerator at 0–4° C unless prolonged beyond 2 weeks. For longer storage, freezing at −15° C is probably the best, but about 15% of dry matter is lost when deep-frozen roots are thawed and put in water, e.g. to separate them from foreign organic matter.

Effect of shading on root growth. Roots derive their supply of assimilated carbon from photosynthesis in the leaves, so their rate of growth presumably depends on the amount of radiation received by the leaves. This was tested in an experiment at Woburn by measuring the effect of covering plots in a barley crop with shades of different densities at different stages of growth.

Barley (Maris Badger) was sown on 11 March, and shading treatments were applied to different plots in each of three periods, the first of three weeks starting on 22 April, and the other two of four weeks, starting on 13 May and 10 June respectively. Shades of 'Tygan' screen-cloth of two densities, transmitting about 80% of daylight (light shade) or 50% (deep shade) were used. For the first week of period 1, or for the first two weeks of the subsequent periods, half of the plots were unshaded and the others had deep shade. For the rest of each period, previously unshaded or shaded plots received either no shade, light shade or deep shade, so there were six combinations of the shading treatments in the two parts of each period. Samples of plants were taken at the beginning and end of the second part of each treatment period from the plots assigned to that period, including unshaded plots. Some later samples were also taken to find how long effects of shading persisted after the shades were removed. The plants were pulled by hand, with some roots attached, and roots remaining in the soil were estimated by washing them from four soil cores per plot cut into layers 0–15, 15–30 and 30–60 cm from the soil surface. From these samples the numbers of shoots, leaf areas and the dry weights of shoots, ears and roots were determined.

At the end of the first and second treatment periods, shading in any part of the period had decreased the dry weight of tops and there was no interaction between treatments in the early or later parts of each period; growth under deep shade for two weeks at any stage decreased shoot dry weight by about 20%. At the end of the third treatment period, shading during the first part of the period but not the second part, decreased shoot weight by about 15%, and also ear weight. The number of shoots was decreased by shading early in the first period when tillering was

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beginning, but later shading had no effect. Shading in the second period decreased the subsequent survival of shoots.

After shading for a week at the beginning of the first treatment period, the weight of roots was not significantly affected. Shading in the following two weeks decreased the weight of roots in the 0–15 cm layer on previously shaded plots only; on these plots the weight of roots was 19 g/m² with deep shade, 23 g/m² with light shade and 34 g/m² with none. This is the type of response expected if plants can use accumulated carbohydrate to maintain root growth during short periods of deficient light; it did not happen during the second treatment period. Deep shade during the later part of the first period after either shading treatment during the earlier part, also decreased the weight of roots in the 15–30-cm layer by 60%, and in the 30–60-cm layer by 75%. Shading during the second treatment period had no significant effects on root weight, though there was evidence of a decrease in the 30–60-cm layer.

At the end of the first treatment period, nearly half the root weight of unshaded plants was in the top 15-cm depth of soil, about 10% in the 15–30-cm layer, and 40% in the 30–60-cm layer. Apparently conditions in the middle layer were less favourable for root growth and proliferation than above or below. A possible explanation of this distribution of roots is that the 15–30-cm layer included a soil pan or compacted zone. Evidence of this was sought by using the 'pinboard' method to examine root distribution.

Soil cores of 6 in. diameter and 36 in. deep were taken with a Proline corer from the crop adjacent to the experimental area on 19 July. From the cores, soil monoliths 15 × 8 cm in cross-section and 90 cm deep were cut and mounted on a pinboard, i.e. a board with nails spaced at 5 cm intervals along the length and across the breadth and projecting 6 cm from its surface. The monolith on the board was immersed in a trough of water and the soil washed away with a fine spray, leaving the roots held by the projecting nails in approximately their original positions in the soil. Compact soil layers were found during washing at depths ranging from 13 to 28 cm below the surface of different monoliths. Roots were densely matted in the top 3–5 cm of soil, then less dense and uniformly distributed down to a depth of 25 cm to 30 cm, which often corresponded with the position of the compacted layer. Below this a few roots penetrated straight downwards to 80 cm or more, with lateral branches throughout, but little intermingling. This distribution of roots was very different from that found in May, but the position of the compacted layer corresponded approximately with the zone where roots grew poorly in May. Whether the hard layer occurs in other fields at Woburn is not known. (Welbank, Gibb and Morgan)

Sugar content of sugar-beet roots. In a field experiment at Broom's Barn in 1967 (*Rothamsted Report for 1967*, p. 95) the effect of decreasing photosynthesis by a sugar-beet crop on the sugar content of the roots was studied by covering plots with shades that transmitted about 45% of the incident light. The shading was repeated on different plots in three periods of 4 weeks. Shading decreased the net assimilation rate by about one-third, but had little effect on leaf area index, so shaded plants gained less dry

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matter and at the end of each period, and at the final harvest in October, the roots had less dry weight and sugar than unshaded plants. Shading did not change the sugar content per cent of dry matter in the root, except for a small decrease in the first period, but it consistently decreased sugar per cent of fresh weight by increasing the water content of the roots, presumably because less water was lost by transpiration, so that the soil–water deficit on shaded plots was less than on unshaded plots. This decrease by shading in the sugar content per cent of fresh weight of the root disappeared by the end of the growth period because the differences in soil–water deficit were eliminated by much rain in October.

To test this explanation, a similar experiment was done at Broom's Barn in 1968. Plots were shaded with the same 'Tygan' screen-cloth shades during three four-weekly periods as before, and others were left unshaded, but some were watered by trickle-irrigation from plastic tubes laid in alternate inter-row spaces. Water was supplied to make up the difference in transpiration between unshaded plots and shaded plots, estimated as 55% of the potential transpiration calculated by Penman's method. Thus, differences between irrigated and shaded plots were intended to measure direct effects of radiation, and those between unshaded plots without and with irrigation effects of radiation operating through change in soil–water deficit. However, even if the amounts of water added were correctly estimated, the distribution of water down the soil profile probably differed between the irrigated and the shaded plots. The amounts of irrigation were: period I, 13 June–11 July, 0·67 in.; period II, 18 July–15 August, 0·75 in.; period III, 21 August–18 September, 0·12 in. The soil-water deficit on unshaded plots without irrigation was never large; it increased to 1·4 in. in late June, and 1·3 in. at the end of July, but in mid-July, mid-August and from late September onwards the deficit was made up by heavy rain, and soil water on all plots was near to field capacity.

Net assimilation rate was unaffected by irrigation but was approximately halved by shading. Leaf area index was slightly increased by irrigation in the first period but not later, and shading decreased it in all periods. So total dry weight, root dry weight and weight of sugar in the root were not changed by irrigation, except for a small decrease in sugar yield in the last period, but were consistently decreased by shading, and the decreases in yield of roots and sugar persisted until harvest in October.

Sugar per cent of fresh weight in the root was decreased by shading from 10·3 to 8·1% in period I, from 13·1 to 12·1% in period II and from 15·5 to 14·3 in period III; at the final harvest it was still decreased by shading in any period, from 14·8 to 14·2%. Irrigation decreased sugar per cent of fresh weight in the root as much as, or slightly less than, shading in each period, but had no effect at the final harvest.

Sugar per cent of dry matter in the root was slightly decreased by shading or by irrigation during the first period, but not during later periods, and neither had any effect at the final harvest.

These results confirm the previous conclusion that decreases in the sugar content of the root per cent of fresh weight by shading reflected changes in water content that were matched by irrigating unshaded plots. Except in

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young plants sugar per cent of dry matter was unaffected by the much smaller photosynthesis of the shaded crop, so sugar yield was less because the dry weight of roots was less, not because the partition of dry matter between sugar and other substances changed.

Other plots in the 1968 experiment were shaded continuously from 13 June to 18 September. The sugar content of the roots from these plots at harvest in October was 13·4% of fresh weight and 70·4% of dry weight compared with 14·8% and 80·4% respectively for unshaded plants. Continuous shading halved the dry weight of roots, from 840 g/m² to 412 g/m², and this, not the change in sugar content, was still the major cause of loss of sugar yield. These results show that the simple concept of sugar storage in the roots as passive accumulation of photosynthate produced in excess of the requirements for growth of the plant is untenable. Continuous shading decreased the dry weight of tops by 176 g/m² and the non-sugar dry matter in roots by 44 g/m², so it depleted the supply of dry matter for growth by 220 g/m², although the shaded plants still contained 290 g/m² of sugar in their roots. (Loach, Phillips and Watson)

Effect of seedling treatment on growth of sugar beet. When sugar-beet seedlings were grown for two weeks in growth cabinets at 20° C with 8-hour or 16-hour photoperiods or continuous fluorescent light and then transplanted in May to pots in an unheated glasshouse with natural illumination, the final weight of the root increased with increase in the length of the daily photoperiod during the seedling stage (*Rothamsted Report for 1967*, p. 99). It was suspected that the pots restricted growth in the later stages, and so limited the effects of the seedling treatment. Accordingly, when the experiment was repeated in 1968 the seedlings were transplanted to the field.

Four treatments were compared: seedlings were raised (1) in continuous fluorescent light in a growth cabinet at 20°, (2) as for (1) but with a 16-hour photoperiod, (3) in an unheated glasshouse with open sides and with natural daylight, (4) from seeds drilled directly in the field. For treatment 3 seeds were sown 10 or 12 days before those for treatments 1 and 2 at the end of March, with the intention that all seedlings should be of similar size at transplanting, but those of treatment 3 were smaller. The seeds were sown in compost in peat pots and transplanted to the field between 26 April and 3 May. The plots with treatment 4 were drilled on 20 March, and the seedlings thinned on 17–21 May.

Seedlings initially in continuous light at first grew faster after transplanting than the others, both in leaf area and in root dry weight. Eventually all treatments had nearly the same maximum leaf area index, about 4, but it was attained later by seedlings raised in 16-hour photoperiod or in the glasshouse. Plants raised in 16-hour photoperiod had a leaf area duration of 7·3 m² weeks, those transplanted from the glasshouse 6·6 m² weeks, and with either of the other treatments, 7·0 m² weeks.

Throughout the growth period the plants grown from seedlings raised in growth cabinets with continuous light or 16-hour photoperiod had a larger ratio of root dry weight: top dry weight than those raised in natural conditions with shorter, cooler days. They also had a larger yield of roots

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at the final harvest at the end of September. The mean fresh weight of roots for treatments (1) and (2), which did not differ significantly, was 21·8 tons/acre, compared with 16·0 tons/acre for the mean of treatments (3) and (4), which also were not significantly different. The weight of tops was similar for all treatments.

The differences between treatments in total dry matter yield were only partly attributable to differences in leaf area duration; they mainly reflect differences in net assimilation rate. Mean E for treatments (1) and (2) in the period from May to September was 50 g/m^2/week, but for treatments (3) and (4) it was 45 g/m^2/week.

Thus, exposing sugar-beet seedlings to longer daily illumination and higher temperature than those of the natural climate for about three weeks before transplanting in the field induced a persistent change in the distribution of dry matter between leaves and roots, causing a larger proportion to move into the root, and increasing the final root yield. However, it did not much affect leaf growth or the yield of tops because the total production of dry matter was increased by increase in net assimilation rate, presumably because the root had more capacity for photosynthate and more of it moved from the leaves. (French and Humphries)

Axillary branches in potato. Axillary buds near the base and near the top of the main stem of potato plants usually develop to form lateral branches, but those in the intermediate part of the stem remain dormant or expand only slightly. The nature of this bud inhibition in the middle zone was studied.

When the apical growing point is removed, dormant axillary buds begin to develop, and the youngest buds remaining usually grow largest. By removing a standard terminal section of the stem at different times, potato plants (Arran Banner) were left with 7, 10 or 13 nodes, and the subsequent growth of laterals was measured. The leaf area and dry weight of the lateral branch produced at a particular node was greater the younger the plant at the time of decapitation. This was true both of branches originating below the soil surface, so-called 'leafy stolons', and those produced in the axils of main-stem leaves. The decline with age in the growth potential of axillary buds was also evident when all except the uppermost axillary bud was removed after the stem was decapitated. The remaining bud grew much more when the others were removed, but grew less the later the time of decapitation. Decapitation also consistently increased the growth in area of the remaining stem leaves, especially the upper ones.

When main stems of similar plants were divided into pieces with one node and placed in moist sand, the axillary buds of younger leaves grew more than those of older leaves. Apparently, the growth of an axillary bud released from inhibitory effects depends directly on the length of time it has been held dormant.

Stopping the growth of the main stem by using growth retardants, e.g. morphactin (p. 104), also caused increased development of axillary buds.

The difference in development of axillary buds seemed not to arise from inherent characteristics of the buds, but to be a correlative effect depending on competitive or inhibitory activities of other plant organs. The present

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view is that the zonation of axillary development along the main stem is caused by change with time in the dominance exerted by the stem apex. The growth of the highest laterals may be associated with the change in the stem apex from vegetative growth to flower production, decreasing either its demand for nutrients or its inhibitory influence. The reason for axillary buds near the base of the stem developing some weeks before flower formation is not clear. Effects of changes in underground parts of the plant, especially tuber initiation and growth, may be involved. (Pethiyagoda)

Growth substances and growth regulators

Growth substances in wheat. Work began on endogenous growth substances in wheat plants, with the object of relating their distribution and concentration in different plant parts to morphological changes during growth and development. Four types of growth substances may be involved, namely auxins and gibberellins, which promote cell expansion, cytokinins, which promote cell division, and growth-inhibiting substances. As a first step, the changes in growth substances during germination and elongation of leaves and in grains growing in the ear were examined.

The wheat tissues were extracted with water, ethanol or ethyl acetate, partitioned into acidic and non-acidic substances and separated on paper chromatograms. Auxins eluted from positions on the chromatograms at appropriate R_f values were assayed by their effect on elongation of wheat coleoptile sections, gibberellins by their effect on α amylase production in pieces of barley endosperm causing release of sugars, and cytokinins by their effect in preventing loss of chlorophyll from sections of mature wheat leaves. Inhibitors were detected by retarded elongation of wheat coleoptile sections and by their interactions with growth promoters.

Germinating wheat grains contained a gibberellin with similar R_f to gibberellic acid, but no detectable auxin. The amount of gibberellin per seed increased for 5 days after the grains were imbibed. The first leaf contained a little auxin on day 7 when it elongated rapidly, but this disappeared by the time growth stopped. The leaves contained gibberellin with the same R_f as that in the grains; the amount increased with the size of the leaf, but the concentration per g of leaf changed little with age.

Marking the first leaves of 6-day-old wheat seedlings to divide them into five parts of equal length showed that later elongation occurred mostly in the basal segment. Assays of separated segments showed that the basal fifth contained most of the gibberellin in the leaf, but auxin was present in both apical and basal segments, with little in between.

Immature grains of maize contain a cytokinin (Zeatin) that is probably associated with growth of the endosperm, but extracts of growing wheat grains, made on six occasions, did not contain detectable cytokinins. Extracts on the 2nd and 3rd occasions, when the grains were still growing, contained some gibberellin. All the extracts contained auxin; most was found on the 4th occasion when the fresh weight per grain was greatest. This auxin had the same R_f on chromatograms as IAA (indol-3-yl-acetic acid).

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No extract of wheat leaves, roots or grains has yet given a positive response in the chlorophyll retention assay for cytokinins. However, an extract of immature grains run on a chromatogram contained a fraction that inhibited, and another that enhanced, the effect of kinetin on chlorophyll retention. Exudates from cut shoots and roots also were assayed, because cytokinins might not be detectable in extracts, but accumulate in exudates collected over several days. However, cytokinins were not found, but exudates contained auxin and gibberellin. (Wheeler)

Effect of CCC on cereals

Wheat. When CCC was sprayed on a wheat crop, the stems were shortened and leaves held more upright, so with the usual 7-in. spacing of rows the sprayed crop intercepted less light than the unsprayed. This suggested that where CCC increases yield without preventing lodging, the increase might be greater with closely spaced rows. Also, it seemed possible that the deeper root system induced by CCC might be more beneficial to closely spaced plants. In an experiment in 1965, CCC increased the yield of spring wheat sown in rows spaced 4 in. apart, but not 8 in. apart.

In 1968, the same possibility was tested with winter wheat (Cappelle Desprez) sown in rows spaced 4 in. or 8 in. apart and given 0·8, 1·6 or 2·4 cwt N/acre. Half the plots were sprayed with 2 lb CCC/acre in 40 gal water on 28 March when the plants had 5 or 6 leaves. The crop was not lodged. The mean yield of grain was 28·8 cwt/acre; closer spacing increased it by 0·9 cwt/acre and spraying with CCC increased it by 1·9 cwt/acre, but there was no indication that CCC had greater effect with closer spacing. The largest grain yield was obtained with 0·8 cwt N/acre, and more N decreased it; the mean yields with 0·8 and 2·4 cwt N/acre were 34·6 and 25·8 cwt/acre respectively. There was no interaction of CCC with N supply.

An experiment with similar treatments was done with spring wheat (Kolibri) sown on 11 March. The three amounts of N fertiliser were applied in the seed bed, and half the plots were sprayed with CCC on 5 May at the 6-leaf stage. Lodging occurred on all unsprayed plots and was increasingly severe with increase in N supply. Spraying with CCC completely prevented lodging on plots with rows spaced at 4 in., but slight lodging occurred with the larger amounts of N on sprayed plots with 8 in. spacing. The mean yield of grain was 31·8 cwt/acre; averaging all amounts of N, closer spacing increased grain yield by 1·3 cwt/acre, spraying with CCC increased it by 4·7 cwt/acre but, as with winter wheat, there was no evidence that CCC was more effective on the closer-spaced crop. The differences in yield were closely related to the severity of lodging. Thus, on unsprayed plots the grain yield decreased with increasing N, but on plots sprayed with CCC it was slightly increased by 2·4 cwt N/acre. Consequently, the increase in yield by CCC was much larger on plots that received the most N.

Growth measurements were made regularly in both experiments, but are not yet completely analysed.

Winter oats. Winter oats are more susceptible to lodging than winter wheat, and so might benefit more than wheat if the straw were shortened

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by CCC. This possibility was tested on a crop of winter oats (Maris Quest) given 0·5, 1·0 or 1·5 cwt N/acre. On 9 April when plants had about 5 leaves, plots with each N dressing were sprayed with CCC at 0, 2·5 or 5 lb/acre. On the average of all N dressings, CCC at 2·5 lb/acre shortened the straw by 11% and at 5 lb/acre by 15%, and its effect decreased with increase in N supply. Lodging occurred in July; it was slight on plots given 0·5 cwt N/acre and was decreased by spraying with CCC, but severe on plots with more N whether sprayed with CCC or not.

The mean yields of grain on unsprayed plots given 0·5, 1·0 or 1·5 cwt N/acre were 25, 23 and 18 cwt/acre respectively. On plots with 0·5 cwt N/acre, where CCC was most effective in shortening the straw and where it decreased lodging, spraying with CCC at 2½ or 5 lb/acre increased the grain yield to 27 and 32 cwt/acre respectively, mainly by increasing the number of grains per panicle; the 1000 corn weight was unchanged. On plots with 1·0 or 1·5 cwt N/acre, CCC had no effect on yield. The N dressings that caused severe lodging gave smaller yields by decreasing the number and size of panicles, and size of the grains. (Humphries and Bond)

Mixed corn (spring wheat and barley). In addition to shortening the stems of wheat, CCC increases the size and depth distribution of the root system, which is thought to explain the increase in yield from CCC that occurs when soil is dry at a critical period near the time when ears emerge; the larger root system may enable the plants to draw on more soil water so that more shoots survive to bear mature ears (*Rothamsted Report for 1966*, p. 88 and *for 1967*, p. 102). The growth of barley stems is affected only temporarily by spraying with CCC, and mature shoots of sprayed plants are not shortened. Assuming that the same is true of the root system, in a mixed crop of barley and wheat treated with CCC the wheat roots may use water and nutrients from soil layers not occupied by barley, so producing a larger yield than from the crops grown separately.

Plots were drilled on 19 March with alternate rows of barley (Zephyr) and spring wheat (Kloka), and other plots had the same number of rows either all barley or all wheat. On 14 May, half the plots were sprayed with CCC at 2·5 lb/acre. Although an attempt was made to sow the same numbers of seeds of the two crops, about 50% more barley plants than wheat plants became established. On 31 May CCC had shortened stems in wheat grown alone by 37% and in the mixture by 30%; stems of barley grown alone were shortened by 15%, and in the mixture by 22%. On 18 June after ear emergence when wheat was taller than barley, CCC shortened wheat grown alone or in the mixture by 30% and barley stems by only 7%. In mid-July stems of sprayed wheat were still about 30% shorter than unsprayed stems, but sprayed barley was as tall as unsprayed. This confirms the previous observation that CCC shortens barley soon after spraying, but sprayed shoots later grow faster than unsprayed.

The grain yield of the unsprayed mixed crop (24·0 cwt/acre) was larger than those of wheat or barley grown alone (18·5 and 22·5 cwt/acre respectively). Spraying with CCC increased the yield of the mixed crop more than of either component grown alone. It increased the grain yield of wheat by 3% to 19·1 cwt/acre, of barley by 6% to 23·8 cwt/acre, and of

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the mixed crop by 14% to 27·3 cwt/acre. The grain produced by the unsprayed mixed crop contained only 19% of wheat and that of the sprayed mixed crop 22%. Presumably the small wheat component was partly a consequence of the smaller proportion of wheat plants in the mixed population. CCC increased the yield of wheat in the mixture by 28%, but that of barley by only 10%.

Explanation of these effects on yield depends on an analysis of growth not yet completed. They may reflect effects on competition for nutrients rather than water, because the summer was unusually wet. (Bond, Humphries and Morgan)

CCC and eyespot. Spraying with CCC decreases lodging of wheat crops by shortening the straw and strengthening the bases of the stems, but some have claimed that it also acts against lodging by decreasing the susceptibility of the crop to infection by eyespot fungus (*Cercosporella herpotrichoides*).

Eyespot infection occurs mainly during the winter so that, if CCC has a direct effect on the fungus, a winter application should be the most beneficial. This was tested in an experiment with winter wheat (Champlein) sown early in October so that the crop reached the 5-leaf stage, at which it can safely be sprayed with CCC, in autumn. The site previously had four successive cereal crops. Plots were sprayed with 2 lb CCC in 32 gal/acre in December, or in early spring, or in both autumn and spring, or were left unsprayed, and received either 100 lb or 200 lb N/acre. About 50% of straws were infected with eyespot and the percentage infection was not changed by spraying with CCC. In July lodging was more severe with the most N. Spraying with CCC in spring decreased lodging on plots given 100 lb N/acre, but spraying in autumn or in both autumn and spring did not. The reason why the double spraying was less effective than the spring spraying is not known. By August most plots were completely lodged. In spite of this, CCC applied in spring to plots given 100 lb N/acre increased the grain yield from 40·7 to 50·1 cwt/acre, presumably because the delay in lodging enabled grain-filling to continue longer and produce larger grains. This is contrary to the effect of CCC on unlodged wheat, which usually decreases grain size. Spraying in autumn, or autumn and spring, had no effect on yield. The plots with 200 lb N gave smaller yields that were not affected by spraying with CCC, even in spring. All these plots were severely lodged by July. The results gave no support to the claim that CCC decreases lodging by controlling eyespot. (Humphries, Bond and Slope, Plant Pathology Department)

Effect of morphactins. The morphactins are a group of growth regulators derived from fluorene-9-carboxylic acid, but their properties differ greatly from those of gibberellins, which are also derivatives of fluorene. They are powerful inhibitors of growth, more active than CCC or B9. Their effects on the growth of potato were studied.

Plants of Majestic potato, grown from uniform sets with a single eye, were sprayed with 12 ml of a solution of morphactin (IT 3456), containing 1 or 10 mg/l, when they were 42 days old and had 16 leaves on the main

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stem. Only the apical growing points and expanding leaves were affected. The areas of main-stem leaves were decreased from the 10th node by the 1 mg/l spray and from the 8th by 10 mg/l. Growth of lateral branches from axillary buds was encouraged, especially at the lower nodes, and the number and size of 'leafy stolons'—branches originating beneath the soil and emerging to bear leaves—were also increased. In a field crop with a greater depth of soil above the set and more competition for light, these branches might not have formed aerial shoots but remained as stolons and produced tubers. Morphactin delayed tuber development, and the more concentrated spray had a larger effect.

Other potato seed pieces were soaked in solutions of morphactin before planting. They produced plants that grew very slowly, had few or no roots and small leaves. The growth rate gradually increased, and the plants eventually had normal morphology. The tops of untreated plants died in early August, but those of treated plants survived into October. The inhibiting effects of morphactin were not overcome by indolylacetic acid, gibberellic acid or kinetin.

Morphactin behaved like gibberellic acid in lengthening stolons, but unlike gibberellic acid it also increased the weight of stolons. Its action differed from those of CCC or B9, which shorten stolons. It was also unlike CCC, but like B9, in increasing the growth of lateral branches. (Pethiyagoda and Humphries)

Effect of 'Ethrel' on barley and oats. No growth regulator that consistently shortens barley has yet been found, although CCC briefly slows growth (p. 103). A growth regulator 'Ethrel' (2-chloroethanephosphonic acid, a quaternary phosphonium compound), recently described, was tested on barley and oats. Plots were sprayed with 1 or 2 lb/acre of active ingredient at the 5–6 leaf stage. Spraying with 'Ethrel' lengthened barley shoots, but not oats, by 2 cm, and caused earlier lodging of both crops. It had no effect on yield. (Bond and Humphries)

Weed studies

Our work on weeds was concerned mainly with grasses, especially blackgrass, now one of the most important annual weeds of cereal crops on heavy land, and the perennial rhizomatous grasses, couch grass, also a common weed of heavy land, and *Agrostis gigantea*, which occurs mainly on light soils.

Alopecurus myosuroides (blackgrass)

Comparison of plants grown from seed of different origins. Ripe seeds in 61 samples collected by the N.A.A.S. in 1966 in 18 counties of England and Wales (*Rothamsted Report for 1966*, p. 95), which had lost their dormancy during storage in the laboratory for a year, were sown in pots of Rothamsted soil in the glasshouse in October 1967 and transferred outdoors in March 1968, to study the variation within the species in morphological and physiological characters. The mean number of shoots produced per plant ranged from 30 to 64, compared with fewer than 40 for plants grown in the

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field. Nearly all shoots produced ears, whereas in the field only about half did so. The plants in pots were also taller; the mean maximum height ranged from 85 to 113 cm. Ripe seeds collected from every pot were later sown in pans in the glasshouse to study variation in dormancy, viability and periodicity of germination.

Periodicity of germination of seeds in the field. To continue the study of periodicity of germination in different seasons, small plots in Little Knott I were left unsown in autumn 1967, when the rest of the field was drilled, and blackgrass seedlings were counted and removed at intervals. Fewer seeds germinated than on the previous site in Broadbalk field (*Rothamsted Report for 1967*, p. 106), which could no longer be used because of the rearrangement of the wheat plots. However, the periodicity of germination of blackgrass was similar to that usual on Broadbalk. Germination started during the first week of October, and 80% of the total seedlings emerged by the end of the first week in November. Seedlings appeared sporadically during November to February, in larger numbers in April and May and then very occasionally until September, when the counts ceased.

Loss of dormancy during storage. Ripe seeds about to shed were collected from the field on 19 August 1968, stored in open tubes until air-dry and the tubes were then corked. To measure how soon the seeds lost their dormancy, batches were taken and set to germinate on a Copenhagen tank at intervals of 10 days, with light for 8 hours daily at 30° C, and darkness for 16 hours at 20° C. In these conditions few seeds germinated by mid-November.

After storage until late December, the time between sowing and germination of the first seeds had decreased from 13 to 6 days, but only 5% of seeds germinated in 8 days, compared with 70% in 8 days for non-dormant seeds collected in 1967 and sown in August 1968.

Development of plants germinating at different times. Blackgrass seedlings at the first-leaf stage were marked as they appeared on small uncropped plots in Little Knott I at the begining of each month from October to January, and in April. Seedlings that emerged in October began to tiller in early December, sooner than in 1966–67, but November plants did not tiller until the end of January. The difference in rate of development persisted, so that October plants had more shoots in June and more ears in July than November plants. Only one plant of those appearing in January survived; it produced more shoots than plants that appeared earlier, as happened in 1967. (Thurston)

Agropyron repens (couch grass) and *Agrostis gigantea*

Germination. *Agropyron* and *Agrostis* are commonly thought to spread mainly by means of their rhizomes, but this may underestimate the part seeds play. To assess this possibility, the behaviour of the seeds is being studied.

Seeds of *Agropyron*, collected in August 1967 from several fields at Rothamsted and elsewhere, were sown in pans of sterilised Rothamsted

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soil in September. After one week, 17–32% had germinated and after two weeks 50–80%. Although the soil was stirred after four weeks, few more seedlings appeared. Seeds of the same collection were stored dry in the laboratory through the winter, and sown in February 1968. All seeds that germinated did so within two months, and the final germination percentages were similar to those for the autumn sowing. Thus, the viability of the seed did not change during storage and the seeds that failed to germinate were apparently not dormant. This suggests that seeds shed naturally, or sown in spring as contaminants of seed corn, have an equal chance of germinating and establishing seedlings.

Recently-collected seeds of *Agrostis* were sown in October 1967 in soil at about ¼ in. depth; 18% of seeds germinated in the first month, increasing to 60% in April when the soil was stirred monthly, but only to 25% when the soil was not disturbed. When the undisturbed soil was then stirred, germination continued slowly, reaching 55% in October 1967, but there was little increase after April in the soil repeatedly stirred throughout.

The seeds of *Agrostis* are very small (mean weight about 0·1 mg) and they are much more sensitive to depth of sowing than the larger seeds of *Agropyron* (mean weight about 2 mg). When *Agrostis* seeds were sown on the soil surface in February, 75% germinated after two months, but only 44% of seeds sown at ¼ in. depth germinated in the same time. Seeds from a bulk of which 70% were found to be viable in a laboratory test were sown either on the soil surface, or at ¼ in. depth, or mixed with the soil throughout a depth of 1½ in. After one month 60% of seeds on the surface germinated, but only 7% of the others produced seedlings that emerged above the soil. In another experiment, started in March to compare a wide range of depths of sowing, the emergence of *Agropyron* seedlings was unaffected by sowing at 2 in. depth, but was halved at 3 in. depth, whereas ¼ in. depth halved the emergence of *Agrostis* seedlings.

Some evidence was found that more *Agrostis* seeds, but not *Agropyron* seeds, germinate in light than in darkness, and this may partly account for the adverse effect on germination of *Agrostis* seeds of covering them with a very thin soil layer.

Development of viability. Inflorescences of *Agropyron* emerge and flower later than those of cereal crops, so the seed they produce can be effective in multiplying and spreading the weed infestation only if the seeds quickly become viable. American work showed that about half the seeds were viable only 12 days after flowering. To test how soon this happens in our climate, inflorescences that flowered freely on about 19 July were collected 18, 26 and 40 days later. Seeds germinated from 13, 35 and 38% respectively of florets of these collections sown in soil. An incubator test showed that 50% of florets of the last collection had viable seeds. The 40-day old seeds germinated sooner, and reached the maximum percentage in four weeks, compared with ten weeks for the 18-day old seeds.

Competition between weeds and crop. The effects of weeds and crop on each other depend on their growth characteristics, and on how they

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compete for light, water and nutrients. To help understanding of these relations three experiments were done: (1) to compare the growth of *Agropyron*, *Agrostis* and spring wheat separately in uniform conditions; (2) to find how *Agropyron* and wheat affect each other when grown together in pots; (3) to measure the effect of shading on the growth of *Agropyron* in the field.

Comparison of the growth of couch grass,* Agrostis *and spring wheat. Chitted seeds of *Agropyron*, *Agrostis* and spring wheat (Kloka) were planted separately in pots of soil, four seeds to a pot, in February. After a month in a cold glasshouse, they were put outdoors, and samples were taken at intervals of 2 or 3 weeks from March to August for growth measurements. Four weeks after sowing, the plant dry weights (*Agrostis* 1·2 mg; *Agropyron* 6·6 mg; wheat 70 mg) reflected the initial seed weights, but by early August *Agrostis* and *Agropyron* plants had equal dry weights of tops (28·9 and 28·1 g respectively), not much less than that of wheat (35·6 g). The grasses had faster relative growth rates than wheat throughout the growth period. Their net assimilation rates in the early stages of growth did not differ from those of wheat; their faster growth rate was a consequence of larger leaf area ratio, i.e. the grasses were leafier than wheat. Tillering began earlier in wheat, but continued longer in the grasses, which eventually had many more shoots. Nearly all surviving wheat shoots produced ears, but only 75% of *Agropyron* shoots and 25% of *Agrostis* shoots. *Agropyron* seedlings began to produce rhizomes at the 4-leaf stage and *Agrostis* at the 6-leaf stage, so that during early growth *Agropyron* had a greater weight and length of rhizome. However, *Agrostis* rhizomes grew faster, and by August the difference between the two grasses in amount of rhizomes was small.

***Competition between wheat and* Agropyron.** During November 1967, single-node pieces of *Agropyron* rhizomes were planted in pots of soil. On 21 February, 13 March and 27 March 1968, the established plants in some pots were defoliated, and half of the pots were sown with germinated seeds of spring wheat. Wheat was also sown in pots without *Agropyron* on the same dates. Later sowing of wheat alone decreased the number of shoots produced per plant but not the number of ears, delayed ear emergence and decreased the yield of grain (16·0, 14·8 and 12·5 g/plant for the three sowing dates respectively). The smaller yield was the result of fewer grains per ear, and grain size was slightly decreased by the latest sowing.

The effects on wheat of competition with *Agropyron* increased with later sowing, making shoots and ears per plant fewer; the latest sown plants averaged only four ears when competing with *Agropyron*, compared with nine when grown alone. The yields of grain per plant were decreased to 12·2, 7·7 and 4·8 g for the successively later sowings. Decrease in size and number of grains, and in number of ears, all contributed to the loss of yield from competition.

The dry weight of the tops and number of shoots of *Agropyron* grown alone were similar for all times of defoliation, but the dry weight of rhizomes per plant decreased from 6·2 g for the first time to 4·9 g for the

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last time. Plants defoliated early had more primary shoots but fewer secondary shoots than those defoliated late, and the number of inflorescences was similar for all times.

Competition with wheat had a much greater effect on the growth of *Agropyron* when the wheat was sown early. The first sowing of wheat on 21 February decreased the final dry weight of *Agropyron* tops from 24 g to 3 g and that of rhizomes from 6·2 g to 0·8 g, the corresponding decreases by the last sowing of wheat on 27 March were much smaller—in tops, from 23 g to 18 g and in rhizomes from 4·9 g to 3·5 g. The effects on numbers of shoots and ears of *Agropyron* were similar to those on dry weight.

In this experiment the plants were widely spaced and frequently watered, so competition between crop and weeds was probably mainly for nitrogen. The results show that, if a spring cereal is grown on land infested with couch grass, early sowing is likely to lessen the loss of crop from weed competition and help to discourage the weed infestation.

Effects of shading on couch grass. The temporary suppression of growth of couch grass in cereal crops during mid-season may be partly attributable to competition for light, i.e. to shading by the crop. The effect of shading on the growth of couch grass in absence of root-competition with a crop was studied by covering small plots in a natural couch-grass infestation in the field with 'Tygan' screen-cloth that transmitted about 45% of daylight. The experimental area was cultivated as for a spring cereal crop at the end of February and on 3 May, when most *Agropyron* shoots had appeared above ground, it was sprayed with a mecoprop/2,4-D mixture to control broad-leaved weeds. Seven plots each 6 ft square (area 3·3 m^2) were covered on 21 May with 'Tygan' shades supported on wooden frames, and comparable areas were left uncovered. At this time the mean number of shoot units (shoots with young tillers) of *Agropyron* was 164/m^2. On 19 June there were 406/m^2 shoots on unshaded plots and 362 on shaded plots, increasing to 741 and 668 respectively, when the plots were harvested on 9 September. At harvest, the tops were cut at ground level and rhizomes with attached roots were dug up and washed free from soil. The dry weight of tops on unshaded plots was 345 g/m^2 and of rhizomes with roots 572 g/m^2. The corresponding weights on shaded plots were 307 and 282 g/m^2. Thus, shading decreased total dry weight of *Agropyron* from 917 to 589 g/m^2, but most of the decrease was in rhizomes, which accounted for 62% of total dry weight on unshaded plots but only 48% on shaded plots. Rhizomes of shaded plants were thinner than those of unshaded plants, but internode length was unaffected. Shading increased the mean height of *Agropyron* shoots from 44 to 51 cm, but had little effect on the numbers of ears. There were no apparent differences in regrowth of couch grass after harvest, when the shades were removed, between previously shaded and unshaded plots. (Williams)

Wild oats. In collaboration with the N.A.A.S., a study of the effects on wild-oat infestations of sowing barley on different dates, with different cultivations and herbicide treatments, was started on two sites in Bucking-

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hamshire, one infested with a mixture of *Avena ludoviciana* and *A. fatua* and the other almost exclusively with *A. fatua*. The changes in the populations of wild oats and their effects on barley yield will be measured in successive crops over several years. (Thurston)

Broadbalk weeds. The rearrangement of the Broadbalk experiment (p. 25), and especially the new cropping scheme, caused large changes in the growth of weeds. The bean crop was treated with simazine, which killed most weed seedlings, mostly *Polygonum aviculare* (knotgrass), except on the farmyard manure plots where simazine was ineffective, but a few late-germinators established themselves. Many potato plots were infested with *Equisetum arvense* (horsetail) that grew much larger than in previous wheat crops, presumably because the potato tops were smaller and shorter when the *Equisetum* shoots emerged in early May than winter wheat is at the same date, and so shaded the *Equisetum* less. This agrees with the fact that *Equisetum* is less well-established on plots where the previous wheat crops were heavier. Pre-planting cultivations destroyed all annual weed seedlings, but in May there were seedlings at the cotyledon or first-leaf stage of species that normally germinate in autumn (*Alopecurus myosuroides*), winter (*Ranunculus arvensis*, corn buttercup), or spring (*Veronica hederifolia*, ivy-leafed speedwell; *Polygonum aviculare*; *Polygonum convolvulus*, black bindweed). Presumably the autumn- and winter-germinating species came from deeply-buried seeds brought to the surface by ridging and so released from dormancy enforced by depth in the soil.

The outstandingly successful weed of the year in wheat was *Polygonum aviculare*, which was not controlled by the ioxynil/mecoprop herbicide applied to control mayweed. In the wheat after fallow many wheat plants were killed by Wheat Bulb fly attack, and the weeds benefited greatly from decreased competition. On three of the most severely affected plots, samples of straw from the windrows before baling were separated into wheat and weeds, and the weed stalks, mostly of *Polygonum aviculare*, accounted for 45 to 90% of the weight of straw. (Thurston)

The Park Grass plots

Changes have continued in the flora of recently limed plots that were previously unlimed (*Rothamsted Report for 1964*, p. 226). Dandelions (*Taraxacum officinale*) were recorded for the first time flowering on all these plots, and red clover (*Trifolium pratense*) was found on plots 1C, 4-2c and 18c, which previously had none; it is now present on all the recently limed, previously acid, plots. (Williams)

Staff and visiting workers

K. Loach left to take a post at the Forest Research Laboratory, Fredericton, New Brunswick, and B. Orchard went to the Research Centre of Tate and Lyle Ltd., Keston, Kent. Gillian N. Thorne returned from Australia in March.

Dr. U. Pethiyagoda of the Tea Research Institute of Ceylon, who was

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awarded a Nuffield Foundation Fellowship, came in March for a year to work on growth regulators. Mr. P. D. Edward came in October as a post-graduate student, with a research grant from the Department of Agriculture and Fisheries for Scotland. Mr. L. A. Morgan and Mr. C. A. Phillips, sandwich-course students of Bath University of Technology, worked with us for six months. Other visiting workers were Dr. J. C. S. Allison from the University of Rhodesia, Mrs. M. Bertenyi Laszlone, from the University of Szeged, Hungary, and Professor S. Tsunoda from Tohoku University, Japan.

E. C. Humphries was invited by the Deutsche Botanische Gesellschaft to take part in a symposium on Morphactins, held at Darmstadt in October.

J. M. Thurston organised the session on Annual Grass Weeds for the IXth British Weed Control Conference, and was appointed Secretary of the Annual Grass Weeds Group of the European Weed Research Council.

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