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BOTANY DEPARTMENT

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For many years the general object of our work has been to add to knowledge and understanding of how the growth and yield of field crops depends on the form and physiological activities of individual plants, how these change with time and are affected by neighbouring plants, by the supply of water and nutrients from the soil, and by physical factors of the environment, especially temperature and the amount and daily duration of sunlight. We also have a long-continued interest in the biology of weed species and how it affects the development of weed infestations.

The topics studied in 1970 include the physiology of cereal grain yield, especially in semi-dwarf varieties of wheat, and their root growth in comparison with other varieties; effects of weather factors on the yield and sugar content of sugar beet; the control of tuber formation in potato; source/sink relations in photosynthesis; effects of water stress on growth; endogenous growth substances in wheat grains; effects of synthetic growth regulators on agricultural crops; seed production and rhizome growth of the perennial grass weeds *Agropyron repens* (couch grass) and *Agrostis gigantea*; germination and viability of seeds of *Alopecurus myosuroides* (blackgrass); effects of mineral nutrient supply on different weed species.

The practical application of much of this work is indirect. Better understanding of the morphological and physiological determinants of crop yield helps plant breeders to define the types of plants to select for particular environments, and may suggest ways of improving crop husbandry. Knowledge of weed biology is essential for the efficient use of herbicides, or other control measures. Synthetic growth regulators offer a direct means of controlling crop growth and yield; many, with diverse properties, are now known, but unfortunately their effects on our agricultural crops have proved to be variable, and more work is needed before they can be used reliably for special purposes, as they are used in horticulture.

Physiology of crop growth and yield

Cereals

Sink capacity of wheat ears. Grain yield of cereals seems to depend on the ability of the ears to absorb carbohydrate, i.e. their sink capacity, and on the amount the leaves photosynthesise after anthesis. Two experiments were done with Kolibri spring wheat to study the factors that determine the sink capacity of wheat ears, especially the number of grains per ear and the potential size of the grains.

In the first experiment we attempted to change the number of grains per spikelet, and hence per ear, by altering the environment either early or late in the period between initiation of spikelets and anthesis, while florets are differentiating. Wheat plants grown in pots outdoors were put in growth rooms for two weeks starting at initiation (six weeks before anthesis), or two weeks after initiation, with the following treatments in both periods: all combinations of bright or dim light for 16 hours per day (127 or 64 W m⁻² of visible radiation), at either 20° or 15°C in both light and dark. The plants were then returned outdoors until mature. The number of grains per spikelet was unaffected. The number of spikelets bearing grains (but not the total number) was increased by warmth (20°) early, and the number of grains per ear increased from 55 (15°) to 58. However, grains in the larger ears were smaller so grain weight per ear was unaffected. No other treatment affected the number of grains per ear. Warmth early increased dry

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weight of the tops and leaf area until anthesis, but had negligible effects on final dry weight. Warmth late had no effects immediately after treatment or at anthesis, but decreased final stem weight by 6%. Bright light during the early treatment period increased dry weight immediately after treatment but not two weeks later or at anthesis, and at maturity decreased grain and straw weight by about 7%. Bright light during the second period increased dry weight and decreased leaf area immediately after treatment, had no effect at anthesis, and at maturity decreased grain weight of the tillers by 10%. The explanation of these effects reversing between the end of treatment and maturity is not clear.

In the second experiment, wheat plants grown outdoors were put in the growth rooms for 32 days immediately after anthesis, with environments as in the first experiment, except that all plants had a temperature of 15°C in the dark, to study the effects on grain size. After 16 days, plants were transferred between environments, so there were 16 treatments, comprising all combinations of the differences in temperature and light intensity early or late during grain growth. The object of the transfer was to find whether adverse conditions early in grain growth limit final grain size, or can be compensated by more favourable conditions later. After treatment in the growth rooms the plants were kept outdoors for a further three weeks until mature. Warmth (20°C compared with 15°C, during the light period) early or late during grain growth increased ear weight immediately after treatment, probably by increasing translocation of carbohydrate to the grain, but decreased final ear weight because it hastened death of the leaves. Warmth decreased dry weight of the rest of the plant by hastening senescence and perhaps also increasing respiration. Final weight per grain and grain yield per pot were least for plants kept at 20°C in the light during both periods, greater for plants transferred between temperatures with no difference between warmth early or late, and slightly but not significantly greater still for plants at 15°C during both periods. Bright light during either period increased the weight of all parts of the plant immediately after treatment and later, but the effects of late treatment on stem weight tended to disappear by maturity. Final weight per grain and grain yield were greatest with bright light and least with dim light throughout both periods, and intermediate for plants transferred between light intensities with no difference whether bright light was given early or late. Increase in temperature of 5°C or doubling the light intensity affected ear growth similarly and independently. The effects of treatment during the second period did not depend on those during the first, so adverse conditions during the early stages of grain growth did not restrict later growth or final grain size; the mean weights per grain for all treatments during the second period ranged from 46 to 52 mg compared with 37 mg for the seed sown. (Thorne and Ford)

Root growth of wheat varieties. Experiments in 1966, 1967 and 1968 explored the effects of nitrogen, phosphorus and potassium fertilisers, and of shading, on the root growth of barley in the field. Last year, spring barley was compared with the other main cereal crops grown in Britain: winter wheat, spring wheat and spring oats. This year the root development of six winter wheat varieties was compared in collaboration with Dr. F. G. H. Lupton of the Plant Breeding Institute, Cambridge, who measured top growth and grain yield, and Dr. P. Newbould and Dr. F. B. Ellis of the A.R.C. Letcombe Laboratory who studied distribution of roots in the soil, and measured their activity in absorbing nutrients, by radioactive tracer techniques. The main object was to find whether short-stemmed wheat varieties derived from the Japanese variety Norin 10 have smaller root systems than taller European varieties.

Four new dwarf winter wheat selections bred by the Plant Breeding Institute, TL363/30, TL365a/25, TL365a/34 and TL365a/37 (all derived from Norin 10) and the varieties

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Cappelle-Desprez and Maris Ranger were each sown in Stackyard Field, Woburn, at 180 lb/acre (202 kg/ha) on 2 October 1969, with 36 lb/acre (40 kg/ha) N, 78 lb/acre (87 kg/ha) P₂O₅, 157 lb/acre (176 kg/ha) K₂O, and 91 lb/acre (100 kg/ha) MgO applied on 1 October 1969, and a spring nitrogen dressing of 1 cwt/acre (126 kg/ha) on 30 April.

The crop was sampled on 9 December 1969, 16 March, 14 April, 12 May and 8 June. On each occasion the tops were cut at ground level from a sample area 0.5 m wide across six rows of each plot for growth measurements by Dr. Lupton. From the same area eight soil cores approximately 7.0 cm in diameter, four within the crop rows and four between the rows, were taken to estimate length and dry weight of roots, by techniques already described (*Rothamsted Report for 1966*, 84, and *1967*, 94).

At the first sampling, cores 50 cm deep were taken, at the second 75 cm and at later samplings 100 cm. Cores were sectioned at 15 cm, then at every 10 cm to 75 cm, and at 100 cm, except on 12 May when sections were cut at 15, 35, 55, 75 and 100 cm. Cores from rows and from spaces between rows were kept separate at the first three samplings. Samples of above ground parts only were taken on 10 August to estimate final grain and straw yields.

At samplings 1, 2 and 3 the cores were compacted by up to 25% of their length. To estimate a correction for this, white emulsion paint was injected into the soil at depths of 35, 55 and 75 cm and coring-tubes were driven in over the injection point. Longitudinal sectioning of the extracted core showed the apparent depths of the injections after compaction, and this was allowed for when cutting up later cores.

Soil was washed off the roots in an automatic apparatus and most of the washed roots were removed from the dead organic matter by a sieve with 2.0 mm holes. A liquid cyclone, similar in principle to those used to separate minerals of different particle size, was used to remove organic debris from the fine roots, and the separation was finished by hand picking.

Two measures of root growth were used—dry weight and root length, because this permits distinction between few coarse or many fine roots, and because root length is thought to be important in determining nutrient uptake. Root lengths and dry weights were determined for all varieties at samplings 1, 2, 3 and 5, but at sampling 4 lengths were determined only for Maris Ranger and Cappelle. The dry weights of both shoots and roots continued to increase throughout the period from 9 December to 8 June (Table 1); the dry weight ratio of root : shoot also increased between December and April from 0.3 to 0.6, but later root weight increased more slowly than shoot weight and the ratio

TABLE 1

Dry weights of roots and shoots, root : shoot ratio, and length of roots; means of all varieties

Sampling date Depth	9 December	16 March	14 April	12 May	8 June
0- 15 cm	11.2	31.4	44.7	66.4	70.5
15- 25 cm	2.3	6.8	10.5	} 15.1	18.1
25- 35 cm	1.4	3.0	4.9		7.3
35- 45 cm	0.6	2.0	3.4	} 7.6	5.7
45- 55 cm		2.0	3.3		4.2
55- 65 cm		2.7	3.5	} 6.5	4.6
65- 75 cm			2.6		4.0
75-100 cm			2.4	4.3	8.3
Total	15.4	47.9	75.3	99.9	122.6
Shoot dry weight, g m ⁻²	49	87	135	292	946
Root : shoot dry weight ratio	0.31	0.55	0.58	0.34	0.13
Total length of roots, km m ⁻²	2.0	8.0	12.7	14.7	20.3

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decreased to about 0.1 in June. The growth rate of shoots increased from December to May, whereas that of roots was nearly constant from March until May and then decreased.

The shoot dry weight did not differ significantly between varieties at any harvest, because the dwarf varieties produced more tillers, which compensated for their shorter height. The only difference in root growth between varieties was that 365a/37 and Maris Ranger had barely half the dry weight or length of roots of the other varieties between 15 and 25 cm on 14 April, and there was a similar but smaller difference at greater depths. Apparently roots of these two varieties did not penetrate below 15 cm as quickly as roots of the others. However, by 8 June the differences were not significant, although the root weights and lengths of 365a/37 and Maris Ranger were still among the smallest. There was no consistent difference between the dwarf varieties and the European varieties in root weight or length. The mean dry weight of roots of the dwarf varieties on 8 June was 129 g m⁻² compared with 111 g m⁻² for Cappelle-Desprez and Maris Ranger.

On 9 December, 72% of roots were in the 0–15 cm layer, although roots had already penetrated to 45 cm deep (Table 1). By 16 March, roots had reached 65 cm, and 35% were below 15 cm. This proportion did not increase until 12 May because of renewed growth in the top layer which kept pace with that at greater depths. Roots had reached between 75 and 100 cm by 14 April and extended deeper than 100 cm on 12 May and 8 June. There was a greater weight of roots in the 0–15 cm soil layer beneath the crop rows than between them at the first three harvests, but the proportion in the spaces increased between 9 December and 14 April. However, the length of roots was similar within and between rows on 16 March, so the greater weight beneath the rows was probably because of the thick root bases attached to the crowns. Below 15 cm there was little evidence of any differences in root dry weight or length between rows and inter-row spaces. As the rate roots grew in the top layer slowed between 12 May and 8 June, the proportion of roots below 15 cm increased to 43%. Root length was distributed between different soil layers in the same proportions as dry weight.

The final grain yields (85% dry matter content) were, in cwt/acre (tonnes/ha): Cappelle-Desprez 29.0 (3.63); Maris Ranger 24.8 (3.11); 365a/25 36.5 (4.58); 363/30 31.8 (3.99); 365a/34 26.7 (3.35); 365a/37 27.6 (3.46). (Welbank and Taylor)

Sugar beet

Effects of temperature and radiation at different stages on growth and sugar content. The study of factors controlling the sugar content of sugar-beet roots, which began in 1967 with field experiments at Broom's Barn on the effects of shading, nitrogen and irrigation was continued with a study of effects of weather, using the new growth rooms to make controlled deviations from the seasonal climatic trend at specific stages of plant development. In a previous experiment of this kind (Thorne, Ford & Watson, *Ann. Bot.* (1967), **31**, 71–101), when sugar-beet plants growing outdoors were transferred for four weeks to temperature regimes equivalent to the long-term outdoor means, and 3°C above and below this, leaf area, leaf number and total dry weight per plant increased with increasing temperature, except with the oldest plants, and the effects, except for those on the youngest batch, persisted until maturity. Later work showed that exposing sugar-beet seedlings to changes in daily radiation and temperature during the first 3 weeks of growth induced persistent changes in total and root dry weights, mainly by affecting net assimilation rate (Humphries & French, *Ann. appl. Biol.* (1969), **64**, 385–393).

The experiment this year intended to re-examine the effects of changing both temperature and radiation at different stages of growth on leaf growth, photosynthesis and dry-matter accumulation by the whole plant, in addition to the effects on root growth and

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sugar content. The treatment periods were related to stages of root development; the first was while the peripheral meristems that determine root structure were being initiated (weeks 1–4), the second while the roots were growing rapidly (weeks 8–12) and the third while sugar was accumulating (weeks 18–22). The treatment in each period compared plants growing outdoors with plants kept in growth rooms with day and night temperatures corresponding to the contemporary mean day and night temperatures outdoors, and temperatures 4°C above and below these. Half of the plants at each temperature received 740 J cm⁻² of visible radiation during a 16 hour day, and half 370 J cm⁻². Day and night humidities were similar to those expected outdoors. Sugar-beet seeds were sown on 1 April in pots containing 10 kg of a 4 : 1 Rothamsted soil : sand mixture and kept outdoors in the glass-roofed cage before and after being in the growth room; plants were sampled at the end of each treatment period and at intervals until final harvest. In addition to conventional growth analysis and sugar estimations, CO₂ uptake was measured at intervals on whole tops or single leaves, with an infra-red gas analyser.

The results are not yet fully analysed, but warmer temperatures during the first two periods apparently increased the total dry weight of the plant and these effects persisted until maturity. Measurements with the infra-red gas analyser showed that none of the treatments affected the subsequent rate of photosynthesis, so the differences in dry matter production were probably caused by differences in leaf area, but this remains uncertain until net assimilation rates have been calculated. (Milford, Ford and Thorne)

Potato

Influence of the shoot on tuber formation. Last year reciprocal grafts were made between scions and stocks of normal potato plants and wildings (genetic variants that produce many more tubers) to find whether tuber number is determined by above or below ground parts of the plant, but results were inconclusive because the wilding used did not produce as many more tubers than the normal plants as expected, and because the stocks of grafted plants produced many lateral branches. The experiment was repeated with modifications and a different wilding stock in 1970.

Single-eyed seed pieces of tubers of normal and wilding stocks of King Edward were planted in pots on 23 March. On 23 April before tubers began to form, grafts were made by an approach-grafting technique between all combinations of the two stocks (normal or wilding) with three scions (normal, wilding or tomato stems). All lateral leaves and branches on the stocks were removed after grafting. Intact normal and wilding plants were also included. Plants were harvested at monthly intervals starting one month after grafting. At the last harvest intact wilding plants had about 20 tubers, and normal plants about 13 tubers (Table 2).

TABLE 2
Mean number of tubers per plant on 28 July

Stock	Intact plants	Grafted plants: Scion			Mean
		Normal	Wilding	Tomato	
Normal	12.5 ^a	13.3	12.5	13.0	20.1
Wilding	20.3	19.8	18.8	21.8	
Mean	16.4 ^c	16.5	15.6	17.4	

Standard errors: ^a 2.06; ^b 1.03; ^c 1.46

Grafted plants on wilding stocks also had about 20 tubers and those on normal stocks about 13. The identity of the scion did not affect tuber number; plants grafted with tomato scions produced as many tubers as those with potato scions. Results were similar

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at the earlier harvests except that at harvest 2 plants with normal scions had more tubers than plants with wilding or tomato scions, but lost more between harvests 2 and 3.

Tuber yield was the same with both stocks, but differed between scions. At the last harvest, the fresh weights of tubers of grafted plants with normal, wilding or tomato scions were, respectively, 12, 35 and 47% less than of intact plants. The total plant dry weight also was independent of the stock, but was less with wilding or tomato scions than with normal scions. The reason for this was that wilding and tomato scions had less leaf area than normal scions; the leaf area duration of grafts with normal scions was only 8% less than of intact plants, but those with tomato or wilding scions were 30% less. The smaller leaf area of plants with tomato scions was partly offset by a larger net assimilation rate. Grafted plants also had a slightly larger net assimilation rate than intact plants.

Hence tuber number and tuber yield were controlled differently: number depended only on the underground parts of the plant, presumably because it depended on the number of underground stem nodes able to form stolons. But tuber yield depended on the above ground parts and was closely related to leaf area duration. (Edward)

Effects of spraying plants with sucrose solution. Tuber initiation and continued growth apparently depends on the supply of photosynthate to the stolon tips, and in a previous experiment (*Rothamsted Report for 1969*, Part 1, 114) an attempt was made to augment the supply by spraying plants with 10% sucrose solution. This increased tuber number but decreased tuber yield. Two more experiments were done, testing solutions with a wider range of sucrose concentrations. In the first, single-eyed seed pieces of Majestic tubers were planted in pots in a cold glasshouse on 10 November 1969, and the plants were sprayed three times weekly with solutions containing 0, 1, 5, 10 or 15% sucrose with 0.025% sulphanilamide to prevent growth of bacteria or fungi, and 0.02% 'Manoxol' as spreader. Plants were harvested on three occasions at monthly intervals. Each increment of sucrose concentration increased the number of tubers formed, the fresh weight of tubers and the total plant dry weight; the 15% sucrose solution increased tuber number by 50% and the yield of tubers by 26%.

A similar experiment, but with Arran Pilot potatoes and solutions with 0, 5, 10, 15 or 20% sucrose, was started on 17 April, and had five harvests at intervals of two weeks. The number of tubers formed and their final fresh weights were unaffected by any of the sucrose sprays. Total plant dry weight was increased by sucrose concentrations up to 10%, but no more by stronger solutions. In both experiments solutions with sucrose concentrations more than 5% hastened tuber initiation.

In the winter experiment 5% sucrose solutions increased leaf area per plant; stronger solutions caused no further increase, but delayed the senescence of leaves, so that leaf area duration increased throughout the range of sucrose concentration. In the spring experiment each increment in sugar concentration increased leaf area per plant and leaf area duration, mainly by greater growth of lateral branches.

Net assimilation rate was increased by the sucrose sprays in both experiments; in the winter one the increase continued throughout the range of concentrations to a maximum of 30% with 15% sucrose, but in the spring one concentrations above 10% decreased net assimilation rate. The increase may partly or wholly reflect absorption of sucrose by the leaves from the spray, not increase in photosynthesis, and the reason for the decrease by the more concentrated sprays in spring and summer may be that sucrose absorbed from the spray accumulated in the leaves and slowed photosynthesis, though some was used in increased growth of laterals.

As spraying with sucrose solution increased the number of tubers in winter but not in

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spring, it seems that tuber formation was restricted in winter by lack of carbohydrate because photosynthesis and leaf growth were slowed by short days, little daily radiation and cold, so that the supply of sugar to the stolon tips was increased by uptake from solutions sprayed on the leaves, but that in spring some other factor than carbohydrate supply determined the number of tubers formed. (Edward)

Effects of water stress on growth. The effects of increasing water stress, that is, of decreasing water potential, in plant tissues on growth was studied by growing plants in pots of soil, allowing pots to lose different amounts of water, and then transferring them to the radiation-cooled growth cabinet (*Rothamsted Report for 1969*, Part 1, 125) where the loss of water was nearly zero, so that the water stress changed very slowly with time. The soil water matric potential (τ) was estimated from the soil water content (θ) determined by weighing the pots. For this purpose the relation between τ and θ was determined over a wide range of θ for three contrasting soils, which will be used as standards in future work—a clay loam from Rothamsted farm, a sandy soil from Woburn, and Kettering loam. The water potential of plants (ψ) was measured with a Scholander pressure bomb.

Kale plants with four leaves, growing in Rothamsted soil, were brought to initial τ values of -0.08 , -0.16 , -0.52 and -3.2 bars, which changed during 7 days in the growth cabinet to -0.10 , -0.46 , -2.0 and -3.7 bars. The fresh weight of leaves per plant, initially 4.7 g, increased to 5.8 g after 7 days in the wettest soil (-0.10 bars), remained unchanged with the two intermediate treatments and decreased to 3.1 g at -3.7 bars. Stem fresh weight and leaf area were also decreased by the most severe water stress, but the dry weight of leaves and stems increased with all treatments. In a similar experiment in Kettering loam, older leaves ceased to expand when τ was about -6 bars, and younger leaves at -10 bars, corresponding to a leaf water potential of -9 bars.

Such experiments with plants growing in soil are unsatisfactory because the soil water potential cannot be specified accurately from the mean water content of the soil in a pot. The water stress at the root surface may differ from that in the soil bulk, and may change with depth. Also, to achieve an adequate range of τ by controlling water loss, plants must be subjected to widely different conditions for several days before the experiment begins. These difficulties can be overcome, and the water potential of the plant defined more precisely, by substituting solutions of polyethylene glycol (PEG) for soil.

When plants of Kolibri wheat were placed in nutrient solution with PEG added to give osmotic potentials of -0.4 , -2 , -5 , -8 or -12 bars, and kept in the radiation-cooled growth cabinet for 5 days with negligible water loss, the water potentials of the plants were, respectively -1.4 , -3 , -6 , -8 and -13 bars, closely similar to the osmotic potentials of the solutions. The growth in length of the youngest leaves was not affected by -2 bars, but with -5 , -8 and -12 bars was decreased by 15, 30 and 80% respectively of that in the nutrient solution alone (-0.4 bars). The fresh weight of leaves was similarly affected and that of stems slightly more: it did not increase at -12 bars. The gain in leaf dry weight was 50% less at -8 bars, and 80% less at -12 bars than at -0.4 bars, stem dry weight was less affected, and root dry weight was apparently unchanged by increasing water stress.

The use of PEG solutions in the radiation-cooled growth cabinet provides a well-controlled and stable system suitable for studies of water stress, and as very little water flows through the plant, probably very little PEG is absorbed.

Comparison of wheat varieties. The water potential of plant tissue is determined by its osmotic potential and turgor pressure. In studies on a single genotype it is not possible to distinguish whether effects of water stress on growth or metabolism are the result of

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change in water potential *per se*, or in osmotic potential or in turgor. However, this may be possible by comparing effects of water stress on genotypes that differ in their water balance, so that the same osmotic potential or turgor pressure is associated with differences in water potential.

An attempt was made to find differences in growth between wheat varieties subjected to water stress, in the hope that these might indicate differences in water balance, in preparation for studies on the effects of water stress on metabolic processes. Seedlings of three varieties of spring wheat, Kolibri, Maris Ensign and Caesar, were grown in nutrient solution in the glasshouse. Some were transferred to solutions with PEG added to give osmotic potentials of -2 , -5 and -10 bars four weeks after sowing when most plants had three leaves, and after six weeks when ears of Caesar but not of the other varieties had emerged. Effects on growth were measured 7 days after the plants were put into the PEG solutions.

Increasing water stress decreased water loss by about 50% at -5 bars and 70% at -10 bars, but the effects were similar in all varieties and both periods. Leaf growth was decreased more by -10 bars than by -5 bars; -10 bars stopped leaf growth of Caesar during the first period but not during the second, perhaps because older leaves are less sensitive to water stress and because Caesar flowers sooner, and its leaves may age faster, than those of the other varieties. The fresh weight and dry weight of plant parts and total leaf area were little affected by -2 bars, or even slightly increased, but were decreased by -5 bars and still more by -10 bars. The effects were less in the second than in the first period.

In general, Kolibri was much less sensitive to water stress than Maris Ensign; Caesar was usually intermediate, but at -10 bars it lost as much dry weight as Maris Ensign. (Lawlor)

Photosynthesis of rooted leaves. Detached leaves of dwarf French bean (*Phaseolus vulgaris*) form adventitious roots on the petioles when placed in nutrient solution. Such a rooted leaf provides a simple system for studying how photosynthesis depends on the capacity of sinks to accept photosynthate because it has no bud and its only growing region using assimilate is the roots, that is, there is one sink for photosynthate. Humphries and Thorne (*Ann. Bot.* (1964), **28**, 391–400) showed that such rooted leaves photosynthesised faster as the size of the roots increased, and slower when roots were removed. Detached leaves of sweet potato (*Ipomoea batatas*) similarly produce roots when the petioles are kept in nutrient solution (Spence, *Rep. Fac. Agric. Univ. West Indies, Trinidad*. 1969–70) but when they are inserted into sand wetted with nutrient solution some roots swell to form tubers. Such rooted leaves with tubers can be used to study source/sink effects on photosynthesis over a wider range of sink size. Tuber formation depends on the depth of the water table in the sand; when it is near the surface tubering is suppressed, although fibrous roots form and grow well. Tubering increases as the water table falls.

Rooted sweet-potato leaves with large tubers produced more dry matter per unit leaf area than leaves with small tubers although these had more fibrous roots and stored some dry matter in the swollen base of the petiole. Thus, with a West Indian cultivar A16/15, the total dry weight of rooted leaves after 14 weeks in sand with a low water table was 3.8 g per 100 cm² of leaf, and with a high water table 3.3 g per 100 cm²; the corresponding tuber dry weights per 100 cm² of leaf were 1.9 and 0.4 g. Cultivars from the West Indies and Japan differed in the weight of tubers formed in the same conditions, and rooted leaves grown in sand culture with a variable water table might possibly be used to select varieties tolerant to wet conditions.

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Tuber formation was also changed by keeping the roots at different temperatures, while the lamina and petiole were at a uniform temperature. At 10° or 15°C no tubers formed, although at 15° roots were abundant. At 25° or 30°C roots were still abundant and some formed tubers. Total dry matter produced per unit leaf area was five times more at 25° or 30° than at 15°.

That net assimilation rate increases when tubers form and depends on the size of the tubers was clearly established, but more direct evidence that photosynthesis is controlled by sink size is being sought by measuring CO₂ uptake.

Leaves of sugar beet and of Dahlia, also, were induced to form tuberous roots by growing them in sand culture with a lowered water table. (Spence and Humphries)

Growth substances and growth regulators

Growth substances in wheat plants. An auxin extracted from immature wheat grains last year was identified almost certainly as indol-3-yl acetic acid (IAA). In a spectrofluorimeter the auxin and IAA behaved similarly, with excitation spectra maxima at 280–285 nm and fluorescence spectra maxima at 365 nm, and both reacted with Salkowski reagent (ferric chloride in perchloric acid) to give crimson solutions with maximum absorption at 520 nm.

Extracts of immature wheat grains assayed for cytokinins last year were found to contain sugars, which affect the bio-assay of cytokinins by the young-wheat-coleoptile test (*Rothamsted Report for 1969*, Part 1, 116). The aqueous residues from ethanolic extracts of wheat grains which, after partitioning at pH 3 with ethyl acetate to remove auxins and gibberellins, contained the cytokinins, were therefore freed from sugars by passing through a column of Amberlite resin, IR-120 (H). Sugars were washed through the column with water, and purines, including cytokinins, which were retained on the resin were eluted with normal ammonia solution. The ammoniacal effluents were concentrated under reduced pressure and separated on paper chromatograms with isopropanol/water/concentrated ammonia solution (8 : 1 : 1). Bio-assay showed two cytokinins, one with an R_f 0.6–0.8 similar to that of zeatin, and the other with R_f 0–0.2. The one with R_f 0.6–0.8 also behaved like zeatin in partitioning from the original aqueous extracts into ethyl acetate at pH 8.5, whereas the other remained in the aqueous fractions.

To estimate what growth substances wheat grains contain, and how they change in amount during growth, samples of growing grains of Kloka spring wheat were taken from anthesis to maturity, from plants grown in the glasshouse with supplementary light during the winter. Auxin, presumably IAA, appeared in the grains soon after anthesis, increased in amount until the fresh weight of the grain was maximal, then disappeared as the grains ripened. A gibberellin, present at anthesis, reached its maximum amount at the same time as the auxin, later than found previously. It also disappeared as the grains ripened. Cytokinins were present at anthesis, and then diminished. Most of the cytokinin activity was attributable to the one with R_f 0–0.2, so the most abundant cytokinin was not zeatin. Samples of grains were also taken from field plants, but the assays are not yet completed. (Wheeler)

Growth substances involved in the formation of adventitious roots. The cut ends of petioles of primary leaves of dwarf French bean (*Phaseolus vulgaris*) form adventitious roots when placed in nutrient solution, and an auxin, probably IAA, appears in the solution (*Rothamsted Report for 1965*, 96), suggesting that root formation is induced by auxin moving to the petiole from the leaf lamina.

Hypocotyls of excised stems of *Phaseolus vulgaris* standing in nutrient solution formed

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adventitious roots sooner than petioles of detached primary leaves. Auxin occurred in the solutions before roots appeared; it increased in amount when roots were produced and then decreased as fewer roots formed. Gibberellins were not detected, but two cytokinins were, one with a similar Rf to zeatin on paper chromatograms and one that ran more slowly. The zeatin-like cytokinin appeared after the other, and both were produced sooner from hypocotyls than from petioles. Cytokinins also appeared in the solutions when cut petioles formed callus but no roots. Exudates from the cut ends of stem stumps still attached to the roots contained cytokinin, but only the one with the smaller Rf than zeatin.

Excised stems or leaves soon die unless they produce adventitious roots, which presumably prolong the life of detached leaves or stems by replacing the cytokinin that usually comes from the root system of intact plants. (Wheeler)

CCC

Effects on cereal crops. There have been indications in previous experiments that CCC, or a derivative of it, may occur in the grain of sprayed crops and affect the behaviour of seedlings. To find whether wheat grains from crops sprayed with CCC soon after ears emerge retain enough CCC to shorten the shoots of crops grown from them, winter wheat (Joss Cambier) and spring wheat (Kolibri) were sprayed with CCC on 25 June 1969. The grain was saved and sown in autumn 1969 (Joss Cambier) or spring 1970 (Kolibri) in comparison with grain from unsprayed crops. On some plots sown with seed from sprayed or from unsprayed crops, the growing plants were sprayed with CCC at the 5-leaf stage. As usual, spraying with CCC shortened the straw and it slightly increased the yield of Joss Cambier. Seed grain of Kolibri from sprayed and unsprayed plots in 1969 gave similar plants, but unexpectedly, grain from sprayed plots of Joss Cambier gave plants that were taller than those from grain on unsprayed plots. The reason for the two varieties differing is unknown, but possibly CCC in the grain stimulated production of a growth substance that persisted for the two months until Joss Cambier was sown but not for the seven months until Kolibri was sown.

CCC shortens wheat straw and can increase yield by preventing lodging, but it can also increase yields of crops that, if unsprayed, would not have lodged. Recently, semi-dwarf varieties have been bred that are resistant to lodging, and two experiments were done to see if CCC affects them. The first compared the semi-dwarf winter wheat Gaines, sown at three rates on 27 October, with Cappelle-Desprez sown at the heaviest seed rate; four amounts of N were tested and three of CCC sprayed on 6 May when the plants had six leaves. The second compared three semi-dwarf spring wheat varieties, Inia, Benoist 257 and VR 6/57 with Kolibri, sown on 22 April; again four amounts of N were tested and three of CCC sprayed at the 5-leaf stage on 28 May.

Cappelle-Desprez yielded 45 cwt/acre (5.6 tonnes/ha) of grain and Gaines sown at the same rate 47 cwt/acre (5.9 tonnes/ha); the yield of neither variety was changed by spraying with CCC. On 1 June, shoots of Cappelle-Desprez sprayed with CCC were 17% shorter than unsprayed shoots. Shoots of Gaines also were shortened but less, up to 12% by most CCC. Gaines did not lodge, and Cappelle-Desprez did only slightly, late in the season. The spring wheat experiment gave a very thin stand, only about 100 plants/m², and the yields were small. Kolibri averaged 25 cwt/acre (3.1 tonnes/ha) of grain, and the best of the semi-dwarf varieties, Inia only 15 cwt/acre (1.9 tonnes/ha). CCC had no effect on grain yield. None of the spring wheats lodged. (Bond and Humphries)

CCC has little lasting effect on barley, but shortens the stems and enlarges the root system of wheat. Experiments were again done to see whether this difference enables wheat and barley sprayed with CCC to absorb water and nutrients from different soil

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zones and so to yield more in a mixed crop than when grown separately. Unfavourable weather delayed sowing until 23 April, when Zephyr barley and Kolibri wheat were sown in plots separately, or in alternate rows. Spring wheat tillers less than barley, and was sown thicker to equalise the numbers of shoots, but on 7 July there were 50% more barley shoots than wheat shoots in the separate crops, and 70% more in the mixed crop. Spraying with CCC (2.5 lb/acre) on 28 May shortened wheat shoots by 20%; it also shortened the lower internodes of barley, but the peduncle and upper two internodes grew longer, so the height of mature shoots was not altered. Previously CCC increased the yield of the mixed crop much more than of the separate crops, but the interpretation of the results was complicated by lodging. There was only a little late lodging this year, when CCC increased the yields of the separate crops slightly but had no effect on the mixed crop. (Bond and Humphries)

'Ethrel'

Effects on cereals. CCC shortens the stems of wheat, but not of barley or oats. Its effect was compared with that of 'Ethrel' on Kolibri spring wheat; both were used at 1 or 2 lb per acre, 'Ethrel' at the 7-leaf stage when it is most effective, and CCC at the 5-leaf stage. Both delayed ear emergence and ripening. In July 'Ethrel' shortened the shoots by 25% and CCC by 8%; both decreased leaf area per plant, 'Ethrel' by 39% and CCC by 17%. There was no lodging, even with the most N given (1.8 cwt/acre). CCC increased grain yield by 5%, whereas 'Ethrel' decreased it by 10%. (Bond and Humphries)

Effects on sugar beet. Plots of sugar beet drilled or transplanted on different dates were sprayed with 'Ethrel' (0.5 or 1.0 lb/acre) when the leaves formed a closed canopy. As in 1969, 'Ethrel' increased the number of living leaves but as it made them smaller, it decreased the leaf area per plant. Sprayed plants had a larger dry weight ratio of root to top, and a smaller leaf area ratio, reflecting an adverse effect on leaf expansion rather than an increase in the sink strength of the root. 'Ethrel' increased net assimilation rate from September onwards, but only enough to offset the smaller leaf area index, and the yield of roots was unaffected. (Humphries and French)

Effects on potato. In Denmark and U.S.A., dipping seed potatoes in 'Ethrel' solution before planting has been shown to increase the number of small tubers and the total yield of the crop. This could help to produce tubers of a size suitable for canning, so seed tubers of an early (Arran Pilot) and a main crop (King Edward) were soaked in water or in solutions containing 60, 120 or 240 ppm 'Ethrel' for 1 hour before they were planted in the field. Samples were taken from the growing crop on eight occasions at two-weekly intervals for growth analysis measurements. 'Ethrel' increased the number and yield of tubers and the proportion of small tubers, most by 60 ppm, and the increases were larger with Arran Pilot than King Edward. Leaf area index of King Edward was increased by all concentrations of 'Ethrel', but of Arran Pilot only by 60 or 120 ppm; 240 ppm decreased it. (Edward, Bond and Humphries)

BABT

Effects on tomato. Treating seeds with 2-n-butyramido-5-bromothiazole (BABT) increased the growth rate of several species, especially tomato (*Rothamsted Report for 1969*, Part 1, 119). This year its effect on yield of tomato fruits was studied by applying to seeds of Kondine Red tomato 1 mg of dust containing 5% or 10% BABT per 250 mg

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of seed. Three trusses were allowed to develop on each plant. The 5% dust hastened growth and increased the yield of the first truss by 30%. The 10% dust increased the size of the plant but not the yield of the first truss. The 5% dust increased the yield of the second truss by 14% and the 10% dust by 30%. Both dusts decreased the yield of the small third truss, but the 5% dust increased the total yield of fruit per plant by 9% and the 10% dust by 6%.

In a similar experiment during the autumn, 5% dust increased the yield of the first truss by 22% and decreased that of the second; the net increase per plant was 9%. The 10% dust increased vegetative growth but it decreased the number of flowers developing on the first truss.

BABT may be useful for stimulating early fruiting, but occasionally for unknown reasons it fails to act, and seems most effective when treated seeds are sown in sterile soil or compost. Very little BABT is needed to stimulate growth; assuming that all the active material in the dust was absorbed by the seedlings, each received only 0.7 ng, so it is improbable that the fruit could contain harmful amounts. (Humphries)

Weed studies

Blackgrass (*Alopecurus myosuroides*)

Periodicity of germination. An experiment on the seasonal periodicity of germination of blackgrass was started in autumn 1969 on a heavily infested site at Mentmore, Bucks., as part of a co-operative study with the European Weed Research Council. The site was uncropped, and weed seedlings were counted and removed at intervals as they emerged.

Germination of blackgrass was delayed by prolonged dry and warm weather in October and early November, and then by cold. Mild wet weather followed and half the year's total of seedlings emerged during the last week of December and first week of January. Germination slowed during January, ceased in February and March, resumed in April and continued at the rate of two or three seedlings per m² per week until the new season's crop of seed started to germinate at the end of July. Seedlings that appeared in June in hot dry weather came from seeds several inches below the surface of the soil, on the faces of large cracks that developed as the soil dried. These seeds presumably remained dormant while the soil was wet, and germinated as air penetrated down the cracks. The seedlings in the cracks were sheltered from the hot sun until they became established, but some died when their roots became detached from the soil as the sides of the cracks crumbled and collapsed.

On five occasions between December and May blackgrass seedlings that had emerged during the previous week in a neighbouring area of winter wheat were labelled and their growth and development were recorded. An area of approximately 1 ft diameter was cleared round each labelled seedling, but the crop and weeds were allowed to grow up to the edge of the cleared area to maintain an environment similar to that in an undisturbed crop. December seedlings that survived were by far the largest plants, 105 cm tall with 24 inflorescences each and 11 g dry weight of tops. Plants from January seedlings averaged only 14 inflorescences and 4 g dry weight of tops, but were nearly as tall as from December seedlings. Later germination gave much shorter plants with fewer inflorescences, that weighed less. The plants from mid-winter seedlings were probably the most damaging to the crop, and also returned most seeds to the soil, supporting earlier observations (*Rothamsted Report for 1968*, Part 1, 106).

Broadbalk weeds. Pre-emergence terbutryne again controlled autumn-germinated *Alopecurus* in winter wheat, except on the dung plot, but the very dry autumn delayed

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germination of many seeds until spring, when the terbutryne was no longer effective. By the end of May all wheat plots had some *Alopecurus*; those on the unsprayed section were flowering, but not the others, reflecting the different ages of the plants. *Veronica hederifolia* was widespread; it flowered and set seed between the time when terbutryne became inactive and the spring spraying with a dicamba/mecoprop/MCPA mixture. *Scandix pecten-veneris* was more abundant than for many years on unsprayed plots, but none was found in sprayed wheat.

The stubble of the sprayed wheat was almost free from annual weeds but had patches of *Agropyron repens* and *Equisetum arvense*. On the unsprayed section annual weeds predominated. The bean stubble was deep in weeds, especially *Polygonum aviculare*; the inter-row cultivations left a band of seedlings within each row, which later spread. The potato plots were very clean; *Equisetum arvense*, the chief survivor of spraying with linuron/paraquat mixture, was hand-pulled.

Equisetum has been increasing on Broadbalk since 1930, slowly until 1960 and then faster. Wet seasons were thought to have caused the increase; 1960 was the wettest during the 30-year period (36.4 in. compared with the mean of 28.0 in.). However, 1961, 1962 and 1963 were average years and 1964 unusually dry. Evidently increase in annual rainfall is not the explanation, but soil moisture content during the period when *Equisetum* is growing may be important. *Equisetum* flourishes in poor wheat crops and is checked by the heavy crops on plots with much N. Apparently it benefits from PK without N more than wheat does.

In 1967-70, after the change in cropping, *Equisetum* increased slightly in abundance on plots of the wheat/potatoes/beans rotation, but decreased slightly elsewhere. The number of infested plots in all four crop sequences changed little. The least competitive crop is potatoes because of the wide rows, and the small size of the tops when the *Equisetum* shoots emerge in spring. Beans also offer little competition early in spring because of the wide rows. Mechanical weeding between rows scarcely affects *Equisetum* but removes other species that might compete with it; however, hand weeding is effective. The most competitive crop against *Equisetum* is weedy winter wheat. (Thurston)

Agropyron repens (couch grass) and *Agrostis gigantea*

Dormancy and germination of seeds. Nearly 3% more of the *Agrostis* seeds sown in autumn 1967 and spring 1968 (*Rothamsted Report for 1968*, Part 1, 106 and 1969, Part 1, 122) germinated this year. More seeds also germinated from those recovered in 1969 from different depths in pots; a third of the seeds had survived under enforced dormancy. Not only did more seeds emerge from the shallow depths, but a greater proportion of the non-emerging seeds remained viable than of those sown more deeply. In an experiment started in October 1968, *Agrostis* seeds were sown either on the soil surface or shallowly in soil cultivated monthly, twice a year during autumn and spring or not at all; most seeds on the soil surface germinated the first month. Seeds in soil cultivated monthly germinated slowly throughout the year; 38% had germinated after a year and 51% after 2 years. With two cultivations a year slightly fewer seeds germinated, mostly during the autumn and spring. In uncultivated soil only 10% of seeds germinated, but when the undisturbed soil was cultivated after nearly 2 years, germination increased to 26% by November 1970. These studies show that *Agrostis* seeds are rarely innately dormant, but dormancy is readily enforced, so even frequent cultivations may fail to eradicate the weed.

Seeds of *Agropyron* collected in the 1969 survey were sown in October and 99% of viable seeds germinated within a month. Seeds from other samples sown in November germinated more slowly; 16% of the viable seeds did not germinate until early spring.

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As in 1968 and 1969, inflorescences of both species were collected from the field at intervals after flowering, to compare how soon seeds become viable in different seasons, and to study the behaviour of seeds of different maturity. In 1970, half the inflorescences collected on each occasion were kept dry and not sown until mid-September. *Agropyron* flowered around 27 June and spikes were collected 18, 27 and 45 days later. By mid-October 9, 43 and 53% respectively of florets placed immediately in soil, and 25, 43 and 60% of those kept dry until mid-September, gave viable seeds. *Agrostis* flowered around 15 July and panicles were collected 9, 19 and 29 days later. By mid-October 77, 255 and 390 seeds germinated per panicle of those put in soil immediately and 167, 328 and 300 of the others. Seeds of the first collection of both species were very green and immature; keeping them dry for a short interval more than doubled their viability. Evidently contamination of crop seed even with very immature *Agrostis* or *Agropyron* seed should be avoided.

Effects of light intensity, photoperiod and nitrogen. Seedlings of *Agropyron* and *Agrostis* receive very different daily illumination during their growth, and probably different supplies of nitrogen, depending on whether they germinate during autumn or spring. To find how light and nitrogen affect their growth and rhizome formation, seedlings of both species were grown in Woburn soil in growth cabinets with all combinations of dim or bright light (62 or 124 W m⁻²), photoperiods of 8 or 16 hour, and 10 or 100 ppm of added N. Temperature was 16°C during the 8 hour common to both photoperiods, and 12° during the remaining 16 hour of each day.

Bright light and more N increased total dry weight of both species, more in combination than separately. Longer photoperiods did not affect the dry weight of *Agrostis*, and increased that of *Agropyron* plants only with more N. The habit of both species was greatly affected by photoperiod; the short days produced decumbent plants with many more shoots and a larger dry weight ratio of leaves to stems than long days. Bright light did not affect the number of shoots but shortened them.

Agropyron initiated rhizomes sooner than *Agrostis* and so usually had more weight of rhizomes. After 75 days, bright light, long photoperiod or more N each approximately doubled the rhizome dry weight of *Agrostis*; the effects of light on *Agropyron* were slightly smaller, and that of N greater, than on *Agrostis*. Longer photoperiod increased the dry weight of *Agropyron* rhizomes only when more N was given, whereas either longer photoperiod or N separately increased the dry weight of *Agrostis* rhizomes and their combined effect was less than on *Agropyron*. Longer photoperiod and N both increased the number and length of rhizomes; bright light also increased their length but had little effect on their number.

Effects of defoliating *Agropyron* seedlings on subsequent growth. Seedlings of *Agropyron* from seeds that germinate in the stubble soon after cereal harvest are likely to be damaged by herbicide, cultivations or both. The effects were compared of cutting off shoots of *Agropyron* seedlings at soil level, or 12 mm above when they had two or four leaves, or when they had six leaves and began to produce rhizomes. On 22 June, seedlings defoliated at either level at the 2- or 4-leaf stages produced as much shoot dry weight as those not defoliated; those defoliated at the 6-leaf stage produced slightly less. Defoliation at any time made rhizomes lighter and least rhizome was produced by plants defoliated at the 6-leaf stage. All defoliation treatments increased the number of shoots and rhizomes; plants defoliated at soil level had fewer and slightly taller shoots but more rhizomes than those defoliated at 12 mm. Hence removing leaves probably most checks the growth of seedlings when done at the time new rhizomes are being initiated.

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Variation between seedlings of *Agropyron repens*. *Agropyron* seedlings established from seed collected from a small area differed considerably (*Rothamsted Report for 1967*, 107), and this variation was studied further by raising seedlings from seeds obtained in 1969 from many sites. Seeds from 15 selections from different areas were grown in Woburn soil with adequate nutrients and sampled on five occasions between April and mid-June. Eight of the selections were grown in larger pots until the end of August, when the shoots and emerged ears were counted at intervals and shoot height measured.

Although there were large differences in growth within selections, the differences between selections in mean shoot weight, number and height were significantly larger than within selections. The mean weight of rhizome per seedling in different selections ranged from 0.5 to 2.1 g \pm 0.07; selections with most rhizome had least weight of shoots suggesting that differences in rhizome weight were genetically determined and not merely a consequence of differences in total dry weight. The number of ears produced per plant differed widely within selections e.g. from 0 to 25. (Williams)

Factors that influence the distribution of weed species. The plots of Broadbalk given different fertilisers have different weed floras. Some weeds are widely distributed, others are much more abundant on some plots than on others. The differences in distribution may be caused by direct effects of nutrient supply on the weed, or by effects on the crop that change the micro-environment within it and alter the competition between crop and weed. Two common weeds on Broadbalk are *Tripleurospermum maritimum* subsp. *inodorum*, scentless mayweed, which is most prevalent on plots given N and P but not K, and *Stellaria media*, chickweed, which occurs mainly on plots given much N. When the weeds or wheat were grown in pots with different amounts of N, P and K, all three responded similarly to increase in N and P, but the growth of mayweed was checked by larger amounts of K that had no effect on chickweed or wheat. (Cox)

Nitrogen also had a great effect on blackgrass (*Alopecurus myosuroides*), a species more abundant and more widely distributed on Broadbalk than mayweed or chickweed; the final dry weight per plant increased almost linearly with the amount of N supplied, and evidently would have continued to increase over a much wider range. The effects of P and K were relatively small, except without N; this reflects the conditions on Broadbalk, where blackgrass plants on plot 5 (P K Na Mg) are 50% larger than on plot 3 (unmanured). The number of inflorescences was greatly increased by N, but little affected by P or K. In general, blackgrass was much more responsive to N, and less to P and K than mayweed or chickweed. (Thurston)

Equipment

Controlled environments. The four large growth rooms in the Controlled Environment building have worked satisfactorily since February, and the four smaller ones also perform to specification after we have modified them considerably. The last two Saxcil growth cabinets arrived in March and all are installed and working well. The cabinets were used by members of seven departments. An automatic alarm system was installed to notify the maintenance engineers when a fault occurs outside working hours. (Thorne, Ford and Young)

Staff and visiting workers

Visiting workers included Dr. J. A. Spence of the University of the West Indies, Trinidad, holder of a Guggenheim Foundation Fellowship, Mr. W. V. Hutcheon of the Cocoa Research Institute of Ghana and two sandwich-course students, Mr. G. R. Ohlson from

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Trent Polytechnic, Nottingham, and Mr. R. J. Penny from Bath University of Technology.

E. C. Humphries went to the Coconut Research Institute of Ceylon under the Colombo Plan, and visited other laboratories and estates in Malaya. He acted as examiner at the University of the West Indies, Trinidad, and visited the University and other laboratories in Guyana.

Gillian N. Thorne and P. J. Welbank visited research institutes and university departments at Wageningen and Groningen.

E. C. Humphries, Joan M. Thurston and E. D. Williams attended the 10th British Weed Control Conference at Brighton. Humphries introduced a programme of research reports on plant growth regulators; Thurston organised a session on weeds, herbicides and plant health, and also arranged a meeting of the European Weed Research Council's annual grass weeds group, held before the Conference.