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ROTHAMSTED RESEARCH

Rothamsted Report for 1966

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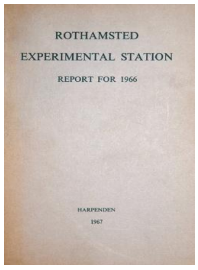

Botany Department

D. J. Watson

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BOTANY DEPARTMENT

D. J. WATSON

D. Burnett left and Mr. Teruhisa Motomatsu, of the Kyushu Agricultural Experiment Station, Chikugo, Japan, came in October for a year. Gillian N. Thorne attended a meeting of a working group of Section UM of the International Biological Programme held at the International Rice Research Institute, Los Baños, Philippines, in May. E. C. Humphries read a paper to the Conference of the European Association for Potato Research at Zurich in September.

In 1966 we continued to work on various aspects of the physiology of growth and yield of crops, and on weed infestations. Methods for the quantitative recovery of roots from field soils were improved, and used to measure the effect of nitrogen supply on root growth of a barley crop. The dependence of cereal grain yield on leaf area during the period of grain growth, and on ear size and grain number, was studied in the field and in growth rooms. Effects of growth regulators were studied in field and glasshouse experiments, particularly those of CCC on wheat and potato crops, on vernalisation of cereal grains, on growth of sugar beet and on protein and chlorophyll contents of leaves. An attempt was made to reconcile conflicting estimates of rates of photosynthesis of crop species obtained from measurements of dry weight increase or CO_2 exchange. New techniques for growing plants in defined states of soil-water deficit that change only slowly with time were used to measure effects of drought on leaf growth. Work on weeds dealt mainly with blackgrass (*Alopecurus myosuroides*).

Root growth of field crops

Methods. Of the methods tested previously for taking soil samples, including roots, from field crops (*Rothamsted Report* for 1965, p. 93), the steel coring tube driven into the ground with a power hammer was the most satisfactory, and was used in 1966. The tubes, made of mild steel, were of 3 in. internal diameter, fitted with cutting shoes of slightly smaller internal diameter and brass liners. A motor breaker, weighing about 65 lb and delivering 2,500 blows per minute, drove a tube to 80 cm depth in Woburn soil in 45 seconds. In Rothamsted soil the time required was 1–2 minutes, depending on how many flints were encountered. The tubes were withdrawn with a chain hoist and tripod. The whole operation of taking a soil sample and removing it from the tube took two men about 4 minutes.

The accuracy of the coring tube for removing known volumes of soil was tested by comparison with a thin-walled bulk density sampler (Dagg, M. & Hosegood, P. H., *E. Afr. agric. For. J.* (1962), **27**, special issue, p. 129). This sampler with a diameter of 10 cm, length 15 cm, and walls only 4 mm thick, is unlikely to compact the soil much during cutting.

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Cores of Woburn soil cut with the coring tube increased in diameter slightly after passing through the cutting shoe. After correction for this expansion, the top 15 cm of the core had a bulk density differing from that of a core cut with the thin-walled sampler by less than 1%. However, sections of cores cut with the coring tube from 15–30 cm depth had bulk densities about 3% greater, and those from 30–45 cm depth 5% greater, than samples from the same depths cut with the thin-walled sampler. Errors in measurement of soil volume caused by compaction were evidently very small in the top 15 cm of cores cut with the coring tube, and not more than 5% in the deeper layers.

Similar tests with the power-driven auger used in 1965 showed that it removed 10–12% less soil from 0–15 cm depth than either the thin-walled sampler or coring tube. From the deeper soil layers it removed up to 8% more soil than would be expected from a hole of the same diameter as the auger, i.e. the hole was larger than the auger diameter, but it removed 12% less than expected from the top diameter of the hole; apparently some soil was compacted round the sides of the hole instead of being brought to the surface. These errors were too small to account for apparent differences in root yields between auger and coring tube samples in 1965.

Effect of nitrogen on root growth of barley. Barley var. Maris Badger was sown on 29 April, with 0·5 cwt/acre P_2O_5 and 1 cwt/acre K_2O combine-drilled, on a site at Woburn previously fallowed. Four rates of nitrogen (0, 0·4, 0·8 and 1·2 cwt/acre N as "Nitro-Chalk") applied immediately after sowing were compared. Sampling began on 14 June, and was repeated on 28 June, 12 July, 3 August and on 6 September, when the crop was ripe.

The crop was pulled by hand from a sample area on each plot, and attached roots were later cut off the shoots. The amounts of roots remaining in the soil were estimated from soil cores extracted from the sample areas. Roots from zones of 0–15, 15–30 and 30–60 cm depth were separately measured, and notes were made of any roots penetrating below 60 cm in the cores. Soil was washed off the roots on a sieve with 0·5-mm holes. Roots and shoots were dried and weighed, and all weights expressed per unit area of land. The dry weight of roots attached to the shoots was added to that in the 0–15-cm zone of the core samples, to give the total dry weight of roots in this depth of the soil. From the second harvest onwards the volume as well as the dry weight of detached roots recovered was measured by displacement of water.

The dry weight of shoots at all harvests, and of ears after they emerged at the end of June, increased with increase in N supply up to 0·8 cwt/acre, but not with further increase to 1·2 cwt. The dry weight of tops (shoots and ears) continued to increase up to the beginning of August, and the effect of N also increased, but there was no subsequent increase in weight, except without N fertiliser. The yield of grain at the final harvest was increased from 28 to 41 cwt/acre by 0·8 cwt/acre N.

The total dry weight of roots on 14 June (about 70 g/m^2) was little affected by N supply, but afterwards it was increased. On 28 June, near to the time of ear emergence, the dry weight of roots of plants receiving

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0 or 1·2 cwt/acre N, respectively, were 72 and 106 g/m², when the corresponding weights of tops were 275 and 535 g/m². The dry weights of roots reached maxima that occurred earlier with increased N supply (28 June with 1·2 cwt/acre N and 3 August without N), and then decreased until the last harvest, when the weights were similar to those on 14 June. The ratio of dry weight of roots to tops decreased with time throughout the experiment and was also decreased by N; between 14 June and 6 September it changed from 0·7 to 0·09 for the crop without N fertiliser and from 0·4 to 0·07 for crops with 0·8 or 1·2 cwt/acre N.

Nearly 80% of the dry weight of roots was in the 0–15-cm soil layer, about 12% in the 15–30-cm layer and 10% in the 30–60-cm layer. Roots penetrating below 60 cm probably equalled about 5% of the total weight above this depth. These fractions varied little with time, and were apparently independent of N supply. Sampling began too late to show whether the rate roots penetrate into deeper soil layers was affected by N. N affected root volume and root dry weight similarly.

Although the dry weight of roots in June was about half that of tops, and may have been relatively larger at early stages of growth, later changes in root weight were small compared with those in tops. Thus, the loss of root dry weight after 28 June from the crop receiving 0·8 cwt/acre N was about 20 g/m², while the weight of ears increased by 500 g/m². Evidently transfer of dry matter from roots to ears can make no appreciable contribution to grain yield. (Welbank and Williams)

Determinants of cereal grain yield

Relation between yields of wheat varieties and post-anthesis leaf area. An experiment in 1963 comparing the old wheat variety Squarehead's Master, sown in December, with the newer varieties Cappelle-Desprez sown in December, Jufy I sown in April and Prestige sown both in December and April, with 0·5 or 1·0 cwt/acre N, showed a close correlation of grain yield with leaf-area duration (*D*) of parts above the flag leaf node between anthesis and ripening, except that Squarehead's Master with 1·0 cwt/acre N yielded less grain than expected from its *D*, probably because it lodged (Welbank, P. J., French, S. A. W. & Witts, K. J., *Ann. Bot.* (1966), **30**, 291). To test whether the same relation between grain yield and post-anthesis *D* holds for other varieties over a wide range of yield, an experiment was planned for 1965–66 to compare Cappelle-Desprez and Jufy I with the newer winter variety Rothwell Perdix and spring variety Kloka that were reputed to yield 6% more than Cappelle-Desprez and 9% more than Jufy I, respectively. Frequent heavy rain prevented autumn sowing of the winter varieties, and eventually all four varieties were sown on 17 February, with 0·4 or 1·0 cwt/acre N applied on 14 April.

Unfortunately, the main purpose of the experiment was partly frustrated because the varieties all gave similar grain yields (means of two N rates: Cappelle-Desprez 42·9, Rothwell Perdix 39·4, Jufy I 43·5, Kloka 40·5 $\pm$ 0·75 cwt/acre). There was no difference between the mean yields of winter and spring varieties. The newer varieties Rothwell Perdix and

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Kloka both yielded less than the older ones, possibly because of more severe yellow-rust infection of Rothwell Perdix or earlier lodging of Kloka than Jufy I.

Leaf-area index was estimated at intervals of 2 weeks, starting before ear emergence, for the whole plant, and separately for the part above the flag-leaf node. Grain yield was determined from small samples, and by combine-harvesting. Numbers of ears per m^2, numbers of grain per ear, and 1,000 grain dry weight were determined at the final harvest. Analysis of the results and the relation of grain yield to *D* and other growth attributes is not yet complete. (Welbank and Williams)

Ear size and grain yield of wheat. When Jufy I spring wheat was grown continuously in growth rooms with differences in day-length or temperature before initiation of spikelets or between initiation and anthesis (*Rothamsted Report* for 1964, p. 106) the resulting differences in grain yield were correlated with changes in number of grains per ear, and apparently independent of leaf area during the period of grain growth. Thus, cold or short days before initiation both increased the number of grains per ear by 8% and grain yield by 6%, but decreased leaf-area duration after anthesis (*D*). Short days between initiation and anthesis decreased grain number by 28% and grain yield by 24% in spite of an increase in *D*. These results suggested that grain yield may have been restricted by the capacity of the ears as sinks for carbohydrate. If so, differences in size of sink, i.e. number of grains, should cause opposite differences in dry weight of the shoots early in the period of grain growth, as was found when the number of grains per ear of barley was altered by excising florets (Nösberger, J. & Thorne, G. N., *Ann. Bot.* (1965), **29**, 579). Unfortunately, this could not then be tested because there were insufficient plants for repeated sampling. A similar experiment was therefore done in 1966, in which wheat plants were treated in the growth rooms either before initiation or between initiation and anthesis, and spent the rest of their growth period in the open air under a glass roof, where more pots can be accommodated than in the growth rooms, and where conditions during the period of grain filling more resemble those in the field. The three growth rooms provided hot (20° C) or cold (15° C) long days (18 hours), or hot short days (14 hours), as in the 1964 experiment, except that the extra 4 hours of light given on the long days was of low intensity from tungsten lamps only.

The results confirmed some of those found in 1964, but showed little evidence that grain yield was controlled by sink size. As in 1964, initiation was later with short or cold days after sowing than with hot long days, but this affected neither the number of grains per ear nor grain yield. Short days increased the number of spikelets per ear on main stems by 1·0, and leaves per shoot by 1·2, compared with 2·0 and 2·1 respectively, in 1964, but decreased the number of grains per spikelet. Shortening the daylength between initiation and anthesis decreased grain yield and the number of grains per spikelet, and increased the dry weight of shoots and roots, as in 1964, but also decreased grain size. The changes after anthesis in dry weight of parts other than the ears were similar whether the plants

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had previously been in short or long days, contrary to expectation if the smaller grain yield of plants from short days resulted from fewer grains providing an inadequate sink. Part of the smaller grain yield of these plants may be attributable to severe mildew they developed during their longer stay in the growth rooms. As in 1964, cold between initiation and anthesis increased the number of ears and grain yield.

In 1964 cool temperature after anthesis delayed senescence of leaves and also increased grain yield, but less than proportionally to the increase in leaf-area duration (see also 5.11). To test whether this was because the ears were unable to accept the extra carbohydrate produced by the larger leaf area, changes after anthesis in dry weight of ears and other parts of plants previously grown outdoors were determined in growth rooms at 20° or 15° C in a 16-hour light period with 8 cal/dm²/min of visible radiation, and 15° C in the dark. In a third room, at 20° C in the light period and 15° C in the dark, the CO_2 concentration of the air was increased about 10-fold to 3,300 ppm, and the intensity of visible radiation was increased to 13 cal/dm²/min, to increase the rate the leaves photosynthesised.

The dry weight of ears was the same with temperatures of 20° or 15° C in the light, but the weights of other plant parts were greater at 15° C. The rates of apparent photosynthesis of flag-leaf laminae at 20° and 15° C were similar. Increasing light intensity and CO_2 concentration had no effect on grain yield, but increased the dry weight of shoots. These results suggest that the ears could not accommodate extra carbohydrate produced by the larger leaf area duration at 15° C, or by increased illumination and CO_2 supply. (Thorne and Ford)

Growth regulators

Effect of CCC on wheat crops. In 1964 spraying spring wheat with the growth regulator CCC (2-chloroethyltrimethyl-ammonium chloride) increased the number of ears, and the grain yield by 2 cwt/acre, although there was no lodging. The explanation of the increased production of ear-bearing shoots was thought to be that shortening of the shoots by CCC allowed more light to penetrate to the base of the plants (Humphries, E. C., Welbank, P. J. & Witts, K. J. *Ann. appl. Biol.* (1965), **56**, 351). However, in 1965 CCC had no effect on grain yield except when the crop was closely spaced (4 in. between rows), although it shortened the shoots as much as in 1964. (*Rothamsted Report* for 1965, p. 90.) It therefore seems unlikely that the increased yield can be attributed to greater penetration of light.

In both 1964 and 1965 CCC-treated plants pulled by hand from the soil had more attached roots than untreated plants. This observation suggested that CCC may increase yield by enabling shoots to avoid water stress in the period near ear emergence, so that more survive to produce ears. This was tested in the Woburn Irrigation Experiment by spraying half of each irrigated and unirrigated plot of Kloka spring wheat with 2½ lb/acre CCC at the five-leaf stage. The experiment also tested 4 rates of N (0·4, 0·8, 1·2 and 1·6 cwt/acre) in all combinations with CCC and irrigation.

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Both irrigation and CCC increased grain yield, and their effects increased with increase in N supply, but CCC had no effect on irrigated plots, and the effect of irrigation was less on plots sprayed with CCC. On plots receiving 1·2 or 1·6 cwt/acre N CCC increased grain yield by 6 cwt/acre, and irrigation by 10 cwt/acre; both increased the number of ears, but CCC decreased 1,000-grain weight.

In an experiment at Rothamsted in 1966 with Kloka wheat given 0, 0·8, 1·6 or 2·4 cwt/acre N, although again there was no lodging even with 2·4 cwt N, CCC increased grain yield by an average of 2 cwt/acre, as in 1964.

Soil-moisture deficits at Rothamsted for the 3 weeks after ear emergence, calculated by Penman's method, were more than 2 in. in 1964 and 1966, when CCC increased grain yield, but less than 1 in. in 1965, when CCC had no effect on the yield of a normally spaced crop. These results agree with those of the Woburn irrigation experiment in showing that CCC increased grain yield when there was a deficit of soil water near to the time of ear emergence, and this may be related to increase in the size of the root system. (Humphries, Welbank and Williams)

Residual effects on growth of wheat grains from plants treated with CCC. When grains harvested from the 1965 wheat experiment were germinated in moist sand at 25° C in the dark, those from plants treated with CCC produced shorter shoots after 3 days than those from untreated plants. The residual effect of CCC on seedling growth was greater with grains from plots that received more nitrogen, possibly because the plants had larger leaves when sprayed, and so acquired a larger dose of CCC. Steeping grains in gibberellic acid solution (5 ppm) before germination made the shoots grow larger, but did not overcome the residual effect of CCC.

Similar results were found in tests with coleoptile sections. Grains from plants treated with CCC and from untreated plants were germinated in sand in the dark for 3 days; sections 10 mm long cut from the coleoptiles, excluding 3 mm at the tip, were floated on water or on solutions of different concentrations of indolylacetic acid or gibberellic acid, separately and in combination, and measured after 16 hours. Coleoptiles from grains of CCC-treated plants grew less on distilled water than those from untreated plants, and this difference persisted in coleoptiles floated on IAA or GA solutions, although their growth was increased.

These results imply either that unchanged CCC was present in grains from treated plants and in shoots arising from them, or that the CCC-treatment decreased the amount of endogenous growth substances present in the grains. (Humphries)

Effects of B9 and CCC on early potatoes. When a crop of Majestic potatoes was sprayed with the growth regulator B9 (*N*-dimethylamino-succinamic acid) on two occasions tuber growth was at first increased, although leaf-area index was decreased. The final weight of tubers was unaffected, but the number was increased (*Rothamsted Report* for 1965, p. 91). Such an early increase in tuber weight might be advantageous with early varieties harvested before maturity. An experiment was therefore done in 1966 to test the effect of spraying an early variety, Arran Pilot, and a second early variety, Maris Peer, with B9 (2 g/l) at the time of tuber

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initiation. Neither tuber growth nor number was affected, possibly because heavy rain fell 6 hours after spraying.

In a small unreplicated trial the effects of B9 applied to the foliage, or CCC applied to the soil, were compared on the following varieties: 1st early, Arran Pilot, Ulster Prince, Ulster Premier; 2nd early, Craig's Alliance, Maris Peer; main crop, Pentland Dell, King Edward. Both B9 and CCC increased the tuber yield of the early varieties (mean increase 6%), but had no effect on the main-crop varieties. The number of tubers of the early varieties was increased by B9, and decreased by CCC. (Humphries, French and Williams)

Lack of effect of CCC on vernalisation of winter wheat and winter barley. The biochemical changes involved in vernalisation of cereal grains are still unknown, but production of gibberellins during the cold treatment may play an essential part. If so, interference with gibberellin production during vernalising by treatment with CCC, which seems to inhibit gibberellin synthesis, should affect flowering and production of ears. In 1965 during vernalisation of seeds of the winter barley Dea at 2° C some seeds were removed from the cold at intervals, immersed in CCC solution for 24 hours and then returned to 2° C to continue the vernalising process, after which they were planted in pots in the glasshouse and grown to maturity. The CCC treatment did not prevent vernalisation and all plants produced ears, but it caused differences in ear weight. In a similar experiment in 1966 imbibed seeds of Dea winter barley and Cappelle-Desprez winter wheat held at 2° C were treated with two concentrations of CCC (100, 1,000 ppm) at the beginning of the cold treatment, or 2 or 4 weeks later. During the interruption of the cold treatment seeds were immersed in water or CCC solution at room temperature for 24 hours and then returned to 2° C to continue vernalising. After 5 weeks' cold treatment the seeds were germinated and uniform seedlings were planted in pots of soil in the glasshouse.

Interrupting the cold treatment affected development more than did CCC. Seeds of barley or wheat transferred to water or CCC solution after 2 or 4 weeks in the cold produced more shoots, but fewer ears, than seeds immersed in water or CCC solution before the cold treatment started, and their ear development was delayed. CCC, especially at 1,000 ppm, also increased tillering and final shoot number, but did not affect the number of fertile ears. Interrupting the cold treatment increased the number of grains per ear both of barley and wheat; it increased the 1,000-grain weight of barley, but decreased that of wheat. CCC had no effect on number of grains per ear or 1,000-grain weight.

Interrupting the vernalisation treatment involved not only a change from 2° C to room temperature but also immersion in water or solution, which may have leached some substance essential for flower formation from the seeds. Both these changes may have contributed to de-vernalisation and lessened ear number. There was no indication that CCC interfered with vernalisation, nor did it affect stem length, although it shortens stems of wheat when applied at the five-leaf stage, but not of barley. (Humphries and French)

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Changes in protein and total N content of bean leaves and their modification by growth regulators. Changes in the protein content of leaves during their expansion, functional life and senescence are presumably associated with the changes with age in metabolic activity, for example, in the rate of photosynthesis. Growth regulators influence the rate leaves grow and senesce, and these effects may be accompanied by changes in protein content. This possibility was tested in experiments with the primary leaves of dwarf French bean (*Phaseolus vulgaris*). The protein and total N contents of a primary leaf increased rapidly to a maximum before the leaf was fully expanded, and then nitrogen was exported, so that when the leaf reached full size it had lost a fifth of its maximum N content. Treating the plant with CCC or B9 decreased shoot growth, and delayed the loss of protein from the primary leaves. If, as this suggests, the decrease in leaf protein is a consequence of shoot growth, removing the growing point should prevent it. The total-N and protein contents of the primary leaves of decapitated plants exceeded those of intact plants, and continued to increase until the leaves were fully expanded. CCC did not increase the total-N and protein contents of primary leaves of decapitated plants, which agrees with the interpretation that CCC delays the loss of N and protein from leaves of intact plants because the smaller shoot demands less nitrogen. Changes in chlorophyll content paralleled those in protein.

Fully expanded primary leaves of dwarf bean, removed from the plant and induced to form roots, became greener and increased in thickness by increase in length of the palisade cells (5.8). Such rooted leaves were kept with their roots in culture solution at 20° C, and the protein content of the lamina was determined at weekly intervals. The protein content doubled in 5 weeks after rooting started, and was then much greater than in comparable attached leaves. (Humphries)

Bound auxins in leaves. Bound auxins in primary leaves of dwarf French bean are released when leaves are macerated in phosphate buffer (pH 8) and incubated at 37° C (*Rothamsted Report* for 1965, p. 96). Further work showed that auxin was not released unless toluene, hibitane or chloramphenicol was added to the macerate. Prolonging the time of maceration or of incubation (up to 4 days at 37° C) increased the amount of auxin released, but the volume of phosphate buffer added had no effect. Auxin was released within a pH range from 6·5 to 8·5. Release was prevented by boiling the leaves before incubation, and decreased by adding ascorbic acid or cysteine (oxidation inhibitors) to the macerate before incubation. Macerated bean leaves released the same amount of bound auxin when hydrolysed for 1 or 2 hours with *N*- or 7*N*-potassium hydroxide at 100° C as when incubated with buffer.

The amount of tryptophane in aqueous extracts of bean leaves increases as the leaves senesce, and when macerated leaves are incubated. Tryptophane added to macerated leaves increased the amount of auxin produced by incubation. These results suggest that tryptophane formed when protein breaks down in senescent leaves, or when macerated young leaves are incubated, contributes to the production of free auxin.

Assays of free and bound auxin in dwarf French bean plants of different

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ages showed that when seeds germinated at 25° C both kinds increased in cotyledons to a maximum 5 days after sowing, and then decreased as the cotyledons shrivelled. In expanding primary leaves both types increased, but as the leaves senesced and lost their chlorophyll the free auxin per leaf continued to increase, while bound auxin decreased. Early removal of the stem apex above the node bearing the primary leaves delayed the loss of chlorophyll and the conversion of bound to free auxin associated with senescence.

Similarly, maceration and incubation released bound auxin in wheat leaves and increased the amount of tryptophane. Also, old wheat leaves with dead or chlorotic patches contained more auxin than young leaves. The free auxin in old leaves, and that released from a bound form, had the same Rf as IAA on paper chromatograms.

Plant growth is mainly controlled by auxin, and the fact that wheat and bean plants contain bound auxin that is released when leaf macerates are incubated, presumably by the action of an enzyme in the tissues, suggests that other growth regulators may act by releasing bound auxin. (Wheeler)

Photosynthesis of different crop species

Experiments in the field, in the glasshouse and in growth rooms show that the net assimilation rates (E) of kale or sugar-beet plants are greater than, often as much as double, those of wheat or barley of similar age growing in the same conditions. Shading experiments (5.12) show that the larger E of sugar beet results from more photosynthesis not less respiration. However, published data show no comparable differences in photosynthesis by single leaves of these species. Nor did we find large differences in CO_2 uptake of whole tops or shoots, or of equally illuminated single leaves, of young plants grown for 26–41 days in a glasshouse during July and August, when measured in a growth room at 20° C in 6 cal/dm²/min of visible radiation. Mean rates of apparent photosynthesis of whole tops of kale and sugar beet, and main shoots of wheat and barley were, respectively, 4·1, 3·6, 3·7 and 4·3 $\pm$ 0·11 mg CO_2/dm²/h, and for single leaves of the same species, 7·0, 7·0, 7·8 and 7·4 $\pm$ 0·34 mg CO_2/dm²/h. Respiration rates at 15° C of whole tops or shoots were also similar for all species, about a quarter of the rates of apparent photosynthesis at 20° C.

An attempt to reconcile these conflicting results was made by measuring CO_2 exchange and E simultaneously. Barley and sugar beet were grown for up to 6 weeks in a growth room with air temperature of 20° C during the light period of 16 hours and 15° C in the dark, in solution culture to avoid the complication of CO_2 production by respiration of soil organisms, and the CO_2 exchange of whole plants, including roots, was measured with an infra-red gas analyser continuously for 6 days, to give the total net uptake of CO_2. E for the same period was calculated from the initial and final dry weights and leaf areas of the plants. Estimates of dry-weight increase, calculated from the uptakes of CO_2, did not differ significantly from the measured increases; the differences were less than 1·5%. However, the sugar beet grew poorly, probably because the culture solution was not aerated, and both its rate of apparent photosynthesis and E were

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less than those of barley, which grew well. The experiment will therefore be repeated on plants grown in aerated culture solutions.

Net assimilation rates of sugar beet and barley enclosed in assimilation chambers for 6 days were, respectively, 88% and 75% of those of unenclosed plants in the same growth room. Light intensity, air temperature in the dark and the temperature of the nutrient solution were the same for enclosed and unenclosed plants, but in the light the air was 7° warmer in the assimilation chambers. However, this temperature difference did not explain the difference in E between enclosed and unenclosed plants. Unenclosed plants were also grown in another growth room with an air temperature of 27° C in the light and 15° C in the dark, and with light intensity, solution temperature and atmospheric humidity the same as in the assimilation chambers in the room with 20° C air temperature in the light. E of unenclosed plants in the 27° C room was less for sugar beet, and greater for barley, than of enclosed plants in the 20° C room. Increasing the air temperature in the light from 20° to 27° C decreased E of unenclosed sugar-beet plants but increased E of unenclosed barley plants. Leaf area was unaffected by enclosing the plants, or by the temperature difference between rooms. Evidently, enclosing the plants in assimilation chambers affected E by changing some factor other than temperature, possibly the conditions of CO_2 supply. (Thorne and Ford)

Effects of drought on leaf growth

Previously, effects of soil-water deficits on leaf growth were studied with kale seedlings growing in pots of soil by measuring relative leaf growth rates (R_L) at intervals after watering stopped, while the soil steadily lost water by transpiration through the plant. Seedlings were grown in a constant environment and watered frequently until the experiment began, some were then left unwatered and others continued to be watered, and the changes in leaf area of both were measured (*Rothamsted Report* for 1965, p. 97). In these conditions R_L decreased linearly with decrease in soil moisture content over a wide range.

To measure R_L with soil water content held nearly constant at different values instead of decreasing rapidly, a growth cabinet was constructed in which transpiration of illuminated plants can be decreased to zero, or made negative by radiative cooling of the leaves (5.9). With soil near field capacity the leaves guttate. A range of transpiration rates between 15% and −5% of that in a conventional growth cabinet can be obtained.

Except for differences associated with size of plant, for which correction was made, R_L of kale seedlings growing at different nearly constant soil-water deficits in the cabinet were similar to those for comparable rapidly changing deficits in a drying cycle. Apart from transient effects, changes in transpiration rate over a range of 30:1 did not alter the drought response. This confirms previous results made in a much narrower range of transpiration rates (1·6:1). Results for smaller and negative transpiration rates have not been fully examined, but there is evidence that leaves of plants in very dry soil continue to grow when the transpiration rate is negative, i.e. when the leaves take up water vapour from the air.

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The present method of varying the soil-water deficit of plants transferred to the radiation-cooled cabinet is to allow them to lose water by transpiration in a conventional growth cabinet for various times, but as the plants grow continuously during the drying cycle, the resulting differences in soil-water deficit are confounded with plant size, which affects R_L. To avoid this in future experiments a cabinet is being constructed to provide intense drying conditions, so that differences in soil-water content can be produced faster.

Another possible method of maintaining constant soil-water status is by adding water to the soil to replace that lost by transpiration. There are two objections to this; one is that the moisture potential corresponding to a particular soil-water content depends on whether it has been reached by drying or wetting. Another is that water added to partially dried soil does not become uniformly distributed in the soil mass, especially when poured on the surface. Whitehead (*New Phytol.* (1965), **64**, 315) sought to overcome this by injecting water from a hypodermic syringe at many points in the soil. Two experiments were done by this procedure; in one the pots were allowed to lose water until the required water content was reached, and water was then added daily to replace further loss. In the other all pots were permitted to dry to near wilting point and were then rewatered to different soil-water contents. In two other experiments water was added to the surface of the soil, not injected throughout the soil mass.

When water was poured on the top of the soil, R_L of the kale seedlings was greater at all soil-water contents than at corresponding contents during a single drying cycle, but when water was injected evenly throughout the soil the discrepancy was much smaller. When pots were injected with water after drying nearly to wilting point there was a transient large increase in R_L comparable to that found in field crops when rain falls after severe drought, but later R_L was related to soil-water content as during a single drying cycle. (Orchard)

Weed studies

Most of the work on weeds was concerned with blackgrass, now one of the most important species, especially in cereal crops, but observations were continued on the final stages of long-period experiments on wild oats, already described in previous Annual Reports.

Blackgrass (*Alopecurus myosuroides*)

Germination and growth in different soils. Seeds collected in 1963 and from three different sites in 1965 sown in pots of three different soils in September 1965 (*Rothamsted Report* for 1965, p. 101) behaved alike, except that the 1963 seed germinated sooner than the others, and seedlings from it matured sooner. Growth was good in the clay soil from Rothamsted, where blackgrass is common, but was poor in the sandy soil from Woburn, where blackgrass does not occur. In the soil from Begbroke, intermediate in texture between Rothamsted clay and Woburn sand, growth in autumn and winter was like that in Woburn soil, but in March plants began to

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grow more vigorously than in Rothamsted soil, eventually becoming taller and heavier with more tillers.

In addition to the differences in texture, Rothamsted soil had more potash than the others, whereas the Woburn soil had 10 times as much phosphate as the Rothamsted or Begbroke soils, but less total nitrogen. Begbroke was neutral, whereas the pH of Rothamsted soil was 5·8 and of Woburn soil 5·5. Which of these differences, if any, accounts for the differences in growth between soils is not yet known.

In pans of the same three soils kept moist and cultivated at intervals about 55% of seeds had germinated by November in Rothamsted and Woburn soils, but only 47% in Begbroke soil. The seeds collected in 1963 had the largest percentage germination, about 70%; presumably they had lost most of their dormancy before sowing. Only 35% of the 1965 collection from Foscot, in Oxfordshire, germinated in 1966, possibly because of damage by infection with twist (*Dilophospora alopecuri*) or ergot (*Claviceps purpurea*) fungi.

No evidence was found of genetic differences in time of germination between seed collected from plants in winter-sown and spring-sown crops (*Rothamsted Report* for 1965, p. 102); the ratio of spring-germinating to autumn-germinating seeds was no greater in seed from spring-sown crops.

Periodicity of germination in the field. Starting soon after the wheat in Broadbalk field was drilled in January, seedlings of blackgrass were counted at weekly intervals as they appeared on small plots on an undrilled area alongside the fallow section. Once a month, after counting, the seedlings were pulled up with as little disturbance of the soil as possible, or treated individually with paraquat. The main flush of germination occurred from mid-February to mid-March. Germination of dormant seeds began in August, and was increasing in October, when the experiment was ended by autumn ploughing. About 40% more seedlings were counted on the plots where they were pulled up than where they were killed with paraquat. The reason for this is not known; the possibilities that some pulled-up seedlings were merely decapitated and grew again to be counted later or that the paraquat treatment killed seedlings other than those treated, both seem very unlikely.

The experiment will be continued to determine how seasonal differences in weather affect the periodicity of germination.

Survey of blackgrass in England. Blackgrass plants bearing ears were collected by officers of the N.A.A.S. from areas where blackgrass is a troublesome weed. About 130 samples were received, with information about the sites from which they came; 94 were from cereal crops, of which 59 were winter wheat, and most of the rest were from herbage-seed crops, mainly grasses; 26 were from spring-sown crops. Of 79 fields with full information on past cropping, 62 had at least three cereal crops in the previous 5 years. This close association of blackgrass with cereal growing agrees with general observation, but infestations in spring-sown crops were more frequent than at Rothamsted (*Rothamsted Report* for 1958, p. 85; 1961, p. 83). The appearance and morphology of the plants were recorded

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and ripe seeds kept, to study the variability within the species. Ergot was found on ears of 18 samples, and twist on two; the ergot infection may be important if the fungus is the same strain as attacks wheat.

The Survey will not give complete information on the geographical distribution of blackgrass, or the frequency of infestations in different areas, because the fields sampled were not a random selection, and only few samples were taken by each collector.

Broadbalk weeds. Broadbalk wheat was severely infested with blackgrass in 1966, in spite of the January sowing, presumably because the wet state of the soil induced dormancy in the seeds and delayed germination until long after the usual time in October. Other winter-germinating species were scarce at the spring survey in mid-May.

The most striking feature of the weeds visible in the stubble in September was the many grass species and the large area covered by them. *Agrostis gigantea* (red top) was found for the first time, in addition to *A. stolonifera* (creeping bent), which is an established member of the Broadbalk flora. *Lolium multiflorum* (Italian ryegrass), possibly introduced by the baler, was common, and *Phleum pratense* (timothy) had spread to plots where it was not previously recorded. *Poa annua* (annual meadow-grass) was also more than usually abundant.

The increase in grass weeds may be a consequence of the use of herbicide sprays to control broad-leaved weeds over the whole field except Section Va. Grass weeds are less prevalent on Section Va than on the sprayed Section Vb, but Vb is no longer in the fallow cycle, and this may partly explain its greater growth of perennial grasses.

Weeds of Scout Farm. Scout Farm is very weedy, and a survey was made to identify the species present. Most of them are the same as on Rothamsted Farm; the chief exceptions are that spurrey (*Spergula arvensis*) occurs on an area of lighter, acid land at the west side of the farm, and hemlock (*Conium maculatum*), a poisonous plant, grows abundantly to a height of 7 ft in rough grass near the dry bed of the River Ver. (Thurston)

The Park Grass plots. The new liming treatments (*Rothamsted Report* for 1964, p. 226) continued to have obvious effects on acid plots not previously limed. Section c (now limed, previously unlimed) of plots 11–1 and 11–2 was much greener than section d (unlimed), because fewer dead culms remained from the previous season, and flowering of *Holcus lanatus* (Yorkshire fog) was again delayed. A few plants of red clover were found on 11–2 section c, which was previously too acid for clover.

In contrast, on acid plots where *Agrostis* sp. and *Anthoxanthum odoratum* (sweet vernal) predominate, section c was less green than the still unlimed section d, the difference being more conspicuous on plot 9 than on plots 1, 10 and 18. This effect persisted throughout the growing season, and was the opposite of that seen in 1965. The new liming treatments have not yet affected the relative abundance of species.

Seedlings of dandelion (*Taraxacum officinale*) grew on bare patches left

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on section c of 11–1 and 11–2 after cutting with a forage-harvester in December 1965, but did not develop beyond the 2–3-leaf stage and died during the summer, probably through competition from *Holcus*.

Ergot was prevalent on ears of *Holcus lanatus*, *Alopecurus pratensis* (meadow foxtail) and *Dactylis glomerata* (cocksfoot). (Williams and Thurston)

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