ROTHAMSTED RESEARCH

Rothamsted Experimental Station Report for 1965

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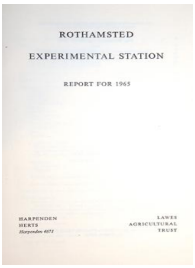

Botany

D. J. Watson

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BOTANY DEPARTMENT

D. J. WATSON

K. J. Witts and P. J. Goodman left and E. D. Williams was appointed to the staff. P. W. Dyson was awarded a Ph.D. degree of London University. E. C. Humphries contributed to a symposium on the action of CCC on cereals organised by Cyanamid International at Wageningen.

The work of the department deals mainly with the physiology of growth of field crops and aims to increase knowledge of how crop yield is determined, and of how growth can be adjusted to achieve maximal yield. It also includes studies of the biology of weed species, to show how weeds persist and multiply, and may be controlled. Growth is studied in field experiments, and in more detail in the glasshouses, controlled-environment rooms and laboratories.

In 1965 we continued to study: the physiological determinants of yield of wheat, sugar-beet and potato crops; the dependence of net assimilation rate on use of photosynthetic products and on respiration; growth regulators; the effects of water stress, atmospheric humidity and CO_2 concentration on growth and yield. New work was started on the growth and depth-distribution of roots of field crops. The weeds studied were mainly blackgrass and wild oats, and the flora of Broadbalk field.

Growth Studies on Field Crops

Wheat

Grain yield of wheat and leaf area duration after flowering. The dry matter that fills cereal grains is mainly the product of photosynthesis after flowering, and the yield of grain therefore depends on the leaf area index (L) of the crop during the time between flowering and ripening. Consequently, L integrated over this period (leaf area duration, D) is correlated with grain yield, and the ratio of grain dry weight to D (the grain : leaf ratio, G), a measure of the mean photosynthetic efficiency of the leaf area present after flowering, tends to be constant. G varies between years, and this can be explained satisfactorily by differences in mean daily radiation and temperature between flowering and harvest. The correlation of D with grain yield is still closer, and the variation in G less, when D is calculated for parts of the plant above the flag-leaf node, in agreement with experimental evidence that most of the dry matter entering the grain comes from photosynthesis in these upper parts of the plant (5.11).

To find whether variation in grain yield caused by differences in sowing date can similarly be explained by differences in post-flowering D, Opal spring wheat was sown on 11 March, 2 April and 28 April 1964 with 0 or 0·6 cwt N/acre as "Nitro-Chalk" applied in the seedbed. The mean dates when 50% of ears had reached anthesis were 26 June, 1 July and 13 July for the early, middle and late sowings respectively, and anthesis was

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delayed about 2 days by N fertiliser. The two earlier sowings were judged to be ripe on 19 August, and the last sowing was barely ripe when cut on 26 August. Samples were taken at intervals between anthesis and harvest to measure *L* of the whole plant and of parts above the flag-leaf node, the dry weights of ears and straw, and the final yield of grain.

The mean grain yields for early, middle and late sowings were 38·5, 37·2 and 29·0 cwt/acre. Nitrogen increased yield of the first two sowings by 6 cwt/acre, but of the last sowing by only 1 cwt/acre. *D* calculated from total *L* was increased by nitrogen from 23 to 31 weeks for the early sowing, from 21 to 29 weeks for the middle sowing and from 17 to only 18 weeks for the late sowing. These figures closely parallel the grain yields, and give grain: leaf ratios increasing slightly but not significantly with later sowing, from 16·5 to 17·8 g/m²/week without N, and from 14·5 to 17·2 g/m²/week with N. The reason for the decrease by N in *G* of the early and middle sowings might be that, when N was given, *L* was super-optimal at anthesis, but a more likely explanation is that N increased the area and persistence of green tissue below the flag-leaf node, which contributes little to grain yield. When *D* was calculated from *L* above the flag-leaf node the values of *G* for early or middle sowings with or without N were identical (43 $\pm$ 1·9 g/m²/week), but those for the late sowing were smaller (34 and 31 g/m²/week without and with N, respectively). This was because flag-leaf *D* was nearly as large for the late sowing as for the earlier ones, though the grain yield was much smaller. Apparently the photosynthetic efficiency of the flag-leaf and peduncle in the post-anthesis period was about 25% less for the late sowing than the earlier ones. The reason is not yet understood. The period of grain growth was delayed 2 weeks by later sowing, so that it occurred in shorter days with cooler temperature, but the effect of this on mean daily radiation and temperature during the period was probably insufficient to explain the smaller *G*. Nor is it likely that the grains of the late sowing were inadequate sinks for photosynthate from the leaves, for although the late-sown crop had fewer ears, it had the same number of grains per ear as the earlier sowings and the weight per grain was less. (Welbank)

Effects of CCC on growth and yield of spring wheat. Spraying wheat with a solution of the growth regulator CCC (2-chloroethyltrimethylammonium chloride) shortens the stems, and so might increase yield by preventing lodging. When attempts to test this were made in 1964 the unsprayed plots did not lodge, although a susceptible variety was sown thickly and given abundant nitrogen. Nevertheless, spraying with CCC increased grain yield by 5%, although it shortened the shoots by 40% and decreased leaf-area index, mainly because leaf-sheath area was less. The cause of the increase in grain yield is not known, but it was associated with more shoots surviving to bear ears. Plants treated with CCC were more erect, and when sown in rows 7 in. apart did not cover the ground between rows so well as untreated plants, so it seemed that sowing in more closely spaced rows might increase interception of light and, perhaps, enhance the increase of yield by CCC. For similar reasons, CCC may have increased yield in 1964 because the seed was sown thickly.

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To test these possibilities, spring wheat var. Opal was sown on 31 March in rows 4 in. or 8 in. apart, at normal and twice normal seed rates (3 and 6 bu/acre) with 0·5 or 1 cwt N/acre as "Nitro-Chalk". Still more N, 2 cwt/acre, was also used, but only with widely spaced rows. Half the plots of each treatment combination were sprayed with CCC ($2\frac{3}{4}$ lb in 40 gal/acre) on 20 May. Growth measurements were made regularly from late May until the crop was ripe, but only on plots that received 1 cwt N/acre, because those with 0·5 cwt N/acre were too irregular. A few plots given much N were affected by lodging, but only two lodged severely, and these not until August, when the crop was nearly ripe.

CCC shortened the straws by a third at ear emergence, somewhat less than in 1964, possibly because the variety was different, and decreased mean straw yield by one fifth. It decreased leaf area index mainly by decreasing the area of leaf sheaths and stems, both before and after ear emergence. In spite of this, grain yield was not decreased, perhaps because CCC had little effect on leaf area duration of parts above the flag-leaf node.

The mean grain yields of plots given 1 cwt N/acre without and with CCC were, respectively, 32·5 and 33·1 $\pm$ 0·8 cwt/acre. In accordance with expectation, CCC apparently had more effect on the closely spaced crop (about 5% increase with 4-in. spacing, and no effect with 8-in. spacing), but the interaction was not significant. On average of all treatments, varying the spacing of rows had no effect on grain yield, but yield was less with the larger seed rate, although it increased post-anthesis leaf area duration. (Welbank, Williams, Humphries and French)

Potato

B9 and growth of a potato crop. Treating potato plants in pots with the growth regulators CCC or B9 (N-dimethylamino-succinamic acid) shortened the shoots and lessened the leaf area, but prolonged the life of leaves and did not affect yield of tubers. It seemed possible that, in a field crop fertilised to give a nearly optimal leaf area index, the growth rate of tubers might be unaffected by leaf area changes caused by CCC or B9, and the longer persistence of leaves might increase the yield of tubers.

The effects were measured of spraying Majestic potatoes twice with B9 at two concentrations (1 or 5 g/litre) with "Triton X-100" as spreader. Enough spray was applied with a knapsack sprayer to wet all the foliage. Seed tubers of different sizes were used in different blocks of the experiment. The first spraying was done on 17 June, when tubers were starting to form, and the second on 1 July, when the first had already slowed stem growth, especially of the upper lateral branches that usually are very long in Majestic. Maximum L, attained at the end of July, was 4·9 for untreated plants and 4·5 and 4·1 for plants sprayed with 1 or 5 g/litre of B9. A month later the effect of spraying was larger. Although sprayed plants had smaller L, at first their tubers grew faster. In late June both concentrations of B9 increased the dry weight of tubers by 10%, and the increase was larger in plants grown from the larger seed tubers.

In contrast with its effect on potato plants in pots, spraying with B9

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caused leaves of the field plants to die earlier. Dry-matter production continued longer in unsprayed than in sprayed plants, because the leaves persisted longer, and the increase in yield by spraying was only 3% at the final harvest on 4 October. Spraying increased tuber number per plant, as well as mean dry weight per tuber. It also increased the water content of tubers and the amount of second growth. The explanation of the increase in yield by spraying in spite of a smaller L may be either that maximal L of the unsprayed plants was above the optimum, or that shortening the shoots allowed more dry matter to be moved into the tubers. Spraying did not affect total dry-weight yield.

As B9 increased tuber yield most in the early stages of tuber growth, it may be more effective for early than main-crop varieties, and this will be tested in 1966. (Humphries, Dyson and French)

Sugar beet

Dependence of net assimilation rate and crop growth rate on leaf area index. An experiment done in 1964 (*Rothamsted Report* for 1964, p. 102) measured the effects of differences in leaf-area index (L) induced by sowing on three dates, by applying nitrogen fertiliser and by removing 0, $\frac{1}{4}$, $\frac{1}{2}$ or $\frac{3}{4}$ of the plants on sample areas of every plot at the beginning of experimental periods, on net assimilation rate (E) and crop growth rate (C); the results have now been analysed. In experiments done in August and September 1954 E decreased slowly with increase in L, so that C continued to increase throughout the range tested up to $L = 6$. Results were very different in 1964. In July E at first increased with increase in L up to 1·5, and then decreased faster than in 1954. Consequently, maximal C occurred when L was about 3. This agrees with results of recent field experiments, in which increasing L above 3 by closer spacing of plants or large nitrogen dressings did not increase yield. The reason for the difference between the results in 1954 and 1964 is not known. One possibility is that the Sharpe's Klein E strain of sugar beet used in both years may have changed during the interval. Seed of the 1958 distribution, the oldest obtainable, sown in 1965 produced a similar L to seed of the 1965 distribution, but the relation of E to L of plants grown from the 1958 seed was not investigated.

Partial regressions of E on root dry weight as well as on L were calculated from the means for the thinning treatments within each sowing date and nitrogen treatment. All the regression coefficients of E on root dry weight were positive and some were significant. This may imply that in the early stages of growth the size of the roots as sinks for photsoynthate may influence the rate leaves photosynthesise, but other explanations are possible, and further work is necessary to decide which is correct. The two later experiments, in August after a drought period and in September after irrigation, gave very variable and inconclusive results.

Plant population and yield. In 1963 spacing sugar beet closer than in current practice had little effect on yield even when the nitrogen supply was also increased (*Rothamsted Report* for 1963, p. 85). The possibility that

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competition for water or other nutrients than nitrogen limited yield when plant number was increased was tested at Rothamsted and Broom's Barn, with plant populations ranging from 20,000 to 67,000/acre in square spacing, abundant water, 0 to 1·8 cwt fertiliser N/acre and, at Broom's Barn, additional phosphorus and potassium.

Until July dry-matter yield increased proportionately with plant number, but later the increase was less than proportionate and eventually disappeared. Additional N increased total yield of dry matter at both centres with all populations, but P and K had no effect, and there was no interaction of spacing with nutrient supply. Irrigation in this wet summer had no effect.

Leaf area index ceased to be proportional to plant population after July, when close spacing with large N supply produced the largest *L*. At Broom's Barn *L* did not exceed 3, but at Rothamsted it reached a maximum of about 5. Maximal *L* differed between populations, but this had little effect on yield. Evidently, with enough N, *L* of all populations was large enough to intercept nearly all incident light.

As in 1963, increasing plant number decreased the proportion of total dry-matter yield contained in the roots, and so did extra N. Root yield was not significantly affected by plant number, but was increased by N, most with the widest spacing. (Goodman)

Root growth of field crops. A serious defect of growth studies on field crops hitherto has been that the weight of roots and their depth distribution have not been measured, because suitable methods were lacking. The requirements are that at the times when samples of above-ground parts are taken for growth analysis, adequate samples of known volumes of soil with the contained roots, from known depths and from the same places in the field as the above-ground parts, can be taken quickly from each plot of a field experiment without damage to surrounding areas, and the roots then separated quantitatively from the soil and from other organic matter.

Possible methods are being investigated at Woburn, where the sandy soil is more tractable than the clay with flints at Rothamsted. Three methods of taking soil samples were tried:

(1) A portable power-driven auger cut 3-in.-diameter holes, and the loose soil it brought up was collected on a tray surrounding the hole. Samples from successive depths were taken by boring the holes in stages and collecting the soil from each stage separately.

(2) A steel coring tube with a cutting edge was driven into the ground with a power hammer to the full depth and pulled out with the soil core inside it, either by a chain hoist and tripod or a crow-bar and a self-locking tube clamp. The core was removed and divided into sections at specified depths. Part of the core was sometimes lost through the bottom of the tube as it was withdrawn, but this may be overcome by redesigning the cutting edge. Removing the core may be facilitated by fitting a tube liner, split longitudinally, that will slide easily out of the tube and prevent the core breaking prematurely.

(3) Another 3-in. coring tube was fitted with a central pipe that carried

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water at high pressure to a nozzle just inside the open end of the tube. As the tube was pushed manually into the soil, radial jets of water carried the soil upwards to an exit pipe at the top of the tube, from which the water was passed on to a wire screen that separated roots and stones from fine soil. This tube penetrated easily, but required much water (12 gal/min). Some water escaped below the cutting edge and up the outside of the tube, flooding the site, and a suction pump fitted to the exit pipe did not prevent the flooding. These difficulties outweighed the main advantage that the roots were separated as the sample was taken.

Samples taken by auger or coring tube were washed on a sieve to separate roots from soil, and dead organic matter removed by hand-picking and flotation. Surface samples may contain much organic debris, and hand separation of the roots is slow and tedious; a quicker and less laborious method is urgently needed. Finally, the roots were dried, weighed and the weights of roots per unit area of crop at different depths calculated from the measured diameter of the sample holes.

Samples were taken on several occasions from two plots of spring wheat with different amounts of nitrogen fertiliser, and from two similar plots of kale. They were too few to give precise estimates, but the results indicate roughly the amounts of roots present and the changes with time. Plants on areas to be sampled were pulled up and their roots cut off, dried and weighed. Detached roots remaining in the soil were then recovered in auger samples. The total dry weight of wheat roots in g/m² to a depth of 60 cm on plots with 0·1 and 0·8 cwt N/acre, respectively were 70 and 160 at ear emergence on 24 June and 30 and 85 on 18 August when the crop was nearly ripe. About 90% of the total root weight was in the top 20 cm of soil and only 1–3% below 40 cm. Detached roots contributed 8 and 20 g/m² to the weights on the last occasion. Samples from the same areas taken with a coring tube 2 days later contained 20 and 45 g/m² of detached roots, more than twice the amount recovered in auger samples. The cause of these discrepancies is not known. Most of the difference was in the top 20 cm of soil, but there were also differences between auger and coring-tube samples in the depth distribution of roots.

The ratio of total root dry weight determined by auger sampling to dry weight of above-ground parts exceeded 0·2 on 24 June, but was only 0·1 on 18 August, with both rates of N. Thus, about one-sixth of the total dry weight of the wheat crop was below ground at ear emergence, but only about one-tenth at maturity.

The total dry weight of kale roots estimated in the same way by up-rooting plants and separating detached roots from auger samples taken to 60 cm depth was about 90 g/m² on 16 July, 13 weeks after sowing, increasing to 150 g/m² in the next 6 weeks. Until then there was little difference between the plots, but on 2 November the crop with 0·5 cwt N/acre had about 250 g/m², and that with 2 cwt N/acre more than 300 g/m². With 0·5 cwt N/acre, the dry-weight ratio of roots : tops was about 0·25 in July, increasing to 0·3 in August and 0·4 by November. With 2 cwt N/acre the ratio was about 0·2 in July, 0·15 in late August and again 0·2 in November. Thus, nitrogen decreased the fraction of the total dry weight of kale present in the roots. More than 90% of the weight of roots was in the top

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20 cm of soil, and much of this was thick, woody main roots; only 1–3% was below 40 cm. (Welbank and Williams)

Laboratory and Glasshouse Studies

Dependence of photosynthesis on use of photosynthate. There is now much evidence that in some circumstances photosynthesis by leaves depends on how fast photosynthetic products can move from the leaves into growing points or storage organs. Thus, the rate potato tubers grow apparently sets a limit to the rate the leaves photosynthesise. To study these effects the relative sizes of sources and sinks of photosynthate must be varied independently. In such an experiment with potato plants grown in pots by a technique that allowed tubers to be excised without disturbing the roots, removing tubers as they were formed greatly slowed the net assimilation rate (5.7). Conversely, making the photosynthetic system smaller by removing some leaves during the period of tuber formation should increase photosynthesis by the remaining leaves, and have little or no effect on tuber yield.

To test this, chitted seed potatoes were planted in pots at the end of April, and a month later, when tubers began to form, some plants were left intact, and enough leaflets were removed from others to make the leaf area 20 or 40% smaller. When the plants were harvested 3 weeks later the leaf area of intact plants had nearly doubled. Leaves grew faster on the partially defoliated plants, so that those that lost 40% of their leaf area initially had only 16% less leaf area than intact plants 3 weeks later. The dry weight of tubers was not significantly changed by removing the leaflets, and the rate of increase in tuber dry weight per unit leaf area increased from 0·16 to 0·22 g/dm²/week in plants 40% defoliated. Although removing leaves did not affect tuber weight, it affected tuber number; the mean tuber number was 19 on intact plants and 13 on those 40% defoliated. (Humphries and Dyson)

Rate of leaf production of sugar beet. An experiment with sugar beet in pots (Humphries, E. C. and French, S. A. W. (1965), *Ann. appl. Biol.* **55**, 159) showed that CCC applied to the soil in April increased leaf production, but gibberellic acid (GA) sprayed on the leaves at intervals in May decreased it. Both effects persisted until the experiment ended in October, and the mean numbers of leaves produced per plant per week from June to October were: no treatment 2·36, CCC 2·70, GA 1·25, $\pm$0·060. This and other evidence suggests that the rate sugar beet and other plants produce leaves may be controlled by internal factors determined at an early stage of growth. To test this, sugar-beet seeds were sown on 6 May in a range of conditions likely to produce large differences in the initial rate of leaf production, viz., (1) in growth cabinets at 20° C with fluorescent light for: 8 hours daily, or (2) 16 hours daily; (3) in a glasshouse with natural daylight (15½ hours photoperiod); or (4) in continuous light in the laboratory. The seedlings were kept in these conditions until 26 May, when they had four leaves. Ten plants from each treatment were then transplanted to pots and moved to a glasshouse where all plants subsequently had the same

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conditions. Living leaves larger than 1 cm^2 and dead leaves were counted at intervals until October. Plants with different initial treatments continued to produce leaves at different rates; the mean rates per plant per week in the period from June to October were (1) 1·87, (2) 2·44, (3) 2·00, (4) 2·21, $\pm$0·063. In otherwise similar conditions (cf. treatments 1 with 2, or 3 with 4) a longer photoperiod immediately after germination caused a persistent increase in the rate. There was also a persistent difference between plants started in the growth cabinets or in the glasshouse (cf. treatments 2 and 3), perhaps an effect of temperature. Leaf production was inversely related to leaf longevity; perhaps leaves died soonest on plants that produced leaves fastest (treatment 2) because nitrogen supply in the pots was limiting, and it might not happen with pretreated seedlings transplanted to the field. (Humphries)

Bound auxin in leaves. In previous attempts to liberate auxins or gibberellins bound to protein in leaves of dwarf French bean (*Phaseolus vulgaris*), incubating macerated leaves in phosphate buffer (pH 6·2) for 24 hours at 37° C produced only a three-fold increase in free auxin. Adding ficin to the macerate increased its auxin content more, but all samples of ficin tested contained auxin. Other proteases (trypsin or papain) did not liberate auxin, and none of the treatments increased extractable gibberellins (*Rothamsted Report* for 1963, p. 87). However, when primary leaves of bean plants, grown at 25° C for 14 days, were macerated in phosphate buffer (pH 8), then kept at 37° C for 2–7 days and the products separated on paper chromatograms, assays with wheat coleoptiles showed a more than hundred-fold increase in auxin. No gibberellin was released from a bound form by this treatment.

The auxin liberated by incubation ran at the same position on chromatograms as indolyl-3-acetic acid (IAA). Incubating longer than 2 days partially destroyed the chlorophyll, and this interfered with the separation on chromatograms. When leaves were killed by immersion in boiling water before they were macerated there was no increase in auxin after incubation, showing that auxin was liberated in macerated leaves by enzyme action. The enzyme is most active between pH 7 and 8. When cell debris was removed from the macerate by centrifuging and the remaining solution incubated, nearly as much auxin was released as by incubating the entire macerate. Thus, both the enzyme and its substrate are water-soluble. Young leaves released less auxin than old leaves, which suggests that either the content of bound auxin or the activity of the enzyme increased with age.

During senescence of primary leaves the free auxin per g fresh weight increased more than the bound auxin decreased, so there was a net increase in total auxin. Release of protein-bound auxin and its movement to the petiole may account for the ability of detached leaves to form roots when the cut petioles are immersed in nutrient solution (*Rothamsted Report* for 1960, p. 102); auxin was found in the solution where roots formed. (Wheeler)

Growth substances in potato. In different potato varieties the durations of dormancy of seed and of tubers are correlated, and gibberellic acid breaks

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the dormancy of both seed and tubers. This suggests that the biochemical basis of dormancy may be similar in seeds and tubers. As a first step in a study of the biochemical control of dormancy, indole compounds in seeds and tubers were extracted by different methods and assayed. Tryptophan and indole-3-acetyl aspartic acid were identified in seeds; both may be precursors of auxin. Indole-3-acetyl aspartic acid was not previously known to occur in potato. It was also found in sprouts grown in light or dark, and in tips of stolons during early stages of tuberisation, but not in the peel of tubers.

Different methods of extraction of peel, and of fractionating the extracts, gave very different results in assays with oat mesocotyls or coleoptiles. When the ether-soluble fraction of a methanolic extract of peel, designed to prevent chemical or enzymic destruction of indole compounds during extraction, was divided between neutral or ammoniacal solvents and run on paper chromatograms, bioassays of the IAA zone of the chromatograms showed more activity with ammonia in the solvent. Possibly the ammonia produced IAA from a precursor. Such a precursor may be physiologically important, and its identity is being sought. IAA was identified by bioassay of electrophoretograms of extracts. The method used separates IAA from gibberellic acid, indole butyric acid, indole acetonitrile and tryptophan.

Earlier work demonstrated a growth inhibitor soluble in acidic ether in dormant tubers that disappeared when the tubers sprouted. The presence of this inhibitor in ether extracts of peel was confirmed, but methanol extracts contained only traces. Extraction with peroxide-free ether discolours the peel, so the inhibitor may be a product of phenoloxidase activity. Although it may be an artefact, its disappearance when dormancy is broken is indirect evidence of a change in the biochemical state of the tuber associated with sprouting.

Other growth-promoting constituents of extracts of different plant parts have not yet been identified. Some of them, in peel and seed extracts, may be 5-OH indole compounds, and 5-OH tryptamine (serotonin) was identified chromatographically and fluorimetrically as a major constituent of the flesh of potato fruit.

Satisfactory bioassays using potato material as test objects are difficult to devise, but some work was done on the use of potato seeds to test for inhibitors of germination, seed-pieces of tuber to test dormancy breaking, callus-tissue formation to test for cell division and cell elongation factors, and sterile culture of stolon tips to assay tuberisation. (Burnett)

Effect of drought on leaf growth. The effect of water stress on leaf growth was further studied by the technique that compares relative leaf growth rates (R_L) of kale seedlings, first grown in a constant environment in pots filled with standard compost and watered frequently, and then either not watered or watered as before (*Rothamsted Report* for 1964, p. 107). As the soil in the unwatered pots dries, R_L of the plants decreases linearly with soil moisture content over a wide range, and the slope of the regression line of R_L on soil moisture content measures the effect of increasing drought on the rate leaves expand (the "drought response"). The method

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has been used to assay treatments that might influence the drought response.

Differences in rate of water loss caused by keeping plants in atmospheric humidities of 37 or 84% R.H., or in the rate of change of soil moisture content produced by varying the size of pot over a four-fold range, had no effect on the drought response, i.e., R_L at a specified soil moisture content was the same with all these treatments. Varying the rate of water loss by starting the experiment with plants of different ages, giving a six-fold range in initial leaf area, apparently had a small effect on the drought response, but this was attributable to decrease in R_L with age that occurred in both watered and unwatered plants. Gibberellic acid, CCC, benzyl adenine and cysteine have been reported to mitigate the harmful effects of drought on plants, but none of them affected the drought response.

The prime difficulty in studying effects of drought on growth processes is that water stress cannot be maintained at a defined intensity. Water is lost continuously from the soil by transpiration through the plant, and in unsaturated soils cannot be replaced uniformly from an external source. If transpiration could be prevented, plants could be grown in nearly constant, or only slowly changing, states of soil water deficit. A growth cabinet was constructed in which the leaves of illuminated plants are cooled by radiation, and the atmospheric humidity is controlled to minimise differences in temperature and in water-vapour pressure between illuminated leaves and the ambient air. Unfortunately, radiation cooling can cope only with illumination less than $\frac{1}{10}$ full sunlight. Light from a panel of fluorescent tubes passes through a perspex box filled with 50% methanol cooled to −18° C, and radiation to the cold methanol cools leaves illuminated with 700 f.c. to about 0·2° C below air temperature. Air temperature and humidity are held constant, and dew-points within 0·1° C of air temperature can be maintained. In these conditions kale guttates freely and dew forms on the leaves. With slightly lower humidities it should be possible to keep transpiration below 5% of its rate from leaves cooled by convection, and also avoid release of water stress in the plant by uptake of dew. Further tests are necessary of the accuracy of transpiration control, and of the adequacy of the light intensity for plant growth. (Orchard)

Growth in Controlled Environments

Effects of atmospheric humidity on growth. In previous experiments, the dry weights and leaf areas of several crop species increased when they were grown in more humid atmospheres, and in one experiment E was decreased (*Rothamsted Report* for 1963, p. 79, and 1964, p. 105), but in further work this year change in humidity had much smaller effects.

Wheat and sugar-beet plants were grown in pots of soil watered generously, in growth rooms illuminated for 16 hours per day with fluorescent and tungsten light of 1,900 f.c. intensity (6·0 cal/cm²/h visible radiation). All rooms had relative humidity of 90% and temperatures of 15° C in the dark, and 20° C in the light. To distinguish effects of humidity on early growth from those on germination, which seemed to be hastened by increased humidity in a previous experiment, all rooms had 70% R.H. in the

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light until all seeds had germinated 8 days after sowing. Thereafter the three rooms were maintained at 50, 70 and 90% R.H. in the light. Six weeks after sowing, total dry weight of sugar beet was 14% greater at 90% R.H. than at 70 or 50% R.H., but there were no significant differences 3 weeks later. Six and 9 weeks after sowing, leaf area was about 20% greater in the wettest than in the driest room, and between 6 and 9 weeks *E* decreased with increasing humidity. Differences in humidity had no effect on dry weight, leaf area or *E* of wheat. Nine weeks after sowing, the green area of the main shoots increased with increasing humidity, but there were most shoots in the driest room. In the similar experiment in 1963 the differences in humidity were maintained during both the dark and light periods, and this may account for the smaller effects on growth in the 1965 experiment, but further work is needed to test this.

Effect of CO_2 concentration on growth. When kale, sugar-beet and barley plants were grown for 6 weeks with 114 cal/cm²/day of visible radiation from fluorescent tubes and tungsten lamps in a 16 h photoperiod, increasing the atmospheric CO_2 concentration from the normal 300 to 1,000 or 3,300 ppm, increased their dry weight by about 30% (*Rothamsted Report* for 1964, p. 106). Another experiment shows that comparable increases occur with 34 and 78 cal/cm²/day of visible radiation.

Sugar-beet and barley plants were grown for 6 weeks in three growth rooms providing the different CO_2 concentrations. Other conditions were the same as before, except that each room was divided, with different light intensities in the two halves. Some plants were sown in the rooms and others were transferred there 25 days after sowing in a glasshouse. Kale sown in the glasshouse was also used, but was in the growth rooms for only 4 weeks. Plants were sampled at approximately fortnightly intervals.

Increasing CO_2 concentration from 300 to 1,000 ppm increased total dry weight of all species by about 40% at most samplings. A further increase to 3,300 ppm increased dry weight by about another 10%. The absolute effects were usually slightly more in brighter light, especially the response to 3,300 ppm CO_2 of plants sown in the rooms. Dry weight was approximately doubled by increasing the light intensity, so that in dim light with the largest CO_2 concentration it was similar to that in bright light with normal CO_2. Light, and usually also CO_2, had slightly greater effects on weight of roots than of tops.

Leaf area was affected less than dry weight by CO_2 and light intensity. It was rarely increased by more CO_2 than 1,000 ppm, and CO_2 had similar effects at both light intensities. The number of tillers of barley, but not leaves of sugar beet or kale, increased with increasing CO_2 concentration. Net assimilation rates have not yet been calculated, but measurements with an infra-red gas analyser of CO_2 uptake by single leaves and whole tops suggest that the differences in growth were caused by differences in rate of photosynthesis. When plants grown in one CO_2 concentration were transferred to another the rate of photosynthesis depended only on the new CO_2 concentration and not at all on the old. (Thorne and Ford)

Effect of age on the photosynthetic and respiratory components of net assimilation rate. The net assimilation rate (*E*) of plants growing in a constant

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environment decreases with age. To find whether this reflects only a slowing of photosynthesis, or whether it also depends on faster respiration, the photosynthetic component (P) and the respiratory component (R) of E, all expressed as change in dry weight per unit leaf area so that $E = P - R$, were measured on three occasions during the growth of sugar beet and wheat by the method of Watson and Hayashi (*New Phytol.* (1964) **64**, 38–47). The method depends on preventing photosynthesis on some days during the experimental period by shading plants. The net assimilation rate (E_N) of plants allowed to photosynthesise on n days out of N is linearly related to n, and the slope of the regression line represents the contribution of one day's photosynthesis to E_N, the net assimilation rate of plants allowed to photosynthesise on all N days. P can therefore be determined by multiplying the regression coefficient by N, and R is given by $P - E_N$.

Between 30 and 90 days after sowing, E of sugar beet decreased from 94 to 44 g/m²/week, i.e., by 50 g/m²/week. In the same period P decreased by 45 g/m²/week and R increased by only 5 g/m²/week. Similarly, between 20 and 50 days from sowing of wheat, E decreased from 63 to 37 g/m²/week, i.e., by 26 g/m²/week. The decrease of P in the same time was 37 g/m²/week, and R decreased with age by 11 g/m²/week. P always greatly exceeded R, and the smallest ratio of $P : R$ was 5, for the youngest wheat plants. Evidently respiration changes played little part in the decrease of net assimilation rate with age, which was caused by a similar or even larger decrease in the rate of photosynthesis.

An alternative method of changing the duration of photosynthesis, by shortening the daily photoperiod, was tested in an experiment with wheat, and gave estimates of P and R almost identical with those obtained by preventing photosynthesis on some days. E was linearly related to photoperiod within the range from 16 to 5 h/day, and shortening the photoperiod had the same effect on E as preventing photosynthesis on an equivalent number of days. (Wilson and Watson)

Photosynthesis of flag-leaf laminae of cereals. Removing half the florets from ears of barley soon after they emerged, slightly slowed photosynthesis of the flag-leaf lamina (5.8). If, as this suggests, photosynthesis by the flag-leaf depends on the capacity of the grains to accommodate the products, photosynthesis of the ear itself may also restrict photosynthesis by the flag-leaf. This might explain the slower photosynthesis of the flag-leaf and peduncle of barley than of wheat, because barley ears photosynthesise more than wheat ears (5.9), but the results of further work do not confirm this.

Plants of two six-row barleys (Brant and Dea), two two-row barleys (Proctor and Plumage Archer), two awnless wheats (Atle and Jufy I) and an awned wheat (Hebrard) were grown in pots in the glasshouse until after ear emergence. Photosynthesis by ears and flag-leaf laminae was measured in a growth room at 20° C and with 5·6 cal/cm²/hr of visible radiation. The rates of photosynthesis of the ears differed between crops and varieties, but there was no indication that photosynthetic rate of the flag-leaf lamina was inversely related to that of the ear. Removing the ear from

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shoots of Atle or Jufy I wheat had no effect on photosynthesis by the flag-leaf 1, 6 or 8 days later. (Thorne)

Weed Studies

Black Grass (*Alopecurus myosuroides*)

Effect of soil disturbance on germination. Seeds of blackgrass were sown in small pots of loose or compacted potting compost in January, and the soil was left undisturbed, or "cultivated" by emptying the pot, mixing the soil and returning it, at 2-, 4- or 8-week intervals. Few seeds germinated in the first 4 weeks, but after 6 weeks 80% of seeds had germinated in pots cultivated twice, 60% in pots cultivated once 2 weeks after sowing and only 20% in pots cultivated once 4 weeks after sowing or undisturbed. Initial compaction of the soil made no difference, probably because the loose soil became compacted by repeated watering. Two months after sowing, germination in pots cultivated every 2 weeks had increased to 85%, but was still about 60% in pots cultivated only once or twice, and 20% in undisturbed pots. Cultivation after 8 weeks of pots previously undisturbed increased the germination to 30%, but with other treatments no more germination occurred between 12 and 21 weeks after sowing. Evidently, frequent disturbance of the soil stimulates blackgrass seeds to germinate. Whether the seeds that did not germinate after 21 weeks were dormant or dead is not known.

Effect of light on germination. Seeds of blackgrass collected on Broadbalk in 1961, 1962 and 1964, and from the National Institute of Agricultural Botany in 1964, were sown on moist plastic sponge in transparent boxes and kept in an incubator at 16° C, either in darkness or in dim light continuously or for 8 hours per day. Mean germination of all samples of seed was 73% in darkness, 84% in continuous light and 86% in short days.

Germination and growth of blackgrass in different soils. The light soils at Woburn and on the Weed Research Organisation farm at Begbroke have no blackgrass, but on the heavy soils at Rothamsted and Boxworth, Cambridgeshire, winter cereals readily become infested. To test whether this difference is determined by soil type or by other factors, ripe seed collected in 1965 from natural infestations of blackgrass at Rothamsted, Boxworth and on a heavy soil at Foscot in Oxfordshire, and in 1963 from another site in Oxfordshire, were sown in September in soil from Woburn, Begbroke and Rothamsted, in shallow pans to estimate germination and in pots to measure plant growth. Boxworth soil was not used, because it is too heavy for pot culture.

By November 20% of Foscot seeds, 30% of Rothamsted and Boxworth seeds and 50% of 1963 seeds had germinated, and the older seeds germinated sooner. More of the seeds from Rothamsted and Boxworth, and of the 1963 collection, germinated in Rothamsted soil than in the light soils, but in contrast, more Foscot seeds germinated in the light soils than in Rothamsted soil. The experiment to test growth in the different soils was

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not completed and will continue in 1966, but the differences in the early stages, and in the germination tests, were too small to explain the absence of blackgrass from the light-land farms. Differences in cropping, and especially the later cultivations for spring than for winter cereals, may keep out blackgrass.

Germination of seeds from winter and spring germinating plants. At Rothamsted blackgrass mostly germinates in November, but elsewhere it is said sometimes to germinate more abundantly in spring. To test whether within the species there are types differing in periodicity of germination, seed was collected in winter-sown and spring-sown crops and sown in September in pans of sterilised potting compost. Germination in the autumn, 2 months after sowing, was the same for seed collected from winter-sown and spring-sown crops in the same place, but there were differences between places. Results to date suggest that differences in germination time are not genetically determined, but that spring germination depends on dormancy induced by autumn weather conditions (*Rothamsted Report* for 1962, p. 64). (Thurston)

Wild Oats (*Avena fatua* and *A. ludoviciana*)

Effect of temperature on dormancy of seeds. Seeds of 14 selections of *A. fatua*, type fA, and eight of *A. ludoviciana*, type lA, grown in pots from seed collected in different countries (*Rothamsted Report* for 1964, p. 112), either intact or with their distal ends cut off to break dormancy, were set to germinate at 10° and 24° C. At 10°, 96% or more of seeds of all selections were viable, i.e., they germinated when the seed was cut, but viability was less at 24°, and more second than first seeds were adversely affected by the warmer temperature.

Viable seed of nine selections of *A. fatua* were almost all dormant and those of another non-dormant at both temperatures; of the remaining selections three had more dormant seeds at 10° and one had more at 24°. The viable second seeds of *A. ludoviciana* were nearly all dormant at both temperatures. There was less dormancy in first than in second seeds at 10°; in two selections all first seeds germinated, but in the others dormancy ranged from 50 to 90%. At 24° dormancy of first seeds was increased to over 90% in half the selections, but increased less or not at all in others. In general, the two species reacted oppositely to temperature; more seeds of *A. fatua* were dormant at 10°, but more of *A. ludoviciana* at 24°. This difference may be related to their difference in time of germination in the field; *A. fatua* germinates mainly in spring and *A. ludoviciana* in winter. There was no obvious connection between country of origin and temperature response.

Fumigation of wild oats seeds. Attempts to kill wild oats seeds attached to grain sacks by heat failed (Williams, G. C. and Thurston, J. M. (1964) *Ann. appl. Biol.* **53**, 29–32), so methyl bromide fumigation was tried, in collaboration with the Ministry of Agriculture, Fisheries and Food, Pest Infestation Division, Liverpool. Seeds of *A. fatua* and *A. ludoviciana* supplied by us were treated and returned for germination tests.

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Seeds with a moisture content of 18% were all killed by fumigation with methyl bromide in 48 hours. When the moisture content was 14% or less some seeds survived and either non-dormant seeds were preferentially killed or dormancy was induced in some non-dormant seeds. When sacks with seeds of *A. fatua* embedded in them were fumigated, only 21% of the viable seeds were killed, but the moisture content of the seeds was only 10%, so more might have been killed had the sacks been moistened before fumigation. (Thurston)

Broadbalk weeds. The whole of Broadbalk, except for Section Va and the fallow strip, was again sprayed with herbicide ("Banlene"), but the effects were less spectacular than in 1964, presumably because of the wet summer. Several annual weeds were more abundant than usual, including *Fumaria officinalis* (fumitory), *Lithospermum arvense* (corn gromwell), *Anagallis arvensis* (scarlet pimpernel), *Euphorbia exigua* (dwarf spurge) and *Avena ludoviciana* (winter wild oat). Blackgrass (*Alopecurus myosuroides*) was present on all plots, and was most plentiful on plots with much nitrogen fertiliser. When the wheat crop lodged in June, blackgrass grew through it and produced a second crop of large ears from the nodes of laid stems. *Medicago lupulina* (black medic), from seeds that germinated after spraying, was abundant in the stubble, and *Aphanes arvensis* (parsley piert) was also frequent in places where *Medicago* was sparse.

Although many seeds of blackgrass were produced, none germinated by mid-November, the usual time, even after the field was ploughed and cultivated. The fungi ergot (*Claviceps purpurea*) and twist (*Dilophospora alopecuri*) were both prevalent on blackgrass ears, but not enough to explain the failure of seeds to germinate. Presumably dormancy was induced by heavy autumn rain, as in 1961 (*Rothamsted Report* for 1961, p. 83), and the seeds will germinate in the spring, so that, although Broadbalk was not sown by the end of the year, exceptionally late sowing may not prevent a blackgrass infestation in 1966.

Soil samples were again taken from selected plots to measure the effects of herbicide sprays on the weed-seed population. Counts of seeds germinating from soil samples taken in 1962 were completed, and showed that even after six years of herbicides without fallow there were still more than 24 million viable seeds/acre, compared with 70 million/acre in the 4th year after fallow without herbicide. This population is still much too large for spraying to be stopped. (Thurston)

The Park Grass plots. Effects of the new liming scheme on the Park Grass plots (*Rothamsted Report* for 1964, p. 226) were apparent only on the very acid plots, where decay of the dead vegetation on areas limed for the first time was hastened in spring. On these parts the grass on plots 1, 4–2 and 18 (mainly *Agrostis tenuis*) was greener, and on 11–1 and 11–2 flowering of *Holcus lanatus* was delayed or diminished. (Williams and Thurston)

To provide a basis for measuring future changes in the flora of the micro-plots into which plots 5 and 6 are now divided, six people estimated by inspection the percentage areas covered with grasses, legumes and other species, and of bare ground on each micro-plot before the new treatments

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were applied. The initial differences between the micro-plots were large; for example, on plot 6 the estimated percentage areas covered by legumes ranged between 5 and 40% and the means of four replicates allotted to each treatment from 20 to 38%, but the treatments may induce large differences in the flora and more uniformity of replicates.

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