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BOTANY DEPARTMENT D. J. WATSON

Work continued on the physiology of crop growth and yield, on endogenous growth substances and growth regulators, and on the biology of weed species-the main subjects studied for some years.

It was intended to begin a programme of experiments in the new growth rooms on effects of climatic factors on various aspects of plant growth. but the rooms were not ready in time, so much of the work extended studies started in 1968 or earlier and described in previous Annual Reports.

Physiology of crop growth and yield

Cereals

Grain yield of semi-dwarf wheats. In 1967 short spring wheats derived from the Japanese variety Norin l0 had slightly smaller grain yields than the taller European varieties Jufy I and Kloka but much less leaf area, so their leaves seemed to be more efficient in producing grain (Thorne, Welbank & Blackwood, Ann. appl. Biol. (1969), 63, 241-251). To test whether this was a consequence of less self-shading by the smaller leaf area of the short varieties, two experiments were done in which leaf area was altered by different sowing rates and amounts of nitrogen fertiliser, so that the short and tall varieties could be compared when having similar leaf areas. Also, we wished to know whether the short varieties responded to changes in sowing rate and nitrogen fertiliser similarly to European ones. The first cxperiment compared Kloka sown at 168 lb/acre (188 kg/ha) with Lerma Rojo 64 and Mexico 120 sown at 84, 168 or 252 lb/acre (94, 188 or 282 kg/ha). All varieties received 0.4, l'0 or 1.6 cwt N/acre (50, 126 or 201 kg/ha). The second experiment, done in collaboration with Dr. R. C. F. Macer of Rothwell Plant Breeders Ltd., compared the short winter variety Gaines sown at 112, 168 or 224 lb/acre with Cappelle Desprez sown at 168 lb/acre. Both varieties received 0.6, l'2, 1.8 or 2.4 cwt N/acre (75, 151, 226 or 301 kg/ha).

All spring varieties had similar maximum yields of 47 cwt/acre (85 $\%$) dry matter) (5.9 tonnes/ha), when given 1.0 cwt N/acre, and slightly less with 1.6 cwt. Trebling the sowing rate of the short varieties increased the number of ears by less than 25% and had no effect on grain yield. Both Gaines and Cappelle had maximum yields of 63 cwt/acre (7.9 tonnes/ha) with 1.2 cwt N/acre, and considerably less with more N. Doubling the sowing rate of Gaines increased the number of ears by 15% , but decreased grain yield by 10%. Gaines always had more ears than Cappelle: when sown at 112 lb/acre, Gaines had the same number of plants as Cappelle sown at 168 lb/acre, but had 30% more ears.

The short varieties would probably have yielded more had they not been heavily infected with mildew, which ethirimol failed to control. Yellow rust was controlled successfully by oxycarboxin.

Averaging all nitrogen treatments, Gaines had leaf area duration after anthesis similar to Cappelle, and the spring short varieties had slightly less than Kloka, although the ranges overlapped. Whenever short and tall varieties had similar leaf areas they also had similar yields of grain and hence their grain leaf ratios (G, grain yield divided by leaf area duration after anthesis) were similar. G of all varieties decreased with increase in leaf area index at anthesis caused by denser sowing or by more nitrogen. So the large Gs of short varieties observed by Thorne et al. (1969) may have been only a consequence of their small leaf area indices. (fhorne)

Root growth of cereals. Previous experiments have explored the effects of nitrogen, phosphorus and potassium fertilisers and of shading on the root growth of barley in the field. This year spring barley was compared with other main cereal crops grown in Britain: winter wheat, spring wheat and spring oats.

Wheat, var. Cappelle Desprez, was sown on 24 October 1968 at 175 lb/acre (196 kg/ha); wheat var. Kolibri was sown at 180 lb/acre (202 kg/ha), and barley var. Maris Badger and oats var. Manod at 140 lb/acre (157 kg/ha), on 27 March 1969. These were similar to usual farm seed rates. All plots received a basal fertiliser dressing supplying 168 lb each of P₂O₅ and K₂O and 113 lb MgO/acre (188 and 127 kg/ha) in October 1968, and nirogen was applied at 90 lb/acre (l0l kg/ha) to half the plots of each variety on 16 April 1969.

The winter wheat was sampled on 3l March 1969, and all crops were sampled on 5 May, 2 June and 30 June (about the time they flowered). On each occasion the above-ground parts of the crop from an area of about I m2 were cut at ground level, and their leaf areas and dry weights measurd. Soil cores approximately 7 cm in diameter were taken from sampled areas, four from within and four from between rows, to estimate the length and dry weight of roots. At the first sampling (winter wheat only), cores 30 cm deep were taken; at the second sampling, cores 60 cm deep were taken from the winter wheat and 30 cm deep from the springsown crops, at the third sampling, 60 cm deep from all crops, and at the fourth 100 cm deep. At the fourth sampling the ground was very dry and hard, and the sampling extended over l8 days after the tops were removed. A fifth sample of above-ground parts only was taken when each crop was ripe (winter wheat, oats and barley on 4 August and spring wheat on 15 August) to estimate final grain and straw yields.

Soil monoliths were taken by the pinboard technique on 9, 16 and 17 June. The soil between 15 and 30 cm depth was yery compact. However, when the soil was washed away from the roots, these seemed to be distributed continuously throughout this pan, with no noticeable discontinuity at its upper boundary.

At the first sampling, when the spring cereals were sown, the winter wheat already had 7.6 g m⁻² dry matter in the shoots and 4.4 g m⁻² in the roots, of which 73% was in the top 15 cm of the soil (Table 1). Root length was distributed between diferent soil layers in the same proportions as root dry weight.

By the second sampling on 5 May the spring cereals had about 30% of

TABLE 1

the shoot dry weight and 25% of the root dry weight of the winter wheat. The nitrogen applied 19 days previously increased the winter wheat shoot dry weight from 58 to 76 g m⁻², but decreased its root dry weight from 36 to 22 g m⁻², chiefly by decreasing roots below 15 cm. Nitrogen did not significantly affect the spring cereals, although the results suggest that root weights were slightly decreased. At this sampling, 45% of the root dry weight of winter wheat was below 15 cm, whereas the corresponding percentage for spring cereals was from 7% (oats) to 13% (barley). The ratio of root : shoot dry weight of winter wheat decreased at the second sampling, and at this stage spring cereals, especially oats and barley, already had less root relative to shoot weight than winter wheat had at the end of the winter (31 March), i.e. they diverted less of their current assimilates into root production during early growth.

The results for later samplings are not yet analysed. (Welbant and Gibb)

Sugar beet

Sugar content of sugar-beet roots. A study of factors that control the sugar content of sugar-beet roots began with field experiments at Broom's Barn in 1967 and 1968 on the effects of sbading and the dependence of sugar content on photosynthesis (Rothamsted Report for 1968, Part l, 97). It was intended to continue the work in controlled environments in 1969 but this was not possible; instead the efects of nitrogen were investigated. Nitrogen fertiliser decreases sugar per cent of fresh or dry weight of the root, and an experiment was done to find how the decrease develops during growth of the crop and whether it is related to anatomical changes in the root, and also to obtain more information on the distribution of the stored sugar.

Sugar-beet plants were grown in an open cage with a glass roof, from seed sown on 25 April in buckets containing 15 kg of Rothamsted soil mixed with 12.5 g K_2HPO_4 and either 6.25 g or 12.5 g ammonium nitrate. Six plants from each of the two amounts of N were taken at intervals of 3-4 weeks for growth measurements and sugar analysis.

The rates of growth in total dry weight of plants with the smaller amount of N during each of the 4 months from June to September were ll0

5.7, 12.8, 8.5 and 5.8 g per plant per week, and of those with the larger amount 7.3 , 16.3 , 14.9 and 15.5 g per plant per week. The effect of N on growth was wholly from increase in leaf area; net assimilation rate was unafected.

The fraction of assimilate that entered the root increased from 40% in June to 90% in September, and the part remaining in the tops decreased correspondingly. This partition of assimilate between tops and roots and its change with time were unaffected by nitrogen supply, but the distribution of assimilate within the tops and roots was altered. The fraction of total assimilate that remained in the leaf laminae decreased from 35% in June to negative values in September, when the growth of new leaves was insufficient to offset the death of old leaves, but the decrease was slower in plants with more N.

Assimilate entering the root may accumulate as sugar, or be used in growth, represented by increase in residual (non-sugar) dry matter. In plants with more N the fraction of total assimilate stored as sugar in the root increased from 30% in June to 65% during August and September, and the fraction used in root growth was 8% in June, increasing to a constant 25% during August and September. In plants with less N, however, a larger fraction of total assimilate, increasing to 95 % at the end of the growth period, was stored as sugar, the fraction that contributed to root growth increased to a maximum of 20% in August and thereafter decreased to zero. At the end of the growth period the roots of these plants were increasing in dry weight only by accumulating sugar, and in size presumably by cell expansion.

At the final harvest, the sugar content of plants with the small and large amounts of N were 88 and 73% of dry weight, and 23 and 20% of fresh weight respectively; the yields of sugar were l0l g and 142 g per plant. The decrease in sugar content per cent of dry weight by increase in N supply was caused not by decrease in the fraction of assimilate that entered the root, but by increase in the fraction used in growth of the root. The decrease in sugar per cent of fresh weight was partly caused by increase in water content of the root.

Sections of the roots were cut 1 cm below the lowest leaf scar and the areas occupied by different tissues measured. Although the heavier roots of plants with more N were larger in cross-sectional area, they had the same number of peripheral meristems as those of plants with less N, but the concentric rings of tissue developed from the meristems were wider; the outermost ring was very small in plants with less N. The rings of tissue consist of vascular zones with vascular bundles embedded in parenchyma, alternating with zones that consist wholly of parenchyma; nitrogen increased the area of both zones in the same proportion. The vascular bundles occupied about 20% of the cross section of the vascular zones, so, as the vascular and parenchymatous zones had approximately equal areas, about 90% of the cross section of roots of plants with either amount of N consisted of parenchyma.

Known volumes of tissue from vascular and parenchymatous zones of each ring were disintegrated, the cells counted and the mean volume per cell estimated. The larger area of the zones in roots of plants with more N

was caused wholly by increase in cell size; the number of cells was not increased.

Similar samples taken from the different tissue zones were used to measure sugar. Differences in sugar content between samples from vascular zones were not related to the area of vascular bundles they contained. Samples of parenchyma from vascular or parenchymatous zones had similar sugar contents. As there was no evidence that sugar was more concentrated in the vascular bundles than elsewhere, and as parenchyma occupies about 90% of the root volume, it follows that most of the sugar in the root was stored in the parenchyma.

The weight of sugar per cell was calculated for all samples taken from different positions in the root sections on different occasions. When plotted against cell volume, the values of sugar per cell seem to conform to a common relation for all sampling times and positions in the root, and both nitrogen treatments. In the range of cell size up to $15 \times 10^4 \mu m^3$ found in young roots, sugar per cell increased nearly proportionally with increase in cell volume, but with larger cell size, up to $60 \times 10^4 \mu m^3$, in old roots and in roots with more N, the sugar per cell increased less than proportionally, so that large cells had a smaller sugar content per unit volume than small cells. Water per cell and residual dry matter per cell were nearly proportional to cell size throughout its range. These results suggest that increase in nitrogen supply may decrease the sugar content per cent of fresh or dry weight of the root by increasing the size of the root cells, and not by a specific effect on sugar storage. Similarly, differences in cell size may account for the variation in sugar content between different regions of the root. (Milford)

Effect of seedling treatment on yield of sugar beet. In 1968, sugar-beet seedlings grown for 3 weeks in controlled environments at 20°C with continuous light, or a 16 hour photoperiod, and then transplanted to the field were compared \yith a crop produced fron seed drilled earlier in the field. The transplants at first grew faster than the drilled plants, but eventually both crops attained the same maximum leaf area index and had nearly equal leaf area durations. However, the transplanted crops had larger net assimilation rates than the drilled crop, presumably because they had a larger ratio of root : top dry weight, and consequently, gave a greater yield of roots.

In a similar experiment, sugar-beet seeds were sown on 21 April 1969 in small peat pots filled with soil, and placed in a growth cabinet at 20'C with a 16 hour photoperiod. The seedlings were transferred to an unheated glasshouse on 15 May, and planted in the field on 20 May. Seeds were drilled in the field on 11 April, and the seedlings thinned on $5-6$ June to the same spacing as the transplants. Samples were taken for growth measurements at intervals of 3 or 4 weeks, and leaf area was measured more frequendy by rating.

The leaf area of transplants was less than of drilled plants until mid-August though greater afterwards, and the transplanted crop also had a smaller mean net assimilation rate, a smaller ratio of root : top dry weight, and less yield of roots.

The reason for the difference between these results and those obtained in 1968 is not known. In 1969 pre-treatment of the seedlings did not increase their root : top ratio as it did in 1968, perhaps because the conditions in the gowth cabinets were not the same; the seedlings were less crowded in 1969. The great difference in weather between the two seasons, especially in rainfall, may have affected the result. (Humphries and French)

Potato

Dependence of net assimilation rate on leaf area. Milthorpe and others at Sutton Bonington found that the rate of tuber growth of potato crops was constant throughout a large part of their growth period, and independent of leaf area index. Nösberger and Humphries (Ann. Bot. (1965), 29, 579-588) showed that, when tubers were removed from plants grown in pots, the net assimilation rate was greatly decreased. Conversely, Dyson and Humphries found that removing 40% or more of the leaf area of potato plants by excising whole leaflets from leaves had no effect on the yield of tubers or total dry matter (Dyson, P. W. (1965), Ph.D. Thesis, University of London). These results support Milthorpe's conclusion that the rate of leaf photosynthesis is controlled by the capacity of the tubers to accept photosynthate.

The effects of partial defoliation on dry matter and tuber growth were further studied in two experiments, one in early spring with Arran Pilot, and the other in summer with Majestic. Single-eyed seed pieces were grown in pots in soil with added fertiliser, and when the plants had 6-9 leaves, before tubers were initiated, approximately a quarter of each leaflet on some plants and a half of each leaflet on others was cut off without cutting the midrib, and the treatment was repeated on new leaves as they appeared. Other plants were left intact. All lateral branches were removed. Plants were harvested at intervals of 3 weeks in Experiment 1 and 2 weeks in Experiment 2. At the final harvest in the first experiment, the mean leaf areas of treated plants were 20 or 41% less than of control plants, and in the second experiment 27 or 41 $\frac{9}{6}$ less. The numbers of stolons and tubers were unaffected by defoliation in either experiment.

In Experiment 1 the tuber yield was decreased by 10 or 19 $\frac{9}{10}$, when 20 or 40% respectively of the leaf area was removed, but the total plant dry weight was unaffected. In Experiment 2 tuber yield was decreased by 37 or 45%, and the total plant dry weight by 28 or 39%, when 27 or 41% of leaf area vas removed. Net assimilation rate was increased by defoliation in Experiment l, but presumably it was unaffected in Experiment ² (for which the values have not yet been calculated) because the loss of dry matter was nearly proportional to the decrease in leaf area. So, in Experiment I the rate of photosynthesis was, apparently, restricted by the sink capacity of the tubers, but not in Experiment 2. In both experiments, a larger fraction of total dry matter was retained in the shoots of defoliated plants than of intact plants, and a smaller fraction passed to the tubers.

Net assimilation rate was increasing throughout Experiment l, but in Experiment 2 it was decreasing from its mid-summer maximum, and

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presumably on this account dry matter production by the leaves of intact plants was not in excess of the sink capacity of the tubers. These results suggest that the rate of photosynthesis of potato crops may be controlled by sint capacity only during the part of the growing season when climatic factors permit large daily rates of dry matter production. (Edward)

Influence of the shoot on tuber formation. Genetic variants called wildings frequently appear in potato crops; they produce many more stolons and tubers, and have shorter stems and leaves with fewer and more nearly circular leaflets, than normal plants. An experiment was done to find whether the increase in tuber number is determined by above or below ground parts of plants, by making reciprocal grafts between wilding and normal plants of the varieties King Edward and Majestic. Tomato shoots were also used as scions. Intact normal and wilding plants were compared with plants consisting of normal or wilding stocks grafted with normal, wilding or tomato scions. The grafts were made on two occasions, before and at the time when tubers were formed.

All grafted plants produced fewer tubers and smaller weights of tubers than intact plants, and grafted plants with wilding scions had more tubers than those with normal scions. With tomato scions, tubers were 40% fewer and 30% lighter than with normal scions. The scions had a greater eflect than the stocks on tuber number and yield. The difference in tuber formation between normal and wilding plants was barely significant, partly because of the variability between replicates, but also because the wilding stocks produced fewer tubers tban usual. Also the stocks of grafted plants produced many lateral branches, which were allowed to grow and may have diminished the effects of the scions, but even in these circumstances the tomato scions had a large effect.

The experiment was inconclusive but suggests that the upper part of the shoot may influence tuber formation and growth in other ways than by supplying photosynthate. (Edward)

Effect of spraying with sucrose solution on formation of tubers. Tuber initiation and continued growth of tuber initials may depend on the concentration of photosynthate at the stolon tips (Milthorpe, F. L. & Moorby, J., Annu. Rev. Pl. Physiol. (1969), 117–138). If so, spraying plants with sugar solution at an appropriate time might increase the number of tubers initiated, prevent resorption of small tubers and increase tuber yield by increasing the supply of sugar from the tops to the stolons.

Two experiments were done to test this possibility. Plants of Majestic potato were grown from l0 g seed pieces, sprouted and allowed to form callus in a wann room, and planted in pots of soil with added fertiliser. The plants were sprayed daily on 5 days each week with water or 10% sucrose solution. At the beginning of the first experiment 10 ppm 'Hibitane' to prevent bacterial growth, and 0.05% 'Triton X' as a spreader, were added to the sugar solution, but they damaged the apical meristems and were replaced by 0.025% sulphanilamide and 0.02% 'Manoxol' (sodium dimethylhexylsulphosuccinate) in the later part of the first experiment and throughout the second. Six harvests were taken at 2-week intervals in the

first experiment and at weekly intervals in the second to measure growth.

In both experiments plants sprayed with sucrose solution had less leaf area per plant, and as spraying also hastened senescence and yellowing of the haulms and leaves, it greatly decreased leaf area duration. Net assimi lation rate was also decreased by spraying in the first experiment, and presumably in the second but the computation is not completed. Consequently, spraying decreased the dry weight of the whole plant and the yield of tubers. However, it increased tuber number per plant by 45% in the first experiment and by 31% in the second, but the tubers of sprayed plants were smaller.

The decrease in net assimilation rate by spraying with sucrose suggests that sugar accumulated in the leaves and depressed the rate of photosynthesis. The increase in tuber number suggests that some sugar from the spray passed to the stolon tips, where it initiated more tubers and sustained their subsequent growth. The smaller size of tubers of sprayed plants may partly be the result of competition between the larger number of tubers for photosynthate which the supply of more sugar from the spray was not enough to offset. The smaller yield of sprayed plants was the result of less leaf area and slower photosyntlesis, and evidently the amount of sugar absorbed from the spray was less than the loss of photosynthate caused by spraying. Nevertheless, the effect of spraying on tuber number suggests that it supplied more sugar, or a derivative of sugar, to the stolon tips at a time critical for tuber initiation and early growth. (Edward)

Growth of individual tubers. Plants of the varieties Majestic and King Edward were grown from single-eyed seed pieces in pots of soil so arranged that tubers were formed in a darkened space above the soil surlace (Nösberger, J. & Humphries, E. C., Ann. Bot. (1965), 29, 579-588). After tubers were initiated, six were selected at random in each pot, nearly 200 in all, and their maximum lengths and breadths measured with calipers every 7 days.

Tuber formation continued for 6 weeks after initiation, and those formed first usually, but not always, became the largest. A few of the early-formed tubers became dominant, and apparently obtained most of the available photosynthate. Others grew more slowly, or after a short time ceased to grow or decreased in size. The later-formed, small tubers usually soon stopped growing and often were resorbed, but some became dominant, and grew much faster than others. Some resumed growth, but only for short periods.

Similar apparently eratic growth behaviour of tubers was described by Moorby (Ann, Bot. (1968), 32, 57). The factors that determine which tubers grow large and which remain small are not known. It may partly depend on apical dominance in the stolons, or on competition between stolons produced from different nodes of the stem. A clearer pattern may emerge when the analysis of the results of this and other experiments is complete. (Edward)

Effects of temperature and light on leaf production by tea (Thea chinensis). In cultivation, the tea bush produces leaves intermittently in flushes

between periods of vegetative inactivity or dormancy, the length of which varies. The causes of bud dormancy in tea are still not understood; it may depend on temperature, light intensity or photoperiod, soil conditions or internal factors. Tea plants were grown in controlled environments, to find how leaf production depends on temperature and light, and whether dormancy can be induced by change in these factors.

Seeds of tea obtained fron the Tea Research Institute of Ceylon were germinated in sand in May, 1968, and transplanted singly to pots of sand irrigated with nutrient solution twice weekly. During the winter the plants were kept in a warm glasshouse with the natural daylight supplemented by fluorescent lamps. The pots were transferred in January to growth cabinets lit with fluorescent tubes and tungsten lamps giving 26 000 lx at the top of the plants. One cabinet had a photoperiod of 16 hours and the other 8 hours. Initially, both cabinets had a temperature of 30'C during the light period and 25'C during the dark, changed after 4 weeks to 25'/20". After a further 12 weeks the light/dark temperatures were changed to 20°/15° and the photoperiod in both cabinets to 12 hours.

None of the conditions induced dormancy; growth and leaf production was continuous. Apparently the rate leaves were produced depended more on photoperiod than on temperature; twice as many leaves were produced in the 16 hour photoperiod as in 8 hours, although in the shorter photoperiod plants were at the night temperature for twice as long. (Humphries and Pethiyagoda)

Growth substances and growth regulators

Growth substances in wheat. An attempt to find whether morphological changes during growth of wheat plants are associated with changes in the distribution and concentration of endogenous growth substances in different plant parts, begun in 1968, was continued. The growth substances were extracted, separated and assayed by methods already described (Rothamsted Report for 1968, Part 1, 101) except that a different assay was used for cytokinins. The previous method sought to measure the effect of plant extracts on loss of chlorophyll from excised mature wheat leaves kept in darkness. Neither the extracts from wheat leaves, roots or grains, nor exudates from cut shoots, assayed by this method in 1968 prevented chlorophyll loss, although kinetin did, but an extract of wheat grains contained a fraction that, though itself inactive, enhanced the effect of kinetin.

When the same assay was done in light, extracts of grains and exudates from cut wheat shoots caused retention of chlorophyll, but neither kinetin nor zeatin did. Leaves of other varieties of wheat and of oats were also tested. When excised leaves of oat, var. Condor, were floated on solutions of zeatin (10^{-6} to 10^{-4} M), kinetin (10^{-7} to 10^{-4} M) or extracts of wheat grains, in darkness at 25°C for 4 days, all delayed the loss of chlorophyll that occurred in leaves floated on water. This assay was used subsequently'

Another bio-assay for cytokinins, described by Rothwell and Wright $(Proc. R. Soc. B. (1967), 167, 202-223)$ was tested with extracts and exudates l16

from wheat. Zeatin and kinetin (10^{-6} to 10^{-4} *M*) increased the elongation of whole coleoptiles of wheat, var. Kloka, excised from seeds after germination in darkness at 25'C for 30 hours. Extracts of immature wheat grains also increased the elongation of coleoptiles, but as sucrose (0.01 to 0.1 \overline{M}) caused more elongation than zeatin or kinetin, the efiects of the wheat extracts can be attributed partly to their sugar contents, and not wholly to cytokinins.

Seeds of wheat, var. Cappelle Desprez, were germinated at 25°C for 3 days, when the coleoptiles and roots were removed, and the seeds remaining were soaked in several changes of ethanol for 24 hours, or macerated in ethanol. More gibberellin was extracted after maceration than from whole seeds, suggesting that the gibberellin is distributed throughout the seed and not confined to the surface layers. Auxin was not detected in extracts from whole or macerated germinating seeds. The gibberellin extracted from wheat seeds travelled on a thin-layer chromatogram at a similar Rf to that of gibberellic acid $(GA₃)$.

In 1968, most of the gibberellin present in the first leaf of wheat seedlings was found to be in the basal fifth that later elongates. Further tests on older seedlings of Kloka wheat with three leaves showed that the youngest leaf, which had not fully emerged from the sheath of the second leaf, had most of its gibberellin in the basal fifth of the leaf lamina. The gibberellin in the second leaf was distributed further along the leaf. The oldest leaf had ceased to expand, and its lamina contained no gibberellin, but the leaf sheath had small amounts. These results agree with much earlier ones with dwarf French bean, which showed that actiyely growing leaves, or parts of leaves, contain gibberellins that disappear when the leaves stop expanding.

Growth substances were extracted from growing grains of Kloka wheat and assayed, at intervals of 2 weks, starting before anthesis. As shown previously (*Rothamsted Report for 1968*, Part 1, 101) an auxin with similar Rf on chromatograms to indol-3-yl acetic acid (IAA) appeared in the grains after anthesis. Most was found when the fresh weight per grain was greatest, and it disappeared as the grains ripened and their fresh weight decreased. A gibberellin with similar Rf to gibberellic acid (GAs) appeared in the grains at anthesis, increasing to a maximum earlier than auxin content, and disappearing before the grains attained their maximum fresh weight. A cytokinin, assayed by the oat-leaf method, occurred in the growing grain. It ran more slowly than kinetin or zeatin on chromatograms and is as yet unidentified. It appeared after anthesis, increased to a maximum before the grains reached full size, and slowly decreased as the grains ripened. (Wheeler)

Effects of growth regulators on potato. The effects of the growth regulators, 'Etfuel' and morphactin, on the growth of potato were compared with those of CCC and B9, about which we already have some knowledge. 'Ethrel' was applied at 0'3 or I lb/acre, morphactin at 0'01 or 0'05 lb/acre, and CCC or 89 at 2 lb/acre, to a crop of King Edward potatoes planted on 19 April. Spraying with the growth regulators was delayed by wet weather until 25 June, when tubers were already formed, and the ground

was covered by foliage. Perhaps because of this late application and dry weather later neither CCC nor 89 caused the usual shortening of stems and darker green colour of the leaves. Immediately after spraying, 'Ethrel' and morphactin caused leaf epinasty, shortened the stems and made them stiffer and more brittle. Plants sprayed with morphactin temporarily had darker green leaves.

CCC and 89 had no effect on maximum leaf area index, but'Ethrel'at I lb/acre nearly halved it, and morphactin at 0.05 lb/acre decreased it by more than 20% , partly by suppressing the production of lateral branches. 'Ethrel' greatly increased the number and length of stolons, and the number of tubers. All the growth regulators produced more tubers and 'Ethrel' produced most; it mainly increased the number of small tubers, but morphactin increased the number in the larger size classes.

CCC and B9 had no effect on the final weight of tubers, but 'Ethrel' and morphactin decreased it, by 16 and 14% respectively with the larger amounts applied. 'Ethrel' and morphactin decreased yield relatively less than leaf area index, implying that they increased net assimilation rate. (Edward, Bond and Humphries)

CCC as a seed dressing. When CCC is used to shorten the straw of wheat, it is sprayed on the crop when the plants have 3-5 leaves. The labour of spraying would be avoided if enough CCC could be applied to the seed before sowing to produce effects on growth similar to those of spraying. To test this, seeds of Cappelle Desprez wheat were wetted with a 40% solution of CCC and air-dried; the weight of CCC so applied was 5% of the weight of the seed. Plots were drilled with untreated and treated seed on 22 October, and in spring received l, 2 or 3 cwt N/acre as 'Nitro-chalk'. CCC-treated seed germinated 2–3 weeks later than untreated seed and fewer seedlings appeared because the second internode was so shortened by CCC that some seedlings failed to emerge above the soil.

There was no lodging in any of the crops. CCC-treated seed gave smaller yields than untreated seed, and produced fewer ears because of the smaller plant population, but on plots that received 2 or 3 cwt N per acre the ears of Ccc-treated plants had more and larger grains, probably because of less competition between plants rather than a direct effect of CCC. (Bond)

Effects of CCC on mixed corn (spring wheat and barley). CCC shortens the stems of wheat, and increases the size and extent of the root system, but has only a temporary effect on barley and does not shorten the mature shoots. These differences suggest that in a mixed crop of wheat and barley sprayed with CCC, the wheat roots may absorb water and nutrients from soil layers not occupied by barley roots, and wheat and barley leaves may intercept light and absorb $CO₂$ in different layers of the crop profile, and so produce larger yields than when the crops are grown separately. This possibility was tested in an experiment done in 1968 (Rothamsted Report for 1968, Part l, 103), which was inconclusive because many fewer wheat plants than barley plants became established, and some plots were lodged. The experiment was therefore repeated.

Plots were drilled on 25 March, some with alternate rows of barley var. ll8

Zephyr and spring wheat var. Kloka, and others with the same number of rows per plot all of barley or all of wheat. There were nearly equal numbers of wheat ind barley plants per metre of row on I May in both the separate and mixed crops, but by 10 June there were more barley than wheat plants in the separate crops, and a still greater proportion of barley in the mixed crop. Spraying with CCC on 22 May had no effect on plant number. Unfortunately, lodging was more severe than in 1968. CCC entirely prevented lodging in wheat sown alone, and decreased it in the mixed crop.

The grain yield of the unsprayed mixed crop, 32.3 cwt/acre (4.05 tonnes/ ha) was less than the mean of the yields of wheat and barley grown separately (40.0 cwt/acre and 31.2 cwt/acre, or 5.02 and 3.92 tonnes/ha, respectively). Spraying with CCC increased the yield of wheat grown respectively). Spraying with CCC increased the yield of which grown
separately by 6% to 42.5 cwt/acre (5.33 tonnes/ha) and of barley by 9% to 34.0 cwt/acre (4.27 tonnes/ha), but had a much greater effect on the mixed crop, increasing its yield by 23% to 39.8 cwt/acre (4.99 tonnes/ha), which was larger than the mean of the yields of the separate crops (38.2 cwt/ acre, or 4.79 tonnes/ha). CCC decreased the proportion of wheat in the grain of the mixed crop from 24 to 14% . It decreased the number of ears, and grains per ear of wheat in the mixture, but increased those of barley, and the size of the barley grains also. (Humphries and Bond)

Effects of 'Ethrel' and morphactin on sugar beet and oats. In the experiment on pre-treatment of sugar-beet seedlings (p. 112) some plots of both transplanted and drilled crops were sprayed on 17 July with 'Ethrel' at I lb/acre or with morphactin at 0'05 lb/acre.

The older leaves of plants sprayed with 'Ethrel' became yellow during the next few days and eventually turned brown. Some younger leaves the next few days and eventually turned brown. Some younger called the end of July. Morphactin caused leaves of some plants to curl. 'Ethrel' hastened the death of leaves immediately after spraying, but later slowed the death rate and increased the production rate of leaves. During the later stages of growth, plants sprayed with 'Ethrel' or morphactin had more leaves than unsprayed plants, but 'Ethrel' made the leaves smaller, and, consequently, decreased leaf area index and leaf area duration; it increased the net assimilation rate.

assimilation rate.

'Ethrel' decreased the dry weights of leaf lamina and petioles and the leaf area ratio. Morphactin had little effect on leaf growth but at the final harvest it increased the weight of leaves by 20% . Both 'Ethrel' and morphactin decreased the yield of roots. (Humphries and French)

Plots of winter oats var. Maris Quest were sprayed with 'Ethrel' at 1 or 2 lb/acre or morphactin at 0.005 or 0.05 lb/acre on 14 May when the mean number of leaves per plant was six. Neither growth regulator had any effect on straw length or yield. (Bond)

Effects of BABT on plant growth. A chemical that accelerates cell division uniformly in all meristematic parts of a plant might increase growth rate of the whole plant without changing the relative proportions of different organs. The natural or synthetic phytokinins stimulate cell divisions in

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excised tissues, but rarely in intact plants. However, compounds containing azole groups have been reported to do so, and to increase plant growth, and one of them, 2-n-butyramido-5-bromothiazole (BABT), supplied by Plant Protection Ltd., was tested on several species. Kaolin mixed with 5 or 10% of the chemical was shaken with seeds to give dosages of 400-1000 ppm of the chemical by weight on the surface of the seed. The seeds were sown in pots of moist compost covered to prevent water loss, so that none of the chemical was removed from the seed by watering before germination.

Treating seeds of Kloka wheat speeded growth of leaves. With 400 ppm the lengths of the first three leaves were increased by 16, 8 and 5% respectively, but later leaves were unaffected. With 1000 ppm, growth of the first three leaves was slightly inhibited, but leaves 4 and 5 were 20% longer, and more tillers were produced. Mustard seedlings from seeds treated with BABT also grew faster. With 400 ppm the first three leaves 20%, and leaves 6 and 7 were also larger but not those produced later; with 1000 ppm the first six leaves were unaffected, and later leaves were smaller than in untreated seedlings.

Seeds of tomato treated with BABT produced plants with larger leaves and a greater yield of fruits, especially on the first truss. Plants grown from untreated seed and from seed treated with 400 or 1000 ppm BABT produced 59 g, 139 g and 300 g of green fruit respectively. (Humphries)

Weed studies

We continued to study the biology of grass weeds, particularly the annual grasses, wild oats and blackgrass, which commonly infest cereal crops, and the peremial rhizomatous grasses, couch grass and Agrostis gigantea, which are troublesome weeds of arable land and the most difficult to control.

Wild oats (Avena fatua)

Competition between barley and A. fatua. Previous work at Rothamsted on competition between wild oats and cereals (Rothamsted Report for 1962, 247-249) was done with cereal yarieties no longer grown, before there were herbicides that act selectively against wild oats in cereals, and its object was to control wild oats by appropriate crop husbandry. Since control by herbicides became possible, we need to know the rates of infestation with wild oats at which the crop yield begins to decrease, and that at which the loss of crop yield becomes large enough to justify the cost of spraying with herbicide. An experiment to obtain such information for *Avena fatua* growing in barley was done jointly with the Botany Section of the A.R.C. Weed Research Organisation.

Two barley varieties, Zephyr and Deba Abed, which, respectively, have upright and prostrate habits during early growth, were sown in rows spaced at 5 in. or 10 in. (12.7 or 25.4 cm) with the same number of seeds per unit length of row; other plots were not sown with barley. Each plot 120

was divided into three parts, in which, 0, 49 or 100 wild-oat seedlings per sq yd $(0, 59, \text{or } 120 \text{ per } \text{m}^2)$ were planted after the barley was drilled, but before it appeared above ground. The wild-oat seeds were chitted in the laboratory, and transplanted at regular spacing unrelated to the barley rows, to obtain evenly distributed populations with known density of plants of similar age, and to avoid leaving dormant wild-oat seeds in the soil. On plots that, in the formal arrangement, had neither barley nor wild oats, fve widely-spaced wild-oat seedlings were planted, to measure growth in the absence of competition. The plots received basal P and K and a small N dressing, because the site was fallowed in the previous year. Samples were taken on four occasions, the last before wild-oat seeds shed, to avoid infesting the site.

At the end of July, the dry weight of wild oats without competition was l3l g per plant, and of those in populations of 49 and 100 per sq yd, 20 g and 12 g, respectively. The dry weights per plant of the two barley varieties were the same, and were unaffected by competition with wild oats, even with 100 plants per sq yd. The dry weight per wild-oat plant, however, was greatly decreased by competition with barley, and more by Deba Abed than by Zephyr. In Deba Abed at 5 in. spacing and with ¹⁰⁰ wild oats per sq yd the dry weight per wild oat plant was 0.6 g. Wild-oat plants in barley had only one inflorescence; those grown alone at 100 per sq yd had an average of three, at 49 per sq yd four and in isolation 34. There were correspondingly large differences in the number of spikelets per plant.

The results suggest that appreciable loss of crop yield may occur only with much denser populations of A . *fatua* than those tested. However, the seedlings may have suffered a temporary check when transplanted and been less competitive with the barley than seedlings from seeds germinated in the crop would be, so it would be unwise to conclude that populations of 100 wild-oat plants per sq yd never afect barley yields.

Blackgrass (Alopecurus myosuroides)

Germination and viability of seeds. Seeds from plants of the 1968 experiment (Rothamsted Report for 1968, Part 1, 105) in which seeds from different parts of England and Wales were grown in pots, were sown in pans to test their germination. Nearly all seeds germinated in autumn, 1968 ; 4% or less, germinated in 1969. The viability of the seed from different selections ranged from 38% to 82% . The parent plants were grown in close proximity out of doors, so this poor viability was probably not caused by failure of pollination but by inclusion of unripe ears; the sample with 82% viability produced 23 new ears (per pot of four plants) during the l0 days before harvest, whereas that with 38 % viability produced 66 new ears.

Periodicity of germination and growth of blackgrass is being studied on a heavily-infested site near Leighton Buzzard, as part of a co-operative study by the Annual Grass Weeds Group of the European Weed Research Council. These comparative studies in the different climates, soils and cultural systems of different countries may help to explain how herbicides that control blackgrass elsewhere in Europe fail in Britain.

Comparison of plants grown from seed of different origins. In 1968 blackgrass seeds from 60 samples collected in 1966 and 1967 from different parts of England and Wales were grown in pots to study their variation in morphological and physiological characters (Rothamsted Report for 1968 , Part 1, 105). This study was repeated, but on only six selections that produced widely different plants. The plants were grown singly in pots, with ten replicates of each selection. Detailed observations were made each month from January to May, and the plants were harvested at the end of July. Seeds were collected as they ripened, to study the duration of dormancy, periodicity of germination and viability.

In general, there was great variability between replicate plants of a selection, and between these plants and those of the same selection grown in 1968. Thus, one selection, expected from the 1968 results to have many shoots, had nearly the smallest mean number of shoots at harvest and included the plant with fewest shoots. Another expected to have few shoots and a prostrate habit, had the largest mean shoot number in May, and only two prostrate plants in the ten replicates. Differences in shoot height were more consistent with those previously found.

The reason for this variability is presumably that the plants are selfsterile, and cross-pollination is essential to produce seed, so that seedlings are all hybrids of mixed origin. This variability may help to ensure adaptability of the species to a wide range of agricultural situations, but it makes growth studies requiring uniform plants very difficult. (Thurston)

Agropyron repens (couch grass) and Agrostis gigantea

Dormancy of seeds. Seeds of Agrostis sown in pans of soil in 1967 and 1968, continued to germinate. The percentage germination of those sown in October 1967 increased from 60 to 70% between October 1968 and October 1969, and of those sown in February 1968 from 70 to 75% . Seeds that did not germinate when sown at different depths in pots of soil in 1968 were recovered and transferred to pans of soil cultivated monthly. About 30% more of seeds originally sown germinated in 1969. Presumably these were made dormant by burial in the soil.

Previous work with *Agropyron* seeds showed that they germinate quickly and have no innate dormancy. Ungerminated seeds recovered from different deptls of soil in pots failed to germinate when transfered to soil in pans; unlike those of *Agrostis* they were not dormant, but had lost their viability.

Effect of light on germination of Agrostis seeds. Previous work suggested that more seeds of *Agrostis*, but not of *Agropyron*, germinate in light than in darkness (Rothamsted Report for 1968, Part 1, 107). Seeds of Agrostis collected in August, 1968, were sown in September, 1968, on the surface ofsoil kept moist in pans; half the pans were covered with aluminium foil, and half left uncovered. More of the same seeds were sown in February, and again in October, 1969, and treated similarly. After 8 months, 81% of fresh seeds, sown soon after ripening, germinated when not covered, but only 18% when kept in darkness. With 6 month-old seed, 92% of 122

uncovered seeds, and 44% of covered seeds germinated. More than 90% of l-year-old seed germinated within amonth of sowing whether covered or not. Thus, light had less effect on germination as the seed aged; tbe germination of fresh seed depended greatly on light, but year-old seed germinated quickly in either light or dark.

Development of viability of seeds. The experiment done in 1968 to find how soon after flowering Agropyron seeds became viable (Rothamsted Report for 1968, Part 1, 107) was repeated. Inflorescences were collected at weekly intervals between 10 and 45 days from flowering, and seeds from them were immediately set to germinate. Flowering occurred a week earlier than in 1968, and more seeds were produced and became viable much sooner. Over 40% of the florets had viable seed after 10 days in 1969, but only 13% after 18 days in 1968. In both years seeds collected later germinated more quickly. The maximum germination in 1969 was more than 70% , 24 days after flowering, compared with 38% after 40 days in 1968.

These results show that viability of Agropyron seeds is attained soon after flowering, and was so accelerated in a dry sunny season that seeds were viable by the time of cereal harvest.

In a similar study on *Agrostis* seeds, inflorescences were collected from field plots at weekly intervals fron flowering (about 23 July), and the florets from single heads were sown on the surfacc of soil in pans. The mean number of viable seeds per head collected one week after flowering was 180, increasing to 370 and 580 in heads collected after 2 and 3 weeks, respectively. Heads collected later had fewer viable seeds than after ³ weeks, possibly because seed had already been shed.

These and other studies show that Agrostis quickly produces many seeds that can germinate rapidly on the soil surface, but become dormant when buried and could remain viable for many years even on frequently cultivated land. Reinfestation from buried seeds may be a serious problem on land infested vith Agrostis.

Survey of seed production by Agropyron. To obtain information on how much seed is produced by Agropyron, and how much of it is viable, N.A.A.S. officers and others collected heads of Agropyron from crops as near to harvest as possible, and supplied information on the distribution of the weed and past cropping of the field. Of the 269 samples received, 84% came from cereal crops, mainly spring barley (57%) and winter wheat (15%) . The lengths of heads were measured, the spikelets and seeds per head counted, and the germination of seeds tested in shallow pans of soil in an unheated glasshouse. Germination after I month was taken as ^a measure of the number of viable seeds. Only 5% of the samples contained no viable seed, and half had more than ten viable seeds per head. More viable seeds per head were formed in winter wheat than in spring barley, and there were very few in samples from potato or sugar-beet crops.

Agropyron is self-sterile, and seed production depends on cross-pollination between compatible genotypes. Morphologically different types of head could be distinguished in 100 samples. Only 25% of samples with

indistinguishable types had more than ten viable seeds per head, compared with 63% of those with different types.

These results contradict the common belief that Agropyron plants in the field produce little seed, much of it not viable. On the contrary, they suggest that seeds could play an important part in spreading couch-grass infestations-

Growth of Agropyron and Agrostis in Rothamsted and Woburn soils. Agrostis gigantea is mainly a weed of light soils, such as at Woburn, but Agropyron repens is common on both light and heavy soils. To find whether this diference in distribution reflects differences in growth of the two species, seeds of both were sown in pots of Rothamsted or Woburn soil given basal P and K, and 0, 25, 75 or 125 ppm nitrogen as ammonium nitrate. The plants were kept in an unheated glasshouse until early April, and afterwards in a cage with a glass roof.

Agropyron seeds are heavier than Agrostis seeds (about 2 mg compared with 0.1 mg), so *Agropyron* plants were heavier initially and continued to be throughout the experiment, although Agrostis had a larger relative growth rate. For the first 8 weeks, both species grew faster in Woburn than in Rothamsted soil, but later they grew faster in Rothamsted soil. Nitrogen increased the weights of both shoots and roots of Agropyron more thaa of Agrostis, and more in Woburn than in Rothamsted soil; 125 ppm N had less effect on *Agrostis* than 75 ppm. In April, but not later, both species had a few more shoots in Woburn soil than in Rothamsted soil and nitrogen increased the shoot number of Agrostis more than of Agropyron. The shoots of both were longer in Rothamsted soil, and N increased shoot length more in Woburn soil.

Agropyron began to produce rhizomes in less than 6 weeks from sowing, but Agrostis not until after 11 weeks. Agropyron had more, longer and heavier rhizomes than Agrostis, At the end of the experiment, the weight of Agropyron rhizomes in Rothamsted soil was twice that in Woburn soil, but Agrostis had equal weights of rhizomes in both soils.

None of these differences provides an obvious reason for the association of *Agrostis* with light soils.

Effects of shading on couch grass. Couch-grass plants growing in cereal crops may suffer from shading as well as from competition with the crop for nutrients or water. An experiment in 1968 on a natural infestation of couch grass to find how shading without root-competition afected its growth (Rothamsted Report for 1968, Part 1, 109) was repeated, with modifications, on plots established in 1968 by planting clonal rhizome fragments. Plots were either unshaded, or shaded from May to mid-July, or from mid-July to September, or throughout both periods, with Tygan screen-cloth, which transmits 45% of daylight.

Plants shaded during the frst period had fewer shoots at mid-July; in September this difference had almost disappeared, but ears were fewer. Shading during the second period had no effect on the numbers of shoots or ears. Shoot height was increased more by late than by early shading. The dry weights of both shoots and rhizomes were decreased more by 124

late shading than by early shading, and the effects on rhizome weight were much greater than those on shoot weight. These results resemble those obtained in 1968. (Williams)

Broadbalk weeds. The most striking feature of the weeds on Broadbalk was the excellent control of *Alopecurus myosuroides* (blackgrass) and most autumn-germinating dicotyledonous weeds by spraying with terbutryne pre-emergence, in autumn 1968. By March, occasional seedlings of Alopecurus, Ranunculus arvensis (corn buttercup), and Veronica hederifolia (ivy-leaved speedwell) were visible, probably from seeds germinating after the terbutryne had gone. In contrast, Alopecurus was very abundant in March on the fallow section and the section after potatoes, which had been ploughed in autumn and not sprayed. Most plots of the unsprayed wheat on section 8 were full of *Alopecurus* by harvest, and there was a heavy infestation in the rows of beans on section 7, although cultivations had eliminated them between rows. Alopecarus on various parts of the field was severely attacked by twist (Dilophospora alopecuri), and ergot (Claviceps purpurea) was unusually abundant on Alopecurus in the beans, some ears having up to 14 ergots. This confirms suspicions that springgerminating *Alopecurus* plants are more susceptible to ergot than autumngerminated ones, probably because they flower at the right time to catch the fungus spores. If this strain of ergot can also attack wheat, then the Alopecurus is helping to carry the ergot across the bean break in the rotation. (Thurston)

Equipment and apparatus

Controlled environments. The eight growth rooms in the Controlled Environment building intended for the Botany Department were not usable for experiments during the year. The four large ones were handed over in August, but required modifications to the humidity control system, which were completed and tested in two rooms by the end of the year. The small rooms require larger coolers to provide the specified temperature range. We expect both sets of rooms will be ready for use early in 1970.

The seven Mark II Saxcil cabinets were used for experiments throughout the year; 13 people from six departments had experiments in them. The two Mark I cabinets also ran continuously. The remaining two Mark II cabinets had not been delivered by the end of the year. (Thorne and Ford)

Water relations. A radiation-cooled growth cabinet similar to that described by B. Orchard (J. agric. Engng Res., (1967), 12, 62-65) but larger, designed and partly made by him before he left the department, was completed and tested. An automatic recording apparatus for measuring water potential of soils or plant tissues with Spanner thermocouple psychrometers was built, incorporating the switch and cam timer control system of Rowse and Monteith (J. scient. Instrum. Ser. 2 (1969), 2, 397-400), but instead of the galvanometer it has an operational amplifier to record the thermocouple output on a strip-chart recorder. This equipment is for use in work on efects of water deficits on plant growth and

metabolism, which was resumed after being interrupted by Orchard's departure. This study requires means to keep constant water deficits for prolonged periods; a common method is to grow plants in nutrient solutions containing polyethylene glycol as osmoticum, but the radiationcooled growth cabinet should enable plants to be grown in soil with a constant or slowly changing water deficit, by preventing transpiration. (Lawlor)

Staff and visiting workers

M. J. Gibb left to join the staff of the Grassland Research Institute. D. W. Lawlor, G. F. J. Milford whose work is supported by a grant from the Sugar Beet Research and Education Committee, R. W. Soffe, P. J. Taylor and A. T. Young, were appointed. Dr. U. Pethiyagoda returned to Ceylon in February. Rosemary R. Cox joined the department as the holder of a Science Research Council Studentship. J. C. Blacklock, a sandwich-course student at Bath University of Technology, worked with us for 6 months. Yisiting workers included Dr. L Kousalova of the Institute of Cereal Crops, Kromeriz, Czechoslovakia, Dr. J. A. Spence of the University of the West Indies, St. Augustine, Trinidad, and Dr. S. M. Sircar, Director of the Bose Institute, Calcutta.

E. C. Humphries and P. J. Welbant attended the XIth International Botanical Congress at Seattle. Gillian N. Thorne was a guest of the University of Nebraska at a Symposium on Physiological Aspects of Crop Yield organised in association with the American Society of Agronomy and the Crop Science Society of America at Lincoln, Nebraska. She also attended an I. B. P. Technical Meeting on productivity of photosynthetic systems at Trebon, Czechoslovakia, and contributed to a Symposium on Potential Crop Production in Britain, arranged by the Welsh Plant Breeding Station and the University College of Wales at Aberystwyth, in which D. J. Watson also took part. Joan M. Thurston was invited to lecture to the Department of Agricultural Botany of Queen's University, Belfast, and to contribute to the 3rd Colloquium on Weed Biology at the Ecole Nationale Supérieure Agronomique, Grignon.