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Rothamsted Report for 1967

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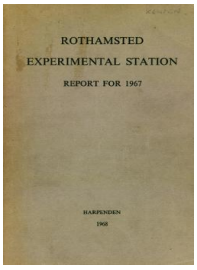

Botany Department

D. J. Watson

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BOTANY DEPARTMENT

D. J. WATSON

The department aims to increase knowledge of how the growth and yield of agricultural crops is determined, how it depends on external conditions and how it can be controlled or changed in advantageous ways. In 1967, as previously, it was concerned with the physiology of growth and yield of field crops, with endogenous growth substances and synthetic growth regulators, and with weeds. Work continued on many of the topics discussed in the 1966 report, including the determinants of cereal grain yield, root growth of field crops, effects of the growth regulator CCC (2-chloroethyltrimethyl-ammonium chloride), the origin of auxin in leaves, the influence of water deficit on leaf growth and the biology of blackgrass (*Alopecurus myosuroides*). In collaboration with the Nematology Department, the role of auxin in gall formation by root-knot nematodes was investigated. Work on sugar-beet physiology, resumed after a short interruption, dealt with the causes of variation in sugar content of the root. A study of the biology of couch grass (*Agropyron repens*) was begun.

Physiology of crop growth and yield

Ear size and grain yield of wheat. Grain yield of cereals seems to depend both on the capacity of the ears to accept photosynthate and on the amount produced by the green parts of the plant. The effects of conditions after anthesis on these two factors in Kloka spring wheat were studied in an experiment similar to one described in last year's Report (p. 88), which was unsatisfactory because the treatments could not start until 2 weeks after anthesis. Plants grown in pots outdoors were transferred at anthesis in June 1967 to three growth rooms. In one of these the temperature during the 16-hour light period with 9·5 cal/dm^2/min visible radiation was 20° C, and in another 15°. In the third room conditions were more favourable for photosynthesis—visible radiation during the light period at 20° C was increased to 15·4 cal/dm^2/min, and the CO_2 concentration was increased approximately three-fold, to 1000 ppm. All three rooms had an 8-hour dark period at 15° C.

Decrease in temperature from 20° to 15° C during the light period had no effect on the apparent photosynthesis of the flag-leaf laminae measured with an infra-red CO_2 analyser; it delayed senescence of the leaves, and hence increased leaf-area duration after anthesis (*D*) by 30%. Ears weighed less at 15° than at 20° until 40 days after anthesis, when those at 20° stopped growing. At 15° ears increased in weight for a further 25 days, so that eventually grain dry weight was 18% greater than at 20°. Shoot and root dry weights increased until 25 days after anthesis at 15° and then decreased to approximately the same values as at anthesis. At 20° they increased slightly during the first 14 days, but then decreased to

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less than the initial value. These changes in weight suggest that most of the current assimilate moved to the grain at 20°, as usually occurs in the field, but that the extra leaf area at 15° produced more photosynthate than could be accommodated in the ears, and so some of it accumulated in the stem and root. Hence leaves seemed less efficient in producing grain at 15° than at 20°; the grain–leaf ratio (*G*) was decreased by 10% from 18·6 g/m²/week at 20° to 16·8 at 15° C.

Extra light and CO_2 increased the rate of apparent photosynthesis of flag-leaf laminae, increased dry weight of ear, shoot and root throughout the grain filling period, and had no effect on *D*. Grain dry weight was 28% greater than with 9·5 cal/dm²/min and normal concentration of CO_2, so *G* was increased correspondingly to 24·4 g/m²/week. Shoot and root increased in weight until 25 days after anthesis and then decreased slightly, as at 15° C with less light and CO_2, indicating that all the extra photosynthate produced by the faster photosynthesis with extra light and CO_2 could not be accommodated in the ears.

The yield of grain from plants left outdoors after anthesis was intermediate between those in the growth rooms at 15° C and at 20° C with extra light and CO_2, and the dry weight of shoot and root was similar to that in the growth room at 20° C without extra light or CO_2.

In the similar experiment in 1966 a 5° C decrease in temperature or extra light and CO_2 also increased shoot and root dry weight, but did not increase ear weight. The reason for this difference between experiments may be either that *D* at 15° C or with extra light and CO_2 was smaller, relative to *D* at 20° C with normal light and CO_2, in 1966 than 1967, or that final grain size depended on the environment during the first 2 weeks of grain filling, before the treatments began in 1966. (Thorne and Ford)

Grain yield of semi-dwarf wheats. A preliminary trial in 1966 showed that some short-strawed wheat varieties had grain yields similar to those of taller British varieties, despite much less leaf area, so in 1967 the mechanism of grain production in six spring wheat varieties descended from the Japanese dwarf wheat Norin 10 was compared with that in Jufy I (J) and Kloka (K) grown on small field plots protected by a bird-proof cage. The semi-dwarf varieties were NBJ115 (N) and Mexico 120 (M), obtained from the Agricultural Research Institute, Wagga-Wagga, Australia, and Penjamo 62 (P), Lerma Rojo 64A (L), Sonora 64 (S) and a recent cross (R) that has given promising lines, obtained from the Rockefeller Foundation in Mexico.

The British and Mexican varieties were slightly infected with yellow rust, but N and M from Australia were so severely infected that their yields were much less than those of other varieties: all the leaf laminae of N were killed soon after anthesis, and it produced only 27 cwt/acre of grain. Grain yields (15% moisture content) of the other varieties were: J 54·6, K 52·4, R 51·4, P 50·2, L 47·0, S 44·1 $\pm$ 1·68 cwt/acre. The differences in yield, except that between J and K, were correlated with differences in numbers of ears per unit area, which in turn were correlated with differences in plant number. Although the Mexican varieties produced thinner plant populations than the British ones, they tillered no more, but more of

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their shoots survived to produce ears. Within the Mexican varieties a thinner plant stand was not compensated either by more tillering or better survival of shoots. These results suggest that the smaller-yielding varieties might have yielded as well or better than Jufy I had they been planted more densely. Differences between varieties in population occurred because there were unintended differences in sowing rate and because some varieties germinated poorly both in the field and in the laboratory.

The mean dry weight of shoots of the Mexican varieties was 57% of that of the British varieties, so grain accounted for 49% of the dry weight of the tops for the Mexican varieties, but only 43% for the British. The Mexican varieties also had much less leaf area than the British. Their leaf-area duration after anthesis averaged 62% of that of the British varieties, but was more efficient in producing grain; the grain : leaf ratio (G) of the Mexican varieties was 35–56% greater than of the British ones. Leaf area above the flag-leaf node accounted for more of the total leaf area in Mexican varieties than in J and K so that, when based on this area, G of the Mexican varieties exceeded that of the British ones by only 24–47%. The Mexican varieties are awned, which may partly account for the apparently greater efficiency of their leaves, because any photosynthesis by the awns was attributed to the leaves. Alternatively, their leaf arrangement may intercept light more efficiently; light penetration was not measured over a sufficient range of leaf-area index to test this. Near the time of anthesis, J and K with leaf-area indices of about 8 absorbed over 90% of the incident radiation, and the Mexican varieties with leaf-area indices of 5 or less absorbed 70–90%.

The Mexican varieties had less leaf area per shoot than the British because their laminae were smaller and because their stems were shorter; their mean height was 61–76 cm compared with 92 cm for Jufy I and 97 cm for Kloka. M was only 43 cm high. Differences in height reflected differences in length of the top four internodes—the only ones that exceeded 2 cm. The top internode (flag-leaf sheath plus peduncle) was shortened relatively less than the lower ones, so its contribution to total height ranged from 44% for J to 53% for S. Short varieties did not have fewer internodes than tall ones. Differences between varieties in the number of leaves produced on the main shoot were not correlated with height.

There were only small differences between varieties in the rate they developed. All initiated spikelets in early May, between 45 and 48 days after sowing, but the Mexican and Australian varieties flowered and ripened about a week earlier than the British ones. (Thorne, Welbank and Blackwood)

Root growth of field crops. The procedure for taking soil samples for recovering roots, using a steel coring tube driven into the ground with a motor breaker (*Rothamsted Report* for 1966, p. 84), was improved in several ways. Use of a three-legged gear puller to grip a ring brazed to the top of the tube hastened extraction of the tube. A method of pulling the brass liners out from the tube with the soil core encased in them was devised, that made sampling of wet soil possible. In favourable conditions the time for taking a core sample was shortened to 2½ minutes; four men were

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required to do all the operations, including dividing up the sample and bagging and labelling its parts.

In May we received from America a hollow soil auger designed by Professor W. F. Buchele of Iowa State University. It is driven by a portable motor, and excavates soil from an annular space, leaving a free-standing core of undisturbed soil in the middle. The core is removed in a non-rotating tube which passes down the middle of the auger. The auger could not be tested until July, when the soil was dry and hard; in these conditions it penetrated very slowly until it reached soft subsoil, from which it was difficult to extract. Contrary to expectation, the core in the central tube was compressed more than cores cut by the coring tube and breaker. The auger will be tested again in less difficult conditions, and with modifications to improve its performance.

Samples were taken with the coring tube from an experiment at Woburn to measure the effects on root growth of barley of applying nitrogen, phosphorus and potassium, separately and in all combinations. Crop samples and four soil cores from each plot, cut into sections at 15, 30 and 60 cm from the surface, were taken on eight occasions from 3 May to 21 August, but examination of the roots from the soil cores is not yet complete. (Welbank, Williams and Gibb)

Sugar content of sugar-beet roots. The wide variation between years in sugar content of sugar-beet roots is troublesome to the sugar factories, not only because a smaller sugar content means less sugar is extracted per ton of roots processed, but also because it decreases the crystallisable fraction of the sugar in the extract, and increases the less-profitable fraction remaining as molasses. For industrial purposes, sugar content is expressed as per cent of fresh weight of roots, and evidently part of the annual variation in this may be caused by differences in water content; how much is the result of differences in sugar per cent of dry matter is uncertain, because the dry-matter content of roots is not determined routinely. The annual variation is presumably caused by weather, acting directly on the crop or by changing soil conditions, and by diseases and pests, the incidence of which also depends on weather.

A study of the causes of variation in sugar content was started with an experiment at Broom's Barn to measure the effects of shading, and of applying additional nitrogen, at different stages of growth. Both treatments presumably restrict the supply of sugar for storage, shading by decreasing photosynthesis and extra N by increasing the requirements of photosynthate for growth. The crop was sown on 4 April 1967, and received 6 cwt/acre Kainit applied in the previous October, and 6 cwt/acre of 20–10–10 compound fertiliser in the seed-bed. The shades, which were of Tygan fabric supported on wooden frames, transmitted about 45% of daylight, and were placed on different plots for three periods each of 4 weeks separated by 1 week, starting on 13 June, 18 July and 22 August respectively. On the same dates 0·6 cwt N/acre as "Nitro-Chalk" was applied to half the shaded plots and to comparable unshaded plots. Samples of about $\frac{1}{1000}$ acre of crop (about 40 plants) were taken in each period from each shaded plot, and from comparable unshaded plots, with and without

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extra N, just before the shades were erected, after 2 weeks, and after 4 weeks when the shades were removed, and from every plot at the final harvest on 25 October.

Shading in all three periods decreased the net assimilation rate by one-third or more, and only slightly increased the leaf-area index, so that it decreased the gains during the period in total plant dry weight and total weight of sugar in the roots. It decreased sugar per cent of fresh weight from 14·6 to 10·0% in period 1, from 15·5 to 13·6% in period 2 and from 17·9 to 17·1% in period 3, but affected sugar per cent of dry matter only at the end of period 1, in mid-July, when it was decreased from 76 to 69%. Evidently, the change in sugar content per cent of fresh weight was mainly or wholly the result of change in water content; shading increased the water per cent of dry matter in the roots by decreasing the transpiration rate of the plants and the water loss from the soil.

At the final harvest in October shading at any time had little or no effect on sugar per cent of either fresh weight or dry weight, but the earlier effects on total weight of sugar in the root persisted, though they were smaller than at the end of the shading period, presumably because shading increased leaf-area index slightly. Evidently when the supply of sugar to the root was restricted by shading, the weights of sugar and of non-sugar dry matter were decreased in similar proportions, implying that sugar stored in the root is not simply what exceeds the requirements for growth.

Nitrogen applied at the beginning of each shading period had no significant effects by the end of the period on the dry weight of any part of shaded or unshaded plants, or on the weight of sugar in the roots, although it increased the area and weight of leaf laminae slightly and decreased sugar per cent of both fresh weight and dry weight in the root.

At the final harvest N applied at the beginning of period 2, but not at other times, decreased root dry weight. Extra N in all periods increased the final dry weight of tops and the leaf-area index, and consistently decreased the sugar content of the roots from about 17 to 16% of fresh weight, and from 76 to 75% of dry weight. Extra N applied in period 2 decreased the yield of sugar, but the earlier and later applications had much smaller effects. All N applications increased the water content per cent of dry matter of all plant parts.

The carbohydrate required for the increased growth induced by additional N was provided mainly by more photosynthesis from the increased leaf area, and little was diverted from sugar storage in the root; averaging all times of N application, the weight of sugar in roots was decreased only from 751 to 724 g/m². As the weight of non-sugar dry matter was scarcely affected, the sugar content per cent of dry matter was slightly decreased. Thus, the effects of both shading and N on sugar content per cent of fresh weight of roots mainly reflected changes in water content. The effect of N depended on persistent internal changes affecting the hydration of the cells, but that of shading was caused by temporary change in soil-water content that disappeared by harvest, presumably because the soil-water contents on previously shaded and unshaded areas had then been equalised by recent heavy rain (6 in. in October). (Watson, Motomatsu, Loach and Hole)

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Photosynthesis by sugar beet and barley. Sugar-beet plants consistently have much larger net assimilation rates (E) than barley plants of similar age growing in similar conditions, but published results show no comparable differences between rates of apparent photosynthesis of sugar beet and barley determined from the CO_2 exchange of whole tops or single leaves. An attempt to account for this anomaly by measuring simultaneously E and the rate of CO_2 exchange of whole sugar-beet and barley plants, grown in solution culture to avoid the complication of respiration by soil organisms, was made in 1966 (*Rothamsted Report* for 1966, p. 92), but failed because the sugar beet grew badly, probably because the nutrient solutions were not aerated. Both its rate of apparent photosynthesis and E were less than those of barley, which grew well. The attempt was therefore repeated.

Sugar-beet and barley plants were grown in soil or in aerated nutrient solutions in a growth room with a 16-hour photoperiod, at 20° C in the light and 15° C in the dark. Barley was sown a week after sugar beet, so that the plants were of similar size and weight when the experiment started 17 days after the barley was sown. Some wheat and barley plants growing in nutrient solution were placed in assimilation chambers through which air from the growth room was circulated, and the CO_2 exchange was measured with an infra-red CO_2 analyser. The remaining plants were fully exposed in the growth room, and their positions adjusted so that the light intensity near the top of the plants was uniform with that in the assimilation chambers (about 9 cal/dm²/min visible radiation). E was determined from the differences in dry weight and leaf area of plants sampled at the start and 6 days later. The experiment was repeated after 2 weeks on older plants of the same sowings, but only with those growing in nutrient solution.

Although the temperature in the assimilation chambers in the light was 5–7° C warmer than outside, it had little effect on growth; it increased leaf area slightly. The mean values of E, in g/m²/week were:

	Exposed		In assimilation chambers	
Grown in:	Soil	Solution	Solution	S.E.
Experiment 1				
Sugar beet	101	102	94	3·2
Barley	72	66	68	1·5
Experiment 2				
Sugar beet	—	91	72	3·3
Barley	—	60	61	1·1

Sugar beet growing in soil or nutrient solution had nearly the same E, but barley had slightly smaller E when grown in nutrient solution. Enclosing the plants in assimilation chambers decreased E of sugar beet, especially in Experiment 2, but not E of barley. As before, sugar beet consistently had much larger E than barley, whether or not the plants were enclosed in assimilation chambers.

The CO_2 uptake of plants in the assimilation chambers was measured during 4 hours near the middle of each daily light period. The mean rates of apparent photosynthesis in mg CO_2/dm²/h were:

	Experiment 1	Experiment 2
Sugar beet	13·4	10·1
Barley	8·4	7·8

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As with the values of E, the rates for barley were about $\frac{2}{3}$ of those of sugar beet.

Continuous measurement throughout several light periods showed that CO_2 uptake changed with time, although conditions in the growth rooms remained constant. With sugar beet the rate increased to a maximum after about 7 hours in the light, and then decreased to the initial value. With barley it continued to increase for about 11 hours and then remained steady. This implies that the difference in apparent photosynthesis between sugar beet and barley measured in short periods will depend on how long the plants have been illuminated.

Estimates of the increments in dry weight during the experimental period, calculated as carbohydrate from the measured rates of CO_2 uptake, were very similar to those actually found for sugar beet, but for barley they were smaller by about 15%. The mean values in cg/plant were:

	Sugar beet		Barley	
	Experiment 1	Experiment 2	Experiment 1	Experiment 2
Observed	87	238	36	245
Calculated	88	233	30	209
S.E.	0·4	11	0·4	3

Evidently, differences in net rate of photosynthesis estimated as E from dry weight increase, such as that between sugar beet and barley, can be reconciled with estimates from CO_2 uptake, provided precautions are taken to ensure that plants are in comparable conditions when the different measurements are made. When discrepancies occur, they are likely to be caused by defects in the more complicated procedures involved in measuring gas exchange. (Ford)

Growth of kale seedlings with slow transpiration rates. The radiation-cooled growth cabinet, in which transpiration by illuminated plants can be nil, or negative, so that the soil-water content changes very slowly with time (*Rothamsted Report* for 1966, p. 93), was used to measure how soil-water deficits affect the leaf growth of kale seedlings transpiring at different rates.

Slowing transpiration by increasing atmospheric humidity in the cabinet had little effect on the soil-moisture content (M_0) at which leaf growth ceased, until the humidity was enough to promote guttation. The relative leaf growth rate in dry soil was then increased by as much as one-third of the rate in wet soil, and consequently M_0, estimated by extrapolation, was apparently decreased. Some or all of the faster growth in dry soil was probably caused by guttation water falling on the soil and causing local wet zones. The amounts of water involved were small, about 1% of the water in the soil mass, but only slightly greater amounts applied by Whitehead's method had a similar effect.

Plants growing in moist soil and transpiring slowly often had a greater initial leaf growth rate than plants transpiring much faster in a conventional growth chamber. As very slow transpiration did not inhibit leaf growth, it seemingly supplied enough mineral nutrients from the soil to the roots. This is important, because drought is thought to inhibit the growth

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of grass swards by preventing nutrient uptake. The potassium and calcium contents of growing seedlings are being determined to measure directly the effects of drought and slow transpiration on nutrient uptake.

Hitherto the water status of the soil has been measured as water per cent dry weight, and the same standard soil has been used in all experiments. To permit meaningful comparisons between different soils and other media and plant tissues in different conditions, water status must be expressed as water potential. An automatic apparatus for measuring water potential by Spanner's method was developed and is being tested. It measures and records water potentials of up to 50 samples at the rate of 30 per hour. Determinations can be made rapidly, so accuracy can be enhanced by averaging replicates. (Orchard)

Persistent effects of raising sugar-beet seedlings in different photoperiods, and of CCC, on subsequent growth. Previous work (*Rothamsted Report* for 1965, p. 95) showed that sugar-beet seedlings grown for 3 weeks after germination with a 16-hour daily photoperiod continued to produce leaves faster than seedlings with 8-hour photoperiod of the same light intensity, when both were transferred to natural illumination in a glasshouse. This effect is not necessarily photoperiodic; it may depend on the difference in total daily radiation. It was studied in two experiments. The seedlings were raised in growth cabinets at 20° C with fluorescent light. In the first experiment seedlings had either 8-hour or 16-hour photoperiods, and in the second either a 16-hour photoperiod or continuous light. After about 2 weeks, when they had two true leaves, they were transplanted singly into pots and moved to an unheated glasshouse in May. Plants were harvested on three occasions, the last after 20 weeks, and growth was measured more often.

Throughout both experiments, plants exposed initially to the longer photoperiod continued to produce leaves faster. They also increased in leaf area faster, and consequently produced more dry matter. The final dry weight per plant was increased by about 10% by increase in the initial photoperiod, either from 8 to 16 hours in the first experiment, or from 16 to 24 hours in the second.

After the plants were moved to the glasshouse CCC solution was applied to the soil three times at weekly intervals in the first experiment, and once in the second; the leaves of other plants in the second experiment were sprayed with CCC on 5 successive days. As in the 1965 experiment, CCC increased the rate leaves were produced over a long period, so treated plants had more leaves throughout the growth period, except that CCC spray injured young leaves, which delayed the increase in leaf production. However, CCC made the leaves smaller. CCC applied to the soil decreased the final dry-matter yield in the first experiment, especially of plants started in an 8-hour photoperiod, but had little effect in the second experiment. (French and Humphries)

Effects of interrupting vernalisation of winter wheat or winter barley, with or without CCC. The vernalisation of cereal grains was unaffected by CCC (*Rothamsted Report* for 1966, p. 90), but interrupting vernalisation by

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immersing the grains in water at room temperature for 24 hours during the period of cold treatment did affect their subsequent development. The effect was further studied.

Imbibed seeds of Cappelle-Desprez winter wheat and Dea winter barley were put in an incubator at 5° C, and at 0, 2 or 4 weeks some were immersed either in water or in CCC solution (100 or 1000 ppm) at room temperature for 24 hours and then returned to 5° C. After 5 weeks, on 19 April, the seeds were planted in pots of soil in the glasshouse. Seeds kept at 5° C for 0, 2 or 4 weeks were also planted, to show the effects of different periods of vernalisation.

As before, CCC did not affect the growth of wheat or barley, except for delaying ear production by wheat in July.

Wheat plants from seeds whose vernalisation was interrupted after 4 weeks produced fewer vegetative shoots than after earlier interruption, but developed ears sooner, so that by mid-July interruption after 0, 2 and 4 weeks gave 9, 5 and 23 ears per pot of 4 plants respectively, but by mid-August the differences were much smaller (23, 17 and 28 ears per pot). Smaller effects on ear number of barley were found in June, but had disappeared in July. Interrupting vernalisation after 2 weeks gave fewer fertile ears and grains per ear, and smaller grain yield of wheat, than interruption after 4 weeks, but it increased the number of grains per ear of barley and so increased the grain yield.

Keeping barley grains at 5° C for 2 weeks gave more ears and larger grain yield than keeping them for 4 weeks, but the reverse was true with wheat. (French and Humphries)

Growth substances and growth regulators

Effects of CCC on winter and spring wheat crops given various amounts of N. CCC (2-chloroethyltrimethyl-ammonium chloride) shortens the straw of wheat, especially spring varieties, so it may permit wheat to be grown with larger dressings of N than usual without risk of lodging and thereby increase yield, if current dressings are too small for maximum yield. This applies especially to winter wheat, with which yield increases over a wider range of N than with spring wheat. This possibility was tested in two experiments, one with winter wheat, var. Cappelle Desprez, and one with spring wheat, var. Kloka, in both of which N at 0, 0·8, 1·6 or 2·4 cwt/acre and CCC at 0 or 2½ lb in 37 gal/acre were applied in a factorial design.

The winter wheat was combine-drilled on 27 October 1966 with 340 lb/acre 0–20–20 fertiliser. The nitrogen was given as "Nitro-Chalk 21" on 18 April and the CCC sprayed on 21 March, when the plants were at the 5–6-leaf stage. Samples of the crop were taken on 22 June, when ears were emerging, on 13 July and 3 August, and on 18 August when the crop was ripe. The spring wheat was combine-drilled on 14 March with 340 lb/acre 0–20–20 fertiliser. The nitrogen was given on 28 March, and the CCC sprayed on 31 May when the plants were at the 6-leaf stage. Crop samples were taken on 29 June, when ears were emerging and on 20 July, 10 August and 23 August when the crop was ripe. Dry weights of shoots and ears,

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components of grain yield and leaf-area indices were estimated in the usual way.

CCC shortened the winter wheat by only 11%, but on 26 June, after a storm, less of the crop had lodged on plots given 1·6 or 2·4 cwt N/acre, and sprayed with CCC, than on unsprayed plots given the same N. However, the crop recovered from this lodging, and on 21 July it was leaning only on parts of unsprayed plots. By 17 August all plots with 1·6 or 2·4 cwt N/acre without CCC were partly or severely lodged, and some sprayed with CCC were partly lodged. The winter wheat was affected by yellow rust, severely on most plots given N, and by take-all.

CCC shortened the spring wheat more than the winter wheat. On 29 June sprayed wheat was about 66% of the height of unsprayed wheat without N, and 71%, 77% and 76% with 0·8, 1·6 or 2·4 cwt N/acre respectively. Like the winter wheat, it was partly lodged on 26 June after the storm, but it recovered and did not lodge again. It was affected by rust and *Rhynchosporium* but not take-all; leaf diseases were less severe than in winter wheat, and increased with increase of N.

The grain yield of winter wheat, estimated from the final samples, was 48 cwt/acre without N, 64 cwt/acre with 0·8 cwt N/acre and 51 cwt/acre with 2·4 cwt N/acre. CCC increased the yield without N to 60 cwt/acre, and although it also increased yield with 1·6 cwt N/acre, this was not statistically significant, and the effect of CCC probably declined with increasing nitrogen. These yields are about 25% larger than those obtained by combine-harvesting, perhaps because some grain was shed between the two harvests, or lost in combine-harvesting. The increase in grain yield by 0·8 cwt N/acre came from more ears and slightly heavier grains. Larger dressings of nitrogen gave little further increase in number of ears, and smaller grains. The increase in yield with CCC came mostly from more ears, with a small contribution from more grains per ear not completely offset by the smaller grains. The smaller yield with more N than 0·8 cwt/acre is probably attributable to diseases, for at ear emergence, and 3 weeks later, the estimated total weight of ears was not smaller with the larger N dressings. Lodging occurred too late in the season to affect yields greatly, and the large dressings of N decreased yield on unlodged CCC-treated plots as much as on unsprayed plots which lodged. Straw yield was 45 cwt/acre without N and 61 cwt/acre with 2·4 cwt N/acre. CCC also increased straw yield, except with 2·4 cwt N/acre, by increasing shoot numbers.

Spring wheat yielded 38 cwt/acre without N, 48 cwt/acre with 0·8 cwt N/acre and 46 cwt/acre with 2·4 cwt N/acre. CCC had no significant effect on grain yield. In contrast to the winter wheat, the yields estimated by sampling agreed well with those from combine-harvesting, perhaps because the spring wheat was combined earlier to avoid grain shedding. Nitrogen increased the number of ears and number of grains per ear, but with 1·6 and 2·4 cwt N/acre these effects were offset by smaller grain size. Whether the smaller grains were caused by disease or by self-shading in the denser crop is uncertain. CCC increased grains per ear and decreased weight per grain slightly, but neither effect was statistically significant. Nitrogen increased straw yields, 0·8 cwt N/acre as much as 2·4 cwt/acre. CCC decreased the straw yield.

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The main object of the experiment, to get maximum yields from large nitrogen dressings by using CCC to prevent lodging, was frustrated by pathogens. (Humphries, Welbank and Williams)

Effects of CCC on barley. Most varieties of wheat are shortened by CCC, but the effects on barley varieties are variable and usually small. Three explanations for this have been suggested, viz. that CCC is either not absorbed by barley, or is not translocated from the site of absorption, or is rapidly metabolised. When dimethylsulphoxide, which aids penetration of some compounds into plant and animal tissues, was added to CCC spray barley plants grown in pots in the glasshouse and sprayed with the mixture were shortened more than plants sprayed with CCC alone. However, this result was not obtained in a field experiment; the final height of the barley crop was little affected either by CCC alone or mixed with dimethylsulphoxide. Soon after the barley was sprayed at the 5-leaf stage the shoots of sprayed plants were shorter, but the difference from unsprayed ones disappeared later. The peduncle and highest internode at maturity were longer on sprayed than on unsprayed shoots. Evidently CCC shortened the lower internodes that elongated soon after spraying, but increased the growth of upper internodes. Grain yield was unaffected by CCC or dimethylsulphoxide. (Humphries and Williams)

CCC and irrigation. In 1966 spraying spring wheat at Woburn at the 5-leaf stage with CCC increased the grain yield without irrigation, but not with (*Rothamsted Report* for 1966, p. 88). This result, and those of experiments in other years (5.8), suggested that CCC increases grain yield when soil water is deficient near the time ears are emerging, probably by increasing the size of the root system and so enabling them to draw water from more soil.

CCC was again tested on the Woburn Irrigation Experiment in 1967, by spraying half of each plot of Kloka spring wheat with 2½ lb/acre CCC on 23 May. The experiment also compared four rates of N. A sample of the crop from discard areas of each plot subdivision was taken on 5 July, about 2 weeks after the ears emerged, when the root weight was expected to be nearly maximal. Two soil cores were then taken from each sampled area, divided into sections from 0 to 25 cm and from 25 to 60 cm depth, and the roots separated from them by washing away the soil on a sieve.

The total weight of roots separated from the soil cores was increased about 14% by CCC without irrigation, but very little by CCC with irrigation. The major effect of CCC on unirrigated plots was to increase the weight of roots in the subsoil between 25 and 60 cm deep by 37%. On irrigated plots it similarly increased the weight of roots between 25 and 60 cm depth by 43%, but this gain was offset by a smaller weight of roots above 25 cm depth. These effects of CCC, though large, were not significant at the 5% level but to measure them with greater precision would have required more core samples than could be taken. Though indecisive, these results are compatible with the concept that CCC increases root growth, particularly in the subsoil.

Although June and July were much drier than in 1966, CCC did not

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increase the yield of unirrigated crops; perhaps the drought was too prolonged for the larger root system with CCC to be effective. CCC increased yield only with the smallest dressing of N, whereas in 1966 its effect increased with increasing N supply. Thus, although there are many examples of CCC increasing yield, the conditions in which it does so have yet to be defined. (Humphries, Welbank and Williams)

Conversion of tryptophan to auxin by phenolic esters in dwarf French bean leaves. When bean leaves die, or young leaves are macerated and incubated, their auxin and tryptophan contents increase (5.11). The possibility that the auxin derives from tryptophan was strengthened by showing that macerated bean leaves produced more auxin when incubated with added tryptophan than without. The endogenous tryptophan is probably produced by protein hydrolysis in dead leaves or in incubated young leaves. Boiled or autoclaved leaves did not produce auxin unless incubated with tryptophan, probably because protein was not hydrolysed in the heated leaves.

The tryptophan produced in macerated bean leaves is probably converted to auxin by phenols in the leaves. Three phenolic esters were separated on chromatograms from ethyl acetate extracts of leaves. H. G. C. King (Pedology Department) showed that alkaline hydrolysis of the esters yields three phenolic acids, caffeic, ferulic and *p*-coumaric acids, and a hydroxy aliphatic acid.

The phenolic esters from bean leaves promoted the extension of wheat coleoptile sections only in dilute alkaline solution containing tryptophan. They also converted tryptophan to auxin in alkaline solutions. Caffeic acid may be the constituent producing auxin from tryptophan because it reacted better than ferulic and *p*-coumaric acids with tryptophan. When the surface of bean leaves was washed with phosphate buffer (pH 7·5) the washings contained phenolic esters resembling those in leaf extracts, but not auxin. These phenols also produced auxin when incubated with tryptophan.

Thus the bound auxin or auxin precursor in bean leaves described in last year's Report (p. 91) is probably a protein or polypeptide that hydrolyses in dying leaves, or in incubated young leaves, to yield amino acids, including tryptophan, which is then partially converted by phenolic esters to auxin. (Wheeler)

Effects of CCC and betaine on growth of dwarf French bean. CCC and betaine are chemically related, but differ in their effects on growth of French bean plants and leaf discs. CCC has more effect than betaine on the growth of whole bean plants, but less on the growth of bean-leaf discs or wheat-coleoptile sections (*Rothamsted Report* for 1964, p. 111). To find the cause of this difference, the effects of CCC and betaine on endogenous growth substances in bean leaves were studied.

Dwarf French bean seedlings grown in sand in an artificially lit cabinet at 25° C, received 5 ml of 2×10^{-2} *M* CCC, or betaine or both or neither, daily for 3 days, starting from the day the hypocotyls appeared above the sand. Soon after treatment began, CCC and betaine were detected in

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aqueous extracts of the primary leaves by treating chromatograms with iodine vapour, but both had disappeared within 3 weeks.

CCC decreased growth of the primary leaves and of stem internodes above the hypocotyl. Betaine did not. Neither CCC nor betaine affected the amount of chlorophyll per primary leaf, but as CCC gave smaller primary leaves these contained more chlorophyll per unit area. Neither CCC nor betaine affected the gibberellin content of primary leaves, but CCC decreased the auxin content of young leaves. CCC prolonged the life of primary leaves, and so delayed the increase of auxin and amino acids that occurs when leaves die. It slightly decreased the amounts of phenolic esters in old primary leaves, and this may account for the smaller auxin content of leaves, assuming that auxin derives from tryptophan by phenolic esters (p. 103).

Thus, CCC retards growth of bean plants probably by decreasing auxin production, but has no effect on the growth of leaf discs, or coleoptile sections, because they are not sites of auxin production. Conversely, betaine affected neither auxin metabolism nor growth of bean plants, so it probably inhibits the growth of leaf discs and coleoptile sections directly. (Wheeler)

Auxin in roots of tomato infested with root-knot nematodes. Larvae of *Meloidogyne* spp. induce galls on the roots of tomato plants, which other workers have associated with increased auxin content of the roots. If this is so, it suggests that the larvae either secrete plant-growth substances that directly cause cells to proliferate or that their feeding changes the endogenous growth substances of the root.

The body contents and secreted saliva of *M. incognita* larvae contained too little auxin and tryptophan to account for the extra occurring in infected roots. Incubating macerated tomato roots at 37° C for 2 days increased the amounts of extractable auxin and tryptophan, showing that the roots contain bound auxin. Incubation produced more auxin and tryptophan from roots with galls than from uninfested roots. Phenolic esters in the tomato roots were not increased by infestation. They increased extension of wheat coleoptile sections only when assayed with tryptophan, presumably by converting tryptophan to auxin.

These results suggest that the feeding larvae cause proteins to hydrolyse to amino acids, including tryptophan, which then reacts with endogenous phenolic esters to produce auxin, which in turn causes cells to proliferate and form galls. (Wheeler with Setty, Nematology Department)

Weed studies

Wild oats

Longevity of seeds. Seedlings continued to appear in pans of moist soil in the glasshouse 4 years after sowing seed of *Avena sterilis* from Israel, and of *A. barbata*, *A. fatua* and *A. ludoviciana* from Australia, and after 6 years from seeds of *A. sterilis* and types resembling *A. ludoviciana* from Greece (*Rothamsted Reports* for 1961, p. 82 and 1964, p. 112). British *A. fatua* and *A. ludoviciana* do not remain dormant so long in the glasshouse.

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Effects of kale seed-crops on wild-oat infestations. Observations on a farm in Suffolk suggested that land where kale had been grown for seed had fewer wild oats than after other crops, and that the difference persisted for several years. To test whether the kale crops left toxic residues, seeds of *A. fatua* were sown in samples of soil taken from four fields where kale seed-crops had been grown for various periods, and from adjacent areas in the same fields where kale had not been grown. Other soil samples were kept without adding seeds, to determine how many wild oats grew from seeds already present. A total of 38 seedlings appeared in three such samples each of 1 kg of soil from no-kale areas, compared with only two from kale areas. In the other fields the populations of wild oat seeds were too small to be compared accurately by such small samples. The numbers of added seeds that germinated in soil from kale areas were not consistently fewer than in soil from no-kale areas.

Thus, there was no evidence that the kale-seed crops left residues toxic to wild-oat seedlings. The wild-oat infestation was smaller after kale than after other crops (mostly cereals), probably because the later sowing and denser shade of the kale meant fewer wild-oat seedlings were established, and these produced less seed than in the other crops.

Effect of sulphuric acid spray for killing pea-haulm on seed production of wild oats. Pea crops are often sprayed with sulphuric acid to kill the haulm before combine-harvesting. To find whether such spraying affects the production of viable seed by wild oats growing in the crop, ears of *A. fatua* were collected from two pea crops in Essex in July just before they were sprayed, and again 4 or 8 days later, before the peas were combined. All florets were removed from random samples of sprayed and unsprayed ears, and the germination of intact seeds, and of seeds with their distal ends cut off to break dormancy, was tested.

On one field, spraying with the boom about 40 in. above the ground killed two-thirds of the seeds, but the dormancy of those surviving was scarcely affected; 83% of viable seeds from unsprayed plants were dormant, and 76% from sprayed plants. Decreasing viable wild-oat seeds by two-thirds is a valuable bonus from the spraying, but the effect on subsequent infestation may be even greater than the killing of seeds indicates. Seeds of wild oats stopped growing immediately after the leaves were killed by spray; they were smaller at the time of combining than those from unsprayed plants, and so were probably less able to produce established seedlings in competition with the subsequent crop.

On the other field spraying with the boom only 30 in. above the ground did not kill any seeds, but 40% had their dormancy broken. The lower boom probably bent the wild-oat ears as it passed, so that, when they sprang upright, the spray was shaken off before it penetrated to the embryos, whereas the higher boom on the other field passed over most ears, and the spray remained on them long enough to kill embryos of the less-mature seeds.

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Blackgrass (*Alopecurus myosuroides*)

Emergence of seedlings from different depths in soil. Efficient use of herbicides applied to the soil requires knowledge of how emergence of weed seedlings depends on the depth of the seeds in the soil. Blackgrass seeds were sown in March in pots of sterilised Rothamsted soil, either on the surface or below the surface at depths increasing by 1-in. intervals to 6 in. Germination was poor, possibly because the time of year was unfavourable; 27% of seeds sown on the surface germinated, and seedlings emerged at the surface from 18% of seeds sown at 1 in. depth, 9% from 2 in., 1% from 3 in. and only 1 seedling out of 300 from 4 in. In France, Barralis (*2e Colloque sur la Biologie des Mauvaises Herbes*, Grignon, 1965) found a similar decrease in emergence with greater depth of sowing, but some seedlings appeared from seed at 12 cm depth.

Periodicity of germination in the field. The experiment on periodicity of germination reported last year (*Rothamsted Report* for 1966, p. 95) was repeated. After the seed-bed cultivations of Broadbalk were completed in October 1966, seedlings of blackgrass were counted every week as they appeared on small plots on an undrilled area beside the fallow strip. The seedlings on all plots were removed by hand-pulling at monthly intervals. After the seedlings were removed, one set of plots was undisturbed and the other cultivated by hand to 4 in. depth. The peak periods of germination for the two treatments coincided, but by September 1967, when the field was ploughed, nearly twice as many seedlings were counted on the undisturbed plots as on the cultivated plots. The most probable explanation is that the cultivation destroyed small unemerged seedlings; it seems unlikely that cultivation prevented germination, induced dormancy or killed seedlings by cooling or drying the soil.

More seeds germinated in autumn and fewer in spring than in the unusual season 1965–66, but germination was later in autumn than expected from previous work on Broadbalk on the dependence of blackgrass infestations on the date of sowing the wheat crop (*Rothamsted Report* for 1958, p. 85). Few blackgrass seedlings were seen before November. The December peak of germination accounted for more than half of all seedlings counted between November 1966 and September 1967, and by the end of February germination had reached 80–90%.

Development of plants germinating at different times. Other plots resembling those used for the periodicity study were cleared of seedlings only once, at monthly intervals on different plots, and the blackgrass seedlings that appeared afterwards were left undisturbed, to find how their growth and development depended on the date of germination.

Tillering began 4 months after germination in the period from November to April, 1 month after germination in June and 2 months after germination in July. Seeds that germinated in January produced plants with most shoots, 15 per plant; those that germinated in February or March averaged 13 shoots, and in November only 8 shoots. Similarly, plants from seeds that germinated in November produced only 4 ears by June, increasing

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uniform material for experiments. Rhizomes from a selection of the plants grown in pots were planted on small plots in October, together with three clones from the Weed Research Organisation, including the standard Headington clone. Types compatible in their times of flowering were planted on neighbouring plots, to provide a source of seed in addition to rhizomes. Rhizomes of *Agrostis gigantea* from different sources were also planted.

Emergence of shoots from rhizome fragments planted at different depths. Rhizome segments 1 in. long with one node or 2½ in. long with two nodes were planted in soil in pots at 1 in., 3 in. and 4½ in. depth. Shoots appeared above the soil surface within a week from most rhizome pieces planted 1 in. deep. After 4 weeks shoots had emerged from all 2½-in. segments planted 3 in. deep, but from only a quarter of the 1-in. segments; none emerged from 4½ in. depth. (Williams)

Weed surveys. Samples of blackgrass plants were collected by N.A.A.S. Officers from all but one of the English counties omitted from the 1966 survey (*Rothamsted Report* for 1966, p. 95) and sent to us for study. As before, most came from clay soils and from cereals, especially winter-sown crops, but blackgrass was also collected from spring cereals on chalk soils in Wiltshire where none was reported in 1966. Only one of 41 samples collected was infected by ergot fungus (*Claviceps purpurea*), compared with 14% of samples in 1967, but whether the difference reflects local or seasonal variation is not known.

The usual annual surveys were made of the weeds on Broadbalk, and a final set of soil samples was taken for the study, started in 1955, of effects on the weed-seed population of returning to continuous wheat after the fallow cycle, and of the use of herbicides. Weeds on other fields of Rothamsted farm and Scout farm and at Woburn were surveyed to assess the efficacy of control by herbicides and cultivations. Perennial grasses, especially *Agropyron repens* and *Agrostis gigantea*, were prevalent except after fallow; field horsetail (*Equisetum arvense*), field bindweed (*Convolvulus arvensis*) and annual meadow grass (*Poa annua*) were more abundant than usual, probably because the preceding summer was wet and winter mild. Onion couch (*Arrhenatherum elatius*) was found surviving a 1-year fallow on Scout farm. (Thurston)

The Park Grass plots

The effects of the new liming treatments (*Rothamsted Report* for 1964, p. 226) on acid plots previously unlimed became more conspicuous. As before, the flowering of *Holcus lanatus* (Yorkshire fog) was delayed, and a similar delay occurred with *Agrostis* sp. and *Anthoxanthum odoratum* (sweet vernal). The treatments have also begun to affect the relative abundance of species. *Trifolium pratense* (red clover) is now present on three newly limed sub-plots previously free from it, and *Festuca ovina* (sheep's fescue) has become more abundant on newly limed areas. On the recently limed parts of plots 11-1c and 11-2c many more species than

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to 6 when growth continued until July, whereas plants from seeds that germinated later, in December–March, had 9–11 ears by July.

Induced dormancy. Comparisons of the numbers of blackgrass seedlings germinating in samples of soil taken in mid-September and early October in 1965–66 and kept in pans in the glasshouse, and of those germinating on field plots, showed that the percentage of dormant seeds in the field changed with time, presumably because dormancy was affected by seasonal changes in soil and weather. Samples taken on 5 October produced 20% fewer seedlings in autumn, but 5% more in spring, and 15% more in late-summer and autumn, than samples taken 2 weeks earlier. Germination in the field did not start until December, and was 60% less in the period October–December, but 35% more in the following spring, 20% more in summer and 5% more in autumn than in samples transferred to the glasshouse in September. Evidently conditions in the field in October and November induced dormancy that was subsequently broken earlier in the field than in the glasshouse. These results, obtained from tests made for other purposes, suggest that the conditions affecting the onset and breaking of induced dormancy need more critical study. (Thurston)

Couch grass (*Agropyron repens*)

Effects of previous cropping. Plots of an experiment cropped with spring wheat, kale or Italian ryegrass in 1965 and with barley in 1966 and 1967, with various amounts of N fertiliser in all years, were scored for the presence of couch grass, on a scale of increasing abundance from 0 to 5, in August when the barley was ripe. The mean scores for plots with different previous cropping were: after wheat 2·5, after kale 1·7, after ryegrass $1{\cdot}3 \pm 0{\cdot}18$. Increasing N in 1965 had no effect on the couch-grass score after ryegrass, slightly increased it after wheat and halved it after kale. There was no consistent effect of N in other years. Evidently wheat competed least effectively with couch grass, and ryegrass most, except that kale given 2 cwt N/acre was as effective as ryegrass. It is noteworthy that these effects of different cropping persisted in the couch-grass infestation after 2 years of uniform cropping.

Selection and propagation of experimental material. Seeds of *Agropyron repens* collected at Rothamsted in August 1966 were germinated in December and the plants grown in the glasshouse until October 1967. The seedlings varied greatly in growth habit and flowering behaviour. Tillering began in mid-February, and secondary shoots from upturned rhizomes appeared in April. The times when shoots elongated differed greatly, and ears began to emerge on different plants from the beginning of June to mid-July. Anthesis occurred about 1 month after ear emergence. The number of ears per plant ranged from 0 to 85, and of seeds per ear from 2 to 38. The species is self-sterile, so seed production depends on compatible types flowering at the same time. Much variation in susceptibility to mildew was found.

This variability within the species makes it necessary to propagate

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usual were found, including some that formerly occurred very rarely or never. *Cerastium holosteoides* (mouse-ear chickweed) occurred on nearly all the recently limed areas of previously unlimed plots, but not on the unlimed areas. (Williams)

Staff and visiting workers

W. Bond, M. J. Gibb and K. Loach, whose work is supported by a grant from the Sugar Beet Research and Education Committee, were appointed. Anne L. Thompson was awarded the B.Sc. degree of the University of London.

Mr. Teruhisa Motomatsu returned to Japan in September. Mr. G. C. Blackwood and Mr. C. C. Hole, sandwich-course students of Bath University of Technology, worked in the department from April to September. Other visiting workers were Mr. Hew Choy Kean, of the Oil Palm Research Station, Selangor, Dr. V. Černý, of the Central Institute for Plant Production, Prague, and Dr. J. Repka, of the College of Agriculture, Nitra, Czechoslovakia.

E. C. Humphries contributed to the 1st International Symposium on Tropical Root Crops, at St. Augustine, Trinidad, and to the Cereal and Physiology sections of the conference of Eucarpia at Wageningen. Gillian N. Thorne went to Australia in October to work in the Phytotron at Canberra, and to visit other research centres. D. J. Watson was Chairman of a session of the 30th Winter Congress of the International Institute for Sugar Beet Research in Brussels.

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