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D. J. Watson

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BOTANY DEPARTMENT

D. J. WATSON

Mr. Jamaludin bin Lamin left in August to return to the Department of Agriculture, Malaya. Other visitors from abroad were Dr. J. P. Riches, of the Botany Department, University of Adelaide, who worked here on water relations of seedlings until the end of January, and Miss M. E. Fitzpatrick, of the Scott Agricultural Laboratories, Nairobi, who was with us in May and June. Many more paid short visits to talk with us about the growth of tea, tobacco, rubber, coffee, cacao, sorghum, maize and vines as well as the crops that are familiar to us.

K. J. Witts was awarded a Ph.D. degree of the University of London. Joan M. Thurston attended the meetings of the European Weed Research Council and the 1st French Weed Control Conference in Paris in December.

In November we acquired some additional laboratory space in the building formerly occupied by the A.R.C. Unit of Plant Morphogenesis and Nutrition, and now to be called the Plant Physiology Laboratory. In part exchange, we surrendered a room to the Library.

Our work continued to deal with two main themes, weeds and the physiology of plant growth and yield. The weed studies were on the biology of weed species, effects of weeds on crop yield, and the nature of interference between weeds and crops. The physiological work included growth analysis studies on field crops, and laboratory and glasshouse investigations of related topics, including particularly the physiology of growth of leaves, and effects of some growth-regulating substances.

WEED STUDIES

Wild oats

More collections of wild oats seeds from several countries in Europe, and also seeds of *Avena sterilis* from Israel and of *A. ludoviciana* and *A. fatua* from Iraq were grown in pots in comparison with the sorts that are common in Britain. This experiment and a similar one in 1960 (*Rep. Rothamst. exp. Sta. for 1960*, p. 103) showed that the time of flowering varied more widely with the country of origin than between species. Thus, *A. fatua* and *A. ludoviciana* from Russia both reached 50% ear emergence in 124 days from sowing, *A. fatua* from Iraq in 97 days, and four selections of *A. ludoviciana* from Iraq in 94–101 days. Similarly, the interval between sowing and 50% ear emergence of *A. sterilis* from Israel was 93 days, from Crete 119 days and from France 134–140 days. Averaging all collections of all varieties in both years, the number of days from sowing to 50% ear emergence varied with the country of origin as follows: Israel 93, Iraq 97, Australia 114, Russia 124, Western Europe 129, Britain 135; it tended to be longer the higher the

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latitude. Early-flowering plants had shorter culms than late-flowering plants of the same sort. The duration of ear emergence was longer in *A. ludoviciana* than in *A. fatua*, and still longer in *A. sterilis*, the species with the highest ear number.

Seeds harvested from these and earlier experiments have been kept in pans of watered soil in the glasshouse to test their dormancy and periodicity of germination. In selections of *A. sterilis* with four-seeded spikelets from the 1958 experiment, most of the first and second seeds germinated in the first year after sowing, the second seeds a little later than the first. Third and fourth seeds started later still; few germinated in the first year, and they continued germinating into the third year. In all years germination occurred only in late autumn and winter. This successive germination of seeds in the order in which they are borne in the spikelet is like that found for *A. ludoviciana*, of which first seeds in the spikelet mostly germinate in the first year after sowing and second seeds in the second year. A Greek selection of *A. ludoviciana* showed a similar germination sequence of seeds within the spikelet; it had more three-seeded spikelets than the British sorts, and the third seeds behaved like those of *A. sterilis*, germinating later than the first or second; a few were still dormant after three years. About half the seeds of a selection of *A. barbata* from Crete germinated in the first year, and fewer in the second and third years; some were still dormant after 3 years. The British sorts of wild oats grown as controls behaved as they did in previous glasshouse trials, except that three sorts had less persistent dormancy than before.

The experiment arranged by the International Research Group for Weed Control on the effects of storage conditions on dormancy and viability of seeds of *A. fatua* (*Rep. Rothamst. exp. Sta.* for 1960, p. 103) give similar results in all six European countries that cooperated. The percentage germination of ripe seeds at the time of collection was less than 10%, and except in Denmark increased rapidly in all storage conditions to 50% by December or January, when the seeds were 5–6 months old. Viability changed little during 1 year of storage, except that many seeds died when kept outdoors in winter in Denmark and Germany. In Denmark there was a sharp decrease in viability after only 3 months outdoors. The Danish results also differed from those of other countries in that the maximum germination in 7 months from harvest was only 20% of viable seeds, and dormancy persisted until February or March.

Dormancy of seeds of *A. ludoviciana* induced by high temperature can be broken by soaking them in a solution of gibberellic acid (*Rep. Rothamst. exp. Sta.* for 1959, p. 82). Further work on this in 1960 was frustrated because the moist plastic sponge on which the seeds were set to germinate was found to be contaminated with a laboratory detergent (Byprox) used in washing it. Soaking in a 1% solution of the detergent for 24 hours at temperatures between 7° and 21° C. inhibited germination of *A. ludoviciana* seeds held subsequently at the same temperature. It also inhibited germination of *A. fatua* seeds at 21°, but a few germinated at the lower temperatures. Ungerminated seeds became swollen and the endosperm was liquefied, but the embryos remained viable, and nearly all germinated within a week when the seed coat was cut. Soaking wild oats seeds

in tap water at 21° C. caused a decrease in subsequent germination at the same temperature that was greater the longer the time of soaking, but there was no effect at lower temperatures. Addition of 25 p.p.m. gibberellic acid to the water in which the seeds were soaked overcame the dormancy induced at 21° C. in seeds of *A. ludoviciana*, especially when the period of soaking was long, but had no effect on germination of *A. fatua*. (Thurston.)

Broadbalk weeds

Unusually late sowing of Broadbalk field, on 18 January 1961, decreased winter-germinating *Ranunculus arvensis* (corn buttercup), but contrary to expectation there was a heavy infestation of *Alopecurus myosuroides* (black grass). Previously, late sowing has suppressed *Alopecurus*, because its germination is usually completed by mid-November, and late seedbed cultivations destroy the seedlings (*Rep. Rothamst. exp. Sta.* for 1958, p. 85). The high density of *Alopecurus* plants may be partly attributable to heavy seeding in the previous season. Decreased competition by the delayed growth of wheat in spring allowed the *Alopecurus* plants to grow large, with numerous inflorescences, but this is unlikely to be the whole explanation of the heavy infestation. The wet, nearly water-logged condition of the soil in autumn that prevented sowing of the wheat may also have induced dormancy in *Alopecurus*, and this is being tested in a glasshouse experiment.

Section 3, after fallow in 1960, was as heavily infested with *Alopecurus* in 1961 as the parts of the field after wheat. It is unlikely that the plants on section 3 came from dormant seeds, as normally only about 3% are dormant, and very little *Alopecurus* seeded in 1959. The seed may have spread from neighbouring sections in 1960, but there was no evidence that the infestation on section 3 was denser at the edges next to cropped sections than in the middle. (Thurston.)

Effect of combine-harvesting on distribution of weed seeds

Completed analysis of the samples taken from Broadbalk field in 1958 (*Rep. Rothamst. exp. Sta.* for 1958, p. 84) showed that of the 24 million weed seeds per acre removed from the field, 7 million appeared in the first grade grain, 12 million in the seconds, 4 million in the rubbish separated from the grain and 1¼ million in the baled straw. Only about 1 million (4%) were left on the ground. The distribution of weed species depended on the seed size. Large seeds, e.g., *Vicia sativa* (common vetch), or inflorescences containing seeds, e.g., *Medicago lupulina* (black medic), appeared in the first-grade grain. Smaller seeds, such as *Polygonum aviculare* (knot grass), occurred mainly in the seconds, and very small seeds, such as *Papaver spp.* (poppies), were about equally divided between the rubbish and the fraction shed on the ground. The baler actually picked up some *Stellaria media* (chickweed) and *Medicago* that had not been cut by the combine. (Thurston.)

Interference between weeds and crop

Weed density and crop yield. In 1960 small plots in non-experimental fields of winter wheat were covered with polythene sheets to

protect the weeds when the crops were sprayed with herbicide in spring, the numbers of weed seedlings of different species present on the plots at the time of spraying were counted or estimated, and the yields of wheat at maturity were determined (*Rep. Rothamst. exp. Sta.* for 1960, p. 105). A multiple-regression analysis of the results showed that only where the autumn-germinating weeds *Galium aparine* (cleavers) or *Stellaria media* (chickweed) occurred were there significant regressions of wheat yield on weed density. Grain yield was decreased by 4% and straw yield by 2% by an increase in *Galium* seedlings of 10 per sq. yd. within the range 0–100 per sq. yd. The corresponding effects of increasing density of *Stellaria* were less than 1% (not significant) by 10 additional seedlings per sq. yd. for grain yield and just over 1% for straw yield over a similar density range to that of *Galium*. *Polygonum persicaria* (redshank) also may have had a small effect on straw yield.

Experiments of this sort are difficult to interpret, because weed density and crop yields may both be affected by fertility differences, either directly or indirectly through variation in numbers of weed seeds in the soil caused by difference in weed growth in previous seasons. An alternative method of measuring the dependence of crop yield on weed density is to sow both weed seeds and crop seeds on land previously treated to minimise the natural weed infestation. This was done in 1960 and 1961 on a garden plot that had been fallowed in 1959. Seeds of *Chenopodium album* (fat hen), *Capsella bursa-pastoris* (shepherd's purse) and *Stellaria media* were broadcast on small plots in March 1960 at three rates (including none) in a factorial arrangement. Soon afterwards the plots were combine-drilled with Jufy I spring wheat and fertiliser. They were irrigated in dry periods to encourage germination and growth of the weeds. The treatments were repeated on the same plots in 1961. The numbers of weed plants established on the plots were at best only about half the expectation from laboratory germination tests; in 1960 there were very few *Capsella* plants, and in 1961 few *Chenopodium* plants. In 1960 only *Chenopodium* significantly affected the yield of wheat; the higher rate of sowing, which gave 38 plants per sq. ft., decreased both grain and straw yield by 6%. In 1961 the experiment was spoilt by an attack of "take-all" that made the wheat yields very variable, and the only significant effect, though barely so, was a decrease in straw yield of 12% by *Capsella*. In spite of the large numbers (160 per sq. ft. at the higher rate) of *Stellaria* plants and their vigorous growth, they apparently decreased yield by only about 9%.

Another estimate of the loss of crop caused by weeds was obtained from the experiment on winter and spring varieties of wheat (p. 86). The spring-sown plots had a uniform population of *Polygonum convolvulus* (black bindweed), with an average density of 30 seedlings per sq. ft., which was controlled by spraying with a 2,3,6-TBA/MCPA mixture in early May. At the time of spraying the weeds on parts of each plot were protected with polythene sheet. The yield of straw on these areas was about 10% less than that of the sprayed crop, but the weeds had no effect on grain yield. (Welbank and Witts.)

Competitive effects of Agropyron repens and Agrostis gigantea

The rhizomatous grasses, *Agropyron repens* (couch grass) and *Agrostis gigantea* (common bent), occupy analogous places in the weed flora of the heavy soil at Rothamsted and the light soil at Woburn, respectively. In the Woburn soil *Agrostis* competes more successfully with wheat for nitrogen supplied late in the growing season than for early supplies (*Rep. Rothamst. exp. Sta.* for 1958, p. 88). Nitrogenous fertiliser applied in May increased the yield of wheat growing in competition with *Agrostis* less than an application in early April, because the wheat secured a smaller fraction and *Agrostis* a larger fraction of the late nitrogen supply than of the early. A pot experiment was done in 1961 to find whether competition between wheat and *Agropyron* depends on nitrogen supply in a similar way, to compare the competitive effects of the two grass weeds in Rothamsted and Woburn soils and to test whether the results depend on the size of pot, as it might do if contact with the walls of the pot affects the growth of rhizomes. Pots were harvested at intervals to measure growth in dry weight and provide material for determining nitrogen uptake.

In Woburn soil the effects of competition with *Agrostis* were as before; *Agropyron* also gave similar results in large pots, but in smaller pots caused a greater decrease of wheat yield with early nitrogen applications than with late. In Rothamsted soil the responses of wheat and both grasses to additional nitrogen were less than in Woburn soil. The competitive effects also were different. *Agrostis* decreased wheat yield more with early than with late nitrogen, but the effects of *Agropyron* were the same for both times of nitrogen application. In Woburn soil both grasses had much larger root systems than wheat, but they were smaller in Rothamsted soil, whereas those of wheat were of similar weight in both soils. These results cannot be fully interpreted until the nitrogen estimations and the statistical analyses of the results are completed. (Witts and Welbank.)

Previous work showed that *Agropyron* depresses the growth of crop plants by root competition for mineral nutrients, particularly nitrogen. The intensity of root competition is likely to depend on light intensity, because in low light intensities the requirement of mineral nutrients for growth may be diminished. In a pot experiment to test this, young sugar-beet plants were transplanted into soil with or without established *Agropyron* plants, three rates of nitrogen supply were compared, and pots were grown in the open or under shades that passed about one-third or two-thirds of the incident light.

Without competition, the growth of sugar-beet plants increased with increase in light intensity, but the difference between the intermediate and high intensities was small. Nitrogen also increased growth at the high and intermediate light intensities, but had little effect in the low intensity. Competition with *Agropyron* had no effect on growth of sugar beet in the low light intensity, but without added nitrogen it greatly decreased growth in the higher light intensities. The effects of competition were almost eliminated by increased nitrogen supply, indicating that the competition was for

nitrogen. These results conform with the hypothesis that low light intensity so diminished the requirement of the sugar-beet plants for nitrogen that their growth was unaffected when part of the supply from the soil was removed by *Agropyron*, but a possible alternative explanation is that low light intensity restricted growth of the roots of both sugar beet and *Agropyron* so that they intermingled less. (Welbank.)

Production of toxic substances in soil by decay of plant material

Decay of rhizomes and roots of *Agropyron repens* in poorly aerated soil produces substances toxic to seedlings (*Rep. Rothamst. exp. Sta.* for 1960, p. 106). Experiments were done to test whether other plant species have a similar effect. Rhizomes of *Agropyron* or of *Agrostis* sp. (probably *tenuis*), or stem bases of *Lolium multiflorum* (Italian ryegrass) or *Medicago lupulina* (cultivated trefoil), both of which are used as green-manure crops, were cut up and mixed with an infertile Rothamsted soil, Woburn soil or with a fibrous loam from Kettering. Enough water was added to puddle the soil, and the samples were incubated in stoppered jars for 3-4 weeks at 20° C. The samples were then extracted with water, and the extracts sterilised and assayed for toxicity by measuring their effects on elongation of radicles and hypocotyls of rape seedlings.

Compared with extracts of soil alone, all the extracts of plant materials inhibited radicle elongation, with no significant difference between species. The toxic effects were slightly greater in Kettering loam than in the other soils. Only *Agropyron* extracts consistently inhibited hypocotyl elongation. The other species, particularly *Medicago*, gave extracts that increased hypocotyl growth, and this stimulation was greater for Woburn soil than for the others. Restriction of radicle growth may have enabled the hypocotyls to secure an increased supply of nutrients from the seed. When incubated alone the Kettering soil gave more inhibitory extracts than the others, and probably the organic matter in this soil was itself enough to produce appreciable amounts of inhibitor by anaerobic decomposition. Evidently the production of toxic substances by decay is far from being a specific property of *Agropyron* rhizomes and roots, but the *Agropyron* extracts had effects on hypocotyl growth not shared by the other species tested. (Welbank.)

PHYSIOLOGY OF GROWTH AND YIELD

Old and new varieties of winter and spring wheat

Spring wheat has been so much improved recently that the grain yield of some new varieties approaches that of winter wheat. To find how this happens despite the much longer growth period of autumn than of spring sowings, and how breeding has affected growth so as to increase yield, a field experiment was done in 1960 to compare old and new varieties of winter wheat (Squarehead's Master and Cappelle-Desprez) and of spring wheat (Atle and July I), without or with nitrogenous fertiliser (0.6 cwt. N/acre) applied at the time of spring sowing. Samples were taken at intervals throughout the growing season to measure dry weight, leaf area and other growth

attributes, and nitrogen content. Mean yields of grain in cwt. dry matter per acre were: Cappelle 35, Jufy I 29, Squarehead's Master 21, Atle 20. Nitrogen increased the yields of Cappelle and Jufy I by 6 cwt./acre, and of Atle by 2 cwt./acre, but it decreased the yield of Squarehead's Master by 5 cwt./acre by causing severe lodging. There was also a little lodging in Squarehead's Master without nitrogen.

Until ear emergence the winter varieties had more shoots and greater leaf area and total dry weight than the spring varieties. Cappelle had less leaf area than Squarehead's Master, but Jufy I had more than Atle. Nitrogenous fertiliser increased leaf area. These differences in leaf area were accompanied by differences in the opposite sense in net assimilation rate (E). Thus, during May and June E of the spring varieties greatly exceeded that of the winter varieties, and nitrogen decreased E . However, when the mean values of E in this period were corrected to constant mean leaf area index (L) by a regression of E on L , the differences between varieties in E and the decrease in E by nitrogenous fertiliser all disappeared, except that mean E for the winter varieties remained slightly, though not significantly, below that of the spring varieties, and this if real may represent an age effect. So it is reasonable to assume that the differences in E between varieties and the effect of nitrogen on E were caused by differences in mutual shading of leaves associated with the differences in L , and not by differences in leaf physiology affecting photosynthetic rate.

After ear emergence the spring varieties continued to have smaller total dry weights than the winter varieties, but their ear dry weights were only slightly less, so that their ear : shoot ratios were greater. Total and ear dry weights and ear : shoot ratio were greater for Cappelle than Squarehead's Master and for Jufy I than Atle. There were only small differences between varieties in number of shoots after ear emergence, so high grain yield and dry weight of ears were associated with large ears, especially in Jufy I, which had the fewest shoots. The leaf area present after ear emergence, which produces most of the dry matter in the grain, measured as leaf area duration (D) after the date of 50% ear emergence, was little greater for winter than for spring varieties, and this is the reason for the similarity in their grain yields. The efficiency of the leaves, expressed as the ratio of final grain yield to D , was the same for winter and spring varieties. However, it was greater for Cappelle than Squarehead's Master and for Jufy I than Atle. It is unlikely that the leaves of the new varieties had higher rates of photosynthesis than the old ones at this time, because before ear emergence there was no difference in E except that attributable to differences in leaf area. The explanation of the apparently greater efficiency in grain production of the leaves of Cappelle and Jufy I is presumably that photosynthesis by the ears of these varieties contributed more to grain yield than ears of Squarehead's Master or Atle. Thus, in both winter and spring wheats, as in barley,* the higher grain yield of new varieties was associated with a larger ear : shoot dry weight ratio that was partly attributable to more photosynthesis by the ears. (Watson, Thorne and French.)

* Watson, D. J., Thorne, G. N. & French, S. A. W. (1958). *Ann. Bot. Lond. N.S.*, **22**, 321-352.

Photosynthesis by ears of Proctor and Plumage Archer barleys

In a previous field experiment (*Rep. Rothamst. exp. Sta.* for 1960, p. 98) shading ears decreased the grain size of Proctor and Plumage Archer barleys equally, but decreased the numbers of grains, and hence dry weight per ear, of Proctor more than of Plumage Archer. However, in the field in 1961, as in all previous pot experiments, shading ears decreased the numbers of grains of both varieties equally. Grain size and dry weight of grain per ear of Proctor were decreased slightly more than those of Plumage Archer. Proctor had more ears per acre, and the contribution by ear photosynthesis to yield of grain per acre, as estimated by shading, was 70% greater for Proctor than for Plumage Archer.

The reversal of the varietal difference in ear : shoot dry weight ratio that occurs between ear emergence and maturity was studied in pots (*Rep. Rothamst. exp. Sta.* for 1960, p. 98), where Proctor and Plumage Archer do not differ in yield, but hitherto not in conditions where Proctor shows its usual superiority of yield. In a field experiment done in 1961 Proctor produced 12% more grain than Plumage Archer, and the ear : shoot ratio was again greater for Plumage Archer at emergence but for Proctor at maturity. This reversal occurred whether or not ears were shaded, and was wholly caused by the greater relative growth rate of Proctor ears. Proctor shoots decreased in weight less than Plumage Archer shoots, the opposite of the varietal difference observed in pots. Leaf-area duration after ear emergence and the efficiency of leaves in grain production of shoots with shaded ears were both similar for Proctor and Plumage Archer.

In this field experiment yields of Proctor and Plumage Archer grown with 7-inch or 14-inch spacings of the rows were compared, to test whether the lack of varietal difference in yield in pots was a consequence of the greater light intensity at the base of the plant in pots than in the field. However, Proctor yielded more than Plumage Archer at the wide as well as the close spacing.

The measurements of CO₂ uptake by photosynthesis and loss by respiration of shoots of Proctor and Plumage Archer made with an infra-red gas analyser in 1960 on plants grown in pots (*Rep. Rothamst. exp. Sta.* for 1960, p. 98) were repeated in 1961 on randomly selected shoots of the two varieties growing in adjacent field plots, starting 7 days after the ears began to emerge. Rates per shoot of apparent photosynthesis and respiration of the ears, and of the flag leaf, sheath and peduncle were slightly greater for Plumage Archer than for Proctor. This was because Plumage Archer shoots had larger ears and greater leaf area; rates of apparent photosynthesis of the leaves per dm.² and of respiration per g. dry weight were similar for the two varieties. Rates per shoot of apparent photosynthesis of ears and leaves remained constant until about 3 weeks after ear emergence and fell to zero during the next 2 weeks. (Thorne.)

Effects of drought on crop growth

When a sugar-beet crop suffering from drought is irrigated, even with quantities of water much less than the soil-water deficit, it may for a time grow faster than a continuously irrigated crop, and so

compensate for slow growth during the drought period (*Rep. Rothamst. exp. Sta.* for 1958, p. 79, and for 1959, p. 77). The extent to which a crop can recover from a check to growth caused by drought depends on the severity of the drought (the soil-water deficit), the size of the plants and the weather during the recovery period. Previous experiments have been done in summer, but another was started in August 1960 to see whether recovery from drought can occur in the unfavourable growth conditions of autumn and winter. Seedlings raised in soil blocks were transplanted to the Dutch-light glasshouse and kept free from water stress by irrigation until 8 September. Some plots then continued to be irrigated, and on others water was withheld until 3 November. On some of the unwatered plots water was then given to make up the soil deficit of 1.7 inches; other plots received only $\frac{1}{4}$ inch of water, and still others continued without irrigation. Samples of plants were taken to estimate dry weight, leaf area and water content in October, early and late November 1960 and in early January 1961.

Growth was slow and the leaf area index (L) never exceeded 1.3. By early November, L was decreased by a quarter on plots unwatered for 2 months, but the small decrease in total dry weight was not significant. When water was then given at the higher rate there was nearly complete recovery in L , but the low rate of watering had small and transient effects much less than in previous experiments. Continued drought for 4 months decreased total dry weight by one-third and halved L mainly by decreasing leaf size; leaf number was only slightly affected. Net assimilation rate was not significantly affected.

No further work was possible until June, as the Dutch-light glasshouse was moved to another site, doubled in size and equipped with automatically-metered spray lines. An experiment was started in June and continued until August, to test whether recovery from drought depends on light intensity, by covering parts of the plots with white cotton shades in the period after rewatering when the soil water deficit had reached 3 inches. The results of this experiment are not yet fully analysed. (Orchard.)

Profiles of photosynthetic rate in field crops

A method of studying the profile of photosynthetic rate, i.e., its variation with height in a field crop, based on measurements of the net assimilation rate (E) of sugar-beet seedlings (phytometers) growing in nutrient solution and supported at varying heights within the crop for periods of about one week, was described in *Rep. Rothamst. exp. Sta.* for 1960, p. 97. Results of experiments in 1960 showed that phytometer E was less inside crops than in the atmosphere above, and decreased towards the ground, but remained positive at ground level in all crops between mid-June and September. Near to the top of the crop, the rate of decrease of E with depth was faster in kale than in sugar beet or potatoes, for which it was similar. Results for barley were variable and need to be repeated. The vertical distribution of leaf area index (L) of the crop, determined by layered sampling, showed that E decreased linearly with increase in the logarithm of L of the part of the crop above the phytometer. The decrease was faster for kale than for

the other crops, and slowest for barley. This difference presumably means that less light penetrates through unit L of kale than of the other species. The results agree with the hypothesis* that E decreases less rapidly with increase of L so that maximum crop growth rate occurs at a much higher L for sugar beet than for kale crops, because a difference in spatial arrangement of the leaves causes more uniform illumination throughout the profile in sugar beet than in kale. (Leach.)

Dependence of photosynthesis on growth

More evidence is accumulating to suggest that the rate of photosynthesis of leaves depends on how rapidly photosynthetic products are used in growth of other parts of the plant. Rooted detached leaves are particularly suitable for studying this problem, because they have a relatively small sink for photosynthetic products that can be varied in size experimentally.

Detached primary leaves of dwarf French bean kept with their petioles dipping in nutrient solution produce adventitious roots, and survive for several weeks with little increase in area before becoming senescent. They have a low net assimilation rate (E) of about 10 g./m.²/week throughout their life. Experiments done at various times from March to December showed that E varied little with season, indicating that it is controlled by internal factors. About three-quarters of the dry matter accumulated after a leaf was detached remained in the lamina, and most of the rest passed to the roots. The dry weight of lamina increased from about 2 mg./cm.² at the time of detachment to 6 mg./cm.² after 6 weeks when the leaf was becoming senescent and E began to decrease. When petioles of detached leaves were treated with indolylacetic acid before they were placed in nutrient solution they formed more roots and had a higher E than untreated leaves (*Rep. Rothamst. exp. Sta. for 1960*, p. 102). In experiments in 1961 root growth was increased by raising the temperature of the nutrient solution from about 12° to 24°, near the optimum for root growth. At 24° a larger fraction of the photosynthate passed into the roots, the rate of accumulation of dry matter in the lamina decreased, and E was increased. Similarly, when the size of the vessel containing nutrient solution was increased from 600 ml. to 3 l. the root system grew larger and E was doubled. These results suggest that photosynthetic products, which accumulated in the lamina because their use in growth was restricted, depressed the rate of photosynthesis, and may eventually have caused senescence of the leaf. (Humphries.)

Sugar beet and spinach beet are varieties of *Beta vulgaris* that differ in the size of their storage roots and the amount of sugar they accumulate, but otherwise are very similar. To find whether this difference is associated with different rates of photosynthesis by the leaves, plants of the two varieties were grown in pots and their dry weights, leaf areas and net assimilation rates were determined by sampling on four occasions in June and July. Total dry weight of sugar beet was always greater than that of spinach beet, and the difference increased with time; it was entirely attributable to the

* Watson, D. J. (1958). *Ann. Bot. Lond. N.S.*, **22**, 37-54.

greater dry weight of the root of sugar beet. The leaf areas of the two varieties were similar, and E of sugar beet was therefore greater than of spinach beet in each interval; on the average it was 56% more. There was no obvious difference between the varieties in leaf arrangement that might affect mutual shading, and respiratory loss of dry matter by spinach beet was probably less than by sugar beet because of its smaller root, so the difference in E can be ascribed to lower photosynthetic efficiency of the leaves of spinach beet than of sugar beet. It may be a consequence of the greater use of photosynthetic products by growth and sugar storage of the root of sugar beet, that is, of the more efficient sink for carbohydrate. However, it is also possible, though unlikely, that the larger storage root of sugar beet is a consequence and not the cause of the higher photosynthetic rate of sugar beet. It may be possible to decide between these alternatives by studying the growth of reciprocal grafts between roots and tops of sugar beet and spinach beet. (Thorne.)

Growth on different soils

The study of the physiological basis of variation in yield of sugar beet between different soils (*Rep. Rothamst. exp. Sta.* for 1960, p. 96) was continued and extended in 1961. Experiments were done at six centres with widely contrasting soils, including three of the four used in 1960. As before, the crop was grown with and without nitrogenous fertiliser at each centre, and at Rothamsted and Broom's Barn two dates of sowing were compared. Samples were taken at fortnightly intervals from May to November, to estimate leaf area and the dry weight and water content of the plant parts, and for subsequent analyses of mineral nutrient and sugar contents.

At the centre with the highest yield in 1960, on a silt soil near Holbeach, the yield of dry matter was still higher in 1961, but at the other two centres for which a comparison between years is possible, at Rothamsted and on a calcareous soil near Stamford, it was much lower in 1961, especially without nitrogenous fertiliser. These differences in yield between sites and years were associated with similar differences in leaf-area index, but it is not yet known whether there were also differences in net assimilation rate. It is intended to repeat the work in 1962 at the same centres as in 1961, and then to make a combined analysis of the three years' results. (Goodman.)

Effects of gibberellic acid on the growth of potato and sugar beet

Our interest in gibberellic acid (GA) is mainly in its effects on leaf growth. Potato plants sprayed with solutions of GA produce larger leaves, and for a time correspondingly more dry matter, but the leaves soon become paler, and later their photosynthetic efficiency decreases, so that the final weight may be unaffected, though in a pot experiment in 1960 the yield of total dry weight and of tubers was increased. The onset of the change in colour was not prevented by increased supply of nitrogen (*Rep. Rothamst. exp. Sta.* for 1959, p. 72, and 1960, p. 99).

The 1960 experiment not only tested nitrogen but also whether the effects of GA depend on the supply of phosphorus or potassium. The plants were sprayed twice with GA solution in May. As before,

GA increased the area of leaves on the main axis, but decreased their length of life. Leaf production on the lateral branch of node 9 was decreased by GA, but was increased at higher nodes. GA had no effect on the size of lateral leaves.

Nitrogen decreased the number of leaves on the main axis, increased their size and lengthened the life of the lower leaves, but shortened it at higher nodes. These effects of nitrogen on longevity were enhanced by GA. Nitrogen increased leaf production and longevity on lateral branches. Phosphorus and potassium had little effect on the growth of leaves on the main axis, but increased the size of lateral leaves in the later stages of growth, and phosphorus lengthened their life. There was no interaction of GA with phosphorus or potassium.

Cells were counted in disks of known area cut from leaves 7, 11 and 15. The disks were stored in EDTA solution, and immediately before counting were incubated with pectinase to separate the cells.* The results were obscured by a gradient, probably of temperature, along the glasshouse; GA decreased the number of cells per disk, particularly in the warmer part of the glasshouse. Mean cell size was similar in leaves 7 and 11, but smaller in leaf 15. GA increased cell size in leaves 7 and 11 but not in leaf 15; it also increased cell number per leaf by about 25%, even in leaf 15, which had not expanded when the plants were sprayed. These results show that GA promotes cell division as well as cell extension in intact leaves. Nitrogen increased cell number, and in leaf 15 phosphorus did also. Potassium decreased cell number per leaf but increased cell size.

In 1961 the effect of GA on leaf growth of sugar beet was studied in a pot experiment. Young sugar beet were sprayed with 50 mg. GA/l. or with water on 2, 4 or 6 occasions at weekly intervals. GA increased leaf size but decreased leaf number, and on balance did not change the total leaf area per plant. Consequently, in contrast to the results for potato, there was no effect on the rate of dry-matter production, either immediately after spraying or later. GA increased the length of the main axis, but much less than in normal bolting, and it did not cause flowers to form. It decreased the length of the petioles. (Humphries and French.)

Gibberellic acid is not known to occur in higher plants, but other gibberellins do. The one in potato leaves that promotes the growth of disks cut from etiolated dwarf French bean leaves (*Rep. Rothamst. exp. Sta.* for 1960, p. 101) and presumably controls the expansion of potato leaves was identified as gibberellin A₅ (5·8). The fate of gibberellic acid sprayed on potato plants was further studied. Spraying with a solution of 50 mg. GA/l. just before the 15th leaf expanded, increased the growth of the 15th leaf. Gibberellins in the 15th leaf of sprayed and unsprayed plants were estimated by bioassays of chromatograms of ethyl acetate extracts. Total gibberellins (including GA) were assayed with disks of etiolated French bean leaves, and GA with lettuce hypocotyls, the growth of which is not affected by gibberellin A₅ or the gibberellin from potato leaves (5·8). The 15th leaf of unsprayed plants did not contain GA. The 15th leaf of sprayed plants contained much 1 week after spraying, but the amount decreased to a low value after 3 weeks. Meanwhile, the

* Humphries, E. C. and Wheeler, A. W. (1960). *J. exp. Bot.*, **11**, 81-85.

total gibberellin content increased to four times that in untreated leaves, indicating conversion of GA to a gibberellin, possibly A₅, inactive on lettuce hypocotyls. However, conversion to gibberellin A₅ of all the GA present one week after spraying would not account for the total gibberellin content after 3 weeks, so gibberellins formed from GA in lower leaves were probably transported to the 15th leaf. The ethyl acetate extracts were also used for chlorophyll estimations. The total chlorophyll content of the 15th leaf was increased by GA, but as the sprayed leaves were larger, they had less chlorophyll per unit area than unsprayed leaves, and this accounts for their being a paler green. (Humphries and Wheeler.)

Effects of a growth regulator, CCC

Some quaternary ammonium compounds have growth-regulating properties opposite to those of GA; in particular, they diminish stem extension and produce stunted plants. One compound 2, chloroethyltrimethyl ammonium chloride, also called chlorocholine chloride (CCC), was tested in the 1961 sugar-beet and potato experiments, alone and in combination with GA. CCC is closely related chemically to betaine, which occurs in sugar beet. It was applied to the soil at the rate of 150 or 200 ml. of a 10⁻²M solution per pot.

When applied to sugar beet simultaneously sprayed with GA, CCC had no effect on leaf growth, but decreased the stem elongation caused by GA. CCC on its own increased the rate of leaf production by 20%, but decreased leaf size and total leaf area. It also decreased the small amount of stem extension that occurs in untreated sugar beet, so that the "crowns" were shorter and flatter. However, it increased the length of petioles, again an effect opposite to that of GA. (Humphries and French.)

CCC alone slightly decreased the area and gibberellin content of the 15th leaf of potato plants. In plants also sprayed with GA, CCC increased the area and gibberellin content slightly, but the GA content was unaffected. Thus, CCC apparently increased transport to the 15th leaf of gibberellins, presumably produced from GA in older leaves. It had no effect on chlorophyll content. (Humphries and Wheeler.)

The effect of CCC on leaf expansion was tested by the bean-leaf-disk method of assay for leaf-growth substances. CCC at 10⁻³M did not affect the growth in darkness of disks cut from etiolated leaves, but decreased their greater growth in light. Growth promotion by GA added to the test solution was decreased or wholly suppressed by CCC. Thus, inhibition of growth of bean leaf disks by CCC depended on the presence in the tissues either of endogenous gibberellin, i.e., during growth in light, or of GA supplied from the external solution. Similar results were obtained with the analogous compound bromocholine bromide. (Wheeler.)

The effects of CCC were also tested on tobacco, mustard and radish. The tobacco plants were grown in nutrient solution without CCC, or with CCC present in the solution continuously or in alternate fortnights, starting when the plants had four leaves. In the continuously treated plants CCC decreased the length of leaves 7-20, but increased the length of leaves produced later. The treated plants maintained a rosette habit and did not elongate until about

20 leaves were formed, when the stem extended rapidly in spite of continued treatment with CCC. The discontinuous supply of CCC had less effect on leaf growth, and ceased to inhibit stem elongation after 15 leaves were formed.

The older leaves of plants treated with CCC, which were shorter than those of untreated plants, were also wider and probably thicker, so the total leaf dry weight was unaffected. Total dry weight per plant was decreased by CCC, but the difference was wholly in the stems. Treatment with CCC increased the chlorophyll content of the leaves.

The mustard and radish plants were grown in soil with 0, 75, 150 or 225 ml. per pot of a $10^{-2}M$ solution of CCC. The 75-ml. dose increased the weight of leaves on the main stem, 150 ml. had no effect and 225 ml. decreased it. CCC had no effect on the number of leaves on the main stem, but increased the number and total area of leaves on lateral branches. The smallest dose of CCC more than halved the dry weight of the main stem, and larger doses had a greater effect, but the changes in weight of stem of lateral branches were much smaller.

The most interesting result is that although treatment with CCC had little or no effect on total leaf weight or area of tobacco, and in mustard increased them, it greatly decreased stem weight of both species, so that the leaf-weight ratio and leaf-area ratio were increased. The decrease in dry matter produced, in spite of an increase in total leaf area, may be another example of restricted use of photosynthetic products slowing photosynthesis (p. 90), here because CCC inhibits stem extension, but there may be other explanations.

Radish was affected differently; the dry weights of all parts of the plant, except the hypocotyl, were decreased by CCC. This may be related to the difference in apical dominance between mustard and radish. (Humphries.)