Report for 1958

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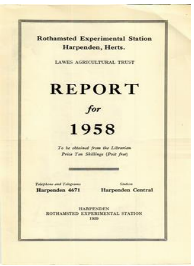

Botany Department

D. J. Watson

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BOTANY DEPARTMENT

D. J. Watson

P. C. Owen resigned in February to take an appointment at Levington Research Station. His work on crop growth in relation to soil water supply was continued by B. Orchard, who joined the department in March.

In September L. H. Fernando returned to Ceylon, after gaining the Ph.D. degree of the University of London.

Dr. Waclawa Potapczyk of the Biochemical Institute, University of Lodz, Poland, who holds a Rockefeller Foundation fellowship, joined the department in October. She is working on kinetin and nucleic acid metabolism, in collaboration with Margaret Holden of the Biochemistry Department.

The Post-Doctorate Fellowship of the National Research Council of Canada awarded to Gillian N. Thorne was extended for three months, and she spent the year in the Botany and Plant Pathology Laboratory of Science Service, Department of Agriculture, in Ottawa, working on plant growth in controlled environments.

Physiology of Leaf Growth

Factors that influence leaf growth, and affect the number, size and longevity of leaves are being studied in the laboratory because variation in yield of crops depends mainly on variation in leaf area. In particular, some substances that are known or are alleged to have growth-promoting properties have been tested on leaves, and an attempt is being made to extract from growing leaves substances that specifically influence leaf expansion.

Effect of gibberellic acid on leaf growth and net assimilation rate

In a previous experiment (p. 242, no. 5.6) when Majestic potato plants were sprayed with gibberellic acid (50 p.p.m. in water) twice with an interval of a week, the area of leaves on the main stem and lateral branches was increased. Net assimilation rate was only slightly decreased by spraying, so that, at the end of the experiment 4 weeks after the second spraying, the sprayed plants had more dry weight than the unsprayed. The additional weight was all in the tubers. However, the leaf area of sprayed plants at this time was decreasing more rapidly than that of the unsprayed, so it was doubtful whether the increase in dry-matter production would have persisted had the plants been allowed to continue growing. This was investigated in 1958, when unsprayed plants were compared with plants sprayed twice with gibberellic acid, and also with others that received four additional sprayings at weekly intervals (six in all) to see whether prolonged spraying had more persistent effects on leaf area and dry-matter production. The spray treatments were tested on plants with a low or a high nitrogen supply. The plants, grown in pots from small sets each with a single eye, were first sprayed when the lower lateral branches on the high-N plants were just beginning to elongate; the low-N plants produced no lateral branches.

At a harvest 3 weeks after spraying began, total dry weight per plant was already increased by gibberellic acid, though not significantly in the low-N plants. As in the previous experiment, the initial increase in dry weight was wholly in stems and leaves, and the weight of tubers was decreased. In the high-N plants spraying decreased the tuber weight to one-quarter of that of the controls, but had a smaller effect on low-N plants. The decrease in tuber weight was much greater than in the previous experiment, although the first harvest was made at a later stage of growth.

At the second harvest, 5 weeks after the first spraying, the dry weight of sprayed plants with the higher nitrogen treatment was about 10 per cent above the controls; all parts of the plant except the roots were increased in weight. In contrast, spraying decreased the dry weights of all parts of the low-N plants.

At the final harvest, 8 weeks after spraying began, high-N plants that had only two sprayings still maintained a greater dry weight than unsprayed plants, but the dry weight of plants sprayed six times was the same as that of the controls. Both spraying treatments decreased the dry weight of low-N plants. These results show that the effectiveness of gibberellic acid depends on both time and frequency of application, as well as on nitrogen status of the plants.

Gibberellic acid increased the areas of leaves both on main axis and lateral branches, especially of low-N plants. At the first harvest the total leaf area of these plants was increased by 40 per cent, and additional sprayings after the first produced no extra increase, though it accentuated the symptoms of nitrogen deficiency. In high-N plants the four additional sprayings after the first two gave a further small increase in leaf area, mainly in terminal leaves of the main axis and on lateral branches.

The number of leaves on the main axis was not affected by gibberellic acid except that, on the high-N plants sprayed six times, small leaves were produced on the terminal inflorescence.

The axillary shoots of the high-N plants were largest at the lower nodes of the main shoot, and were smaller at intermediate nodes than at the upper ones. Spraying with gibberellic acid increased the leaf area of the upper and lower branches, but greatly decreased the area and number of leaves on the branches at nodes 10 and 11. The size of leaves on the main axis was maximal at about node 14, so the restricted growth of the axillary shoots at nodes 10 and 11 may be from competition for nutrients with developing branches below them and expanding leaves above them. If so, this competition was enhanced by gibberellic acid.

The net assimilation rate of unsprayed plants was independent of nitrogen supply. Spraying with gibberellic acid greatly decreased the net assimilation rate of low-N plants, so that in spite of increased leaf area less dry matter was produced. The decrease was smaller in high-N plants and was not significant. (Humphries.)

Effect of ascorbic acid on leaf growth

It has been reported * that ascorbic acid promotes leaf growth and accelerates flowering of some plants, including Chinese cabbage (*Brassica chinensis*). Experiments repeating precisely the conditions in which ascorbic acid was said to be effective failed to confirm the effect. Ascorbic acid solutions freshly prepared every hour were applied to cotton-wool wrapped round the growing point. Other plants were sprayed with ascorbic acid solution. Both methods of application slightly inhibited the growth of the two youngest leaves unfolding at the time of treatment, but had no effect on subsequent leaves or on time of flowering. (Humphries.)

Biological assay of leaf growth-substances

Gibberellic acid (GA) and kinetin (K) affect leaf growth (p. 242, nos. 5.5 and 5.6), and these substances were used to examine the suitability of biological tests for assaying growth substances extracted from leaf tissues. Both GA and K were active at concentrations of $10^{-5}M$ and $10^{-6}M$ in the wheat-coleoptile-section and etiolated-pea-epicotyl-section tests, which have long been used to assay 3-indolylacetic acid (IAA) and related auxins. They both promoted extension growth of wheat coleoptile sections, but less than did IAA. Growth of pea epicotyl sections also was accelerated by GA, but was slightly inhibited by K. In neither test was there any interaction of GA and K; their effects appeared to be additive.

To measure activity in promoting leaf expansion, an assay method based on the growth of leaf tissue is obviously essential, and etiolated primary leaves of 6-day-old " Selected Canadian Wonder " dwarf-bean seedlings grown in darkness at 25° C. were used. Disks 6 mm. in diameter were cut from the leaves in a dim red light, and floated on the test solution containing 1 per cent sucrose, with the adaxial surface in contact with the solution. After 24 hours in darkness at 25° C., the increase in diameter of the disks was measured. This test confirmed that GA and K both accelerate leaf expansion. At concentrations of 10^{-5} or $10^{-6}M$ their effects were less than that caused by fluorescent light of 400 f.c. intensity. The effect of K was eliminated in the presence of light, but that of GA was slightly increased. Light and GA had much smaller effects when the abaxial surface of the disks, instead of the adaxial, was in contact with the solution, presumably because the stomata were blocked. GA was less effective with no sucrose in the solution. Usually a vein formed a diameter of a disk, and IAA (10^{-5} or $10^{-6}M$) caused no expansion in a direction perpendicular to the vein, but increased the length of the vein, and consequently the disks rolled up in the form of cylinders. This effect of IAA in promoting the growth of the veins but not the lamina is well known.

To reduce the variability of the test, the bean seeds were graded by weight before planting. The test was more sensitive to GA with small seeds, which suggests that large seeds supply more GA, or related substances, to the primary leaves, but this has not yet been

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* Chinoy, J. J., Nanda, K. K. & Garg, O. P. (1957). *Physiol. Plant.* **10**, 869.

confirmed by assaying extracts of the seeds. The growth-promoting effect of K appeared to be independent of seed size.

Ascorbic acid, reported by other workers to promote leaf expansion (p. 77), was inactive in the leaf-disk test at a concentration of $10^{-4}M$, and inhibited expansion of the disks at $10^{-3}M$. Carbanilide (1 : 3 diphenylurea, the coconut milk factor of F. C. Steward) slightly increased the growth of the leaf disks and had its maximal effect at $10^{-3}M$. (Wheeler.)

Growth substances extracted from primary leaves and cotyledons of dwarf bean

Dwarf-bean plants were grown in a light intensity of about 950 f.c. from fluorescent tubes, supplemented by red and infra-red radiation from incandescent ballast lamps to prevent stunting. Plants were removed at various stages of growth and their primary leaves extracted with ethyl acetate. The extracts were partitioned with dilute acid or alkali to separate basic and acidic substances, and finally fractionated by paper partition chromatography, using ammoniacal *iso*propanol solvent. The chromatograms were cut into segments which were assayed by the etiolated-dwarf-bean-leaf-disk test. A zone of growth activity with an R_F value similar to that of a marker GA spot occurred consistently on chromatograms of leaf extracts containing acidic substances. The activity of this zone was highest for extracts of primary leaves made at the stage when they were expanding most rapidly. More growth activity was found on chromatograms of an extract of bean leaves grown in light than on those from an extract of a similar number of leaves grown in darkness. Zones of growth activity with a similar R_F value were found also on chromatograms of cotyledon extracts containing acidic substances. These results suggest that GA, or similar substances, is a normal constituent of bean leaves, and that its presence is related to leaf expansion. (Wheeler.)

A method of estimating the number of cells in leaves

The number of cells in a plant tissue can be estimated either by direct counting on cleared preparations under the microscope or by disintegrating the tissue and counting the cells in a suspension on a haemocytometer slide. The usual method of disintegration is to digest the tissue with chromic acid, but this may give misleading results with leaf tissue, because some cells may be completely digested and the estimated number may decrease with time of digestion. A somewhat gentler technique has therefore been developed, in which leaves or leaf disks are incubated with pectinase preparations in the presence of the disodium salt of ethylenediamine-tetracetic acid (EDTA). The EDTA greatly facilitates the separation of leaf cells, possibly by chelating the calcium of the calcium pectate in the middle lamella. The method works well with dwarf-bean and tobacco leaves, but is not applicable to every kind of leaf, e.g., with holly and ivy the lower and upper epidermal cells are separated as sheets of cells, while with leaves of grass or barley no breakdown appears to occur. An investigation of factors affecting cell numbers in leaves of dwarf bean has been started. Primary leaves of plants grown at 20° C. in a 12-hour daily light period each had approximately 3×10^7 cells; complete darkness apparently prevented the last cell division because leaves of plants grown in the dark had only about half this number of cells. (Humphries.)

Mode of action of kinetin and gibberellic acid on leaf expansion

The method of counting free cells in a suspension of leaf-tissue digested with pectinase in presence of EDTA was used to investigate how gibberellic acid and kinetin influence leaf expansion. Cell counts were made on disks of etiolated primary leaves of dwarf bean, treated with GA or K in the same conditions as were used to assay effects on leaf expansion (p. 77). K appeared to increase the numbers of cells in darkness, and to decrease the number in light. The effect of K on cell number was smaller than that of fluorescent light of 400 f.c. intensity. GA had no effect on cell number; implying that it increased leaf expansion solely by increasing the size of cells. (Humphries and Wheeler.)

Growth promotion by pectinase preparations

A pectinase preparation in dilute solution was effective in promoting extension growth of wheat coleoptile and pea epicotyl sections. It was more effective with EDTA at 10^{-3} or $10^{-4}M$. A similar mixture of pectinase and EDTA had only a slight, but significant, effect on expansion of leaf disks. Current theories of the structure of the cell-wall and cell expansion suggest that the growth-promoting effect of pectinase may be attributable to increased plasticity of the cell-wall brought about by breakdown of pectin. (Wheeler.)

GROWTH ANALYSIS

The effect of soil moisture deficit on plant growth

During a prolonged drought period in 1955 the leaf-area index (L) and net assimilation rate (E) of an unirrigated sugar-beet crop at Woburn were both much below those of a crop irrigated to maintain minimal water stress, but after a little rain, much less than the estimated water deficit, the relative leaf growth rate and E were greatly increased and rose above those of the continuously irrigated crop, so that temporarily the unirrigated crop produced dry matter at a greater rate than the irrigated crop (*Rep. Rothamst. exp. Sta. for 1955*, p. 77). An attempt was made to reproduce this effect at Rothamsted in 1957 with a sugar-beet crop protected from rain by a Dutch-light glasshouse, so that the whole water supply was under control (*Rep. Rothamst. exp. Sta. for 1957*, p. 89). Three treatments were compared: (*a*) continuous irrigation, (*b*) drought interrupted by a single large application of water, and (*c*) drought interrupted by frequent small applications. The crop receiving (*a*) had a higher L throughout, and consequently produced a higher yield of dry matter. Immediately after the waterings in treatments (*b*) and (*c*), E was a little higher than for treatment (*a*), but the effect was always much less than that of rainfall after drought in the Woburn field experiment, and the rate of dry-matter production per unit area of crop was always greater for (*a*) than for (*b*) or (*c*).

Another experiment was done in the Dutch-light glasshouse in 1958, comparing the following treatments:

(*a*) *Minimal water stress* maintained by frequent waterings.

(*b*) *Early drought.* The plants were subjected to three drought cycles during June and July, and at the end of each cycle the plots were watered just before permanent wilting point was reached (in the top 12 inches of soil). At the end of the drought period the water deficit was 6 inches. During August and September the plots were watered as for treatment (*a*).

(*c*) *Late drought.* The plots were watered as for (*a*) until the end of June, and then received no water, except for 1 inch applied in late September. The water content of the soil (to 12 inches depth) was constant at about permanent wilting point (14 per cent) during August and early September.

All the plots were watered uniformly until the beginning of June, when the drought periods of treatment (*b*) began. After that, the total amounts of water applied were: (*a*) 14 inches; (*b*) 10 inches; (*c*) 5½ inches. To reduce variability between plants, sugar-beet seedlings were raised in soil blocks and selected for uniformity before planting out in early May. Samples of plants were taken on six occasions between the beginning of July and the end of September.

By the end of July, plants that had suffered the early drought of treatment (*b*) had a slightly lower dry weight than the others, and this was wholly due to a decrease in L, for E was unaffected. However, in the fortnight after watering was resumed at the end of July, E for treatment (*b*) was higher than for the others and L also increased, whereas it decreased for treatment (*a*). Throughout August and September, L of treatment (*c*) fell steadily below that of treatment (*a*), which remained nearly constant. All the effects of drought on L were the result of decreased leaf expansion, because leaf number per plant was unaffected. Watering of the (*c*) plots in September after the prolonged drought period had no detectable effect on E or L. At the final harvest the dry-weight yields for treatments (*a*) and (*b*) were similar, but that for treatment (*c*) was slightly less. Statistical analysis of these results is not yet completed, and the significance of some of the effects mentioned is uncertain.

Thus, there is evidence that watering after the early drought period, but not after the late drought, produced a spurt of growth involving temporary increases in both E and relative leaf-growth rate similar to, but much less than, that observed in the field at Woburn in 1955. The reason for watering after drought in the 1957 and 1958 experiments at Rothamsted producing so much smaller effects than at Woburn is not yet known; it may depend on differences in soil or in seasonal weather. The lack of response to the watering in September of sugar beet previously unwatered since the end of June may be because the roots were then actively absorbing only from lower depths of the soil, and had become almost independent of treatments applied to the surface. (Orchard.)

Measurement of the CO_2 *flux of a field crop*

An attempt is being made by J. L. Monteith, of the Physics Department (see p. 38), to determine the flux of CO_2 into a field crop through photosynthesis in the light, and out of it from respiration in the dark, by measuring continuously the gradient of atmospheric CO_2 concentration immediately above the crop. If the estimates are valid, they should, when integrated over a suitable period, conform with the increase in dry weight of the crop. To test this, samples were taken at intervals from the sugar-beet crop to determine the changes with time in its yield of dry matter. Leaf-area index was also measured, so that the magnitude of the CO_2 flux can be related to the size of the photosynthetic system. The physical and biological measurements agreed well for early periods of growth, but the calculations for the later periods are not complete. (Orchard.)

Measurement of leaf area

An instrument has been developed for measuring the areas of sugar-beet leaves in the range from 10 to 1000 sq. cm. by a scanning method. The leaf is placed against a white background and a light beam, interrupted by a shutter, is made to traverse the background and the leaf by means of a rocking mirror. The mirror is moved forward between each traverse in the direction at right angles to the scanning direction, so that the whole area of the background is scanned once. Pulses of light reflected from the background, but not from the leaf, are perceived and amplified by a photomultiplier, subtracted electronically from the total number of pulses sent out, and the result counted by a scaler. In effect, the instrument is made to count the pulses that are not reflected. A single pulse corresponds to 0·5 sq. cm. of scan.

Pulses which fall on the edge of a leaf can give rise to errors, which have been minimized by making the scanning spot cover approximately half the width of the unit scan in each dimension, and adjusting the instrument to count any pulse which just touches the leaf as fully on the leaf. If the disposition of the pulses with respect to the leaf edge is random, there is a probability of 0·5 that a unit scan falling symmetrically on the boundary will be counted, and this probability will increase as more of the unit scan falls on the leaf and vice versa. Good compensation for the edge effect has been achieved; if the error it causes were appreciable it would cause curvature in the relation of area to counts, but no such curvature was found. This source of error makes the instrument unsuitable for measuring small, divided or narrow leaves.

The standard error of a single determination, based on repeated measurements of test areas between 8 and 384 sq. cm., was 3 per cent of the mean. Leaves that will lie within a rectangle of 50 × 30 cm. can be measured, and can be scanned in 10 seconds. The instrument is suitable for routine use in its present form, but requires careful adjustment and shows instability while warming up. Some of its present defects can be avoided by slight changes in construction, and it is hoped to develop similar instruments suitable for small, dissected and narrow leaves, and possibly for field use. (Orchard.)

Net assimilation rate of cultivated and wild beet

Further examination of data collected in 1956 comparing net assimilation rates (E) of wild sea beet (*Beta vulgaris* subsp. *maritima*)

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and Kleinwanzleben sugar beet (*Rep. Rothamst. exp. Sta. for 1956*, p. 86) showed that, although the wild and cultivated beet had the same E when the leaf area index (L) was near to 1, they differed in E when L was larger. There was an inverse relation between E and L for the three wild beet types tested, similar to that previously found between strains of sugar beet. In a period when mean L for sugar beet was about 2·5, its E was much greater than that of the leafiest wild type, for which L was also about 2·5, but was little different from that of the wild type with the smallest L (about 1·5). This suggests that the development of sugar beet from its wild ancestors by selection and breeding has not affected the intrinsic photosynthetic efficiency of the leaves, but has improved the photosynthetic performance of the plants in another way; it has diminished the effect of mutual interference between leaves so that when they are crowded together their mean efficiency in dry-matter production is not so much impaired. This change is probably related to the form of the plant; the wild-beet plants had a prostrate habit, with leaves overlapping more than in sugar beet, the leaves of which are more nearly upright, so that they shade each other less and tend to receive direct sunlight over a larger fraction of the total leaf surface. If this interpretation is correct, it provides an example of the great importance of the spatial disposition of leaves, as well as their total area, in relation to yield. (Watson and Witts.)

Varietal differences in barley

In a comparison of field crops of Plumage Archer, Proctor and Herta barleys * no differences between the varieties were found up to the time of ear emergence in leaf-area index, total yield of dry matter or net assimilation rate, and after ear emergence, the leaf-area index of Plumage Archer was about the same as that of Proctor and greater than that of Herta. It was therefore concluded that Proctor and Herta produced higher grain yields because their ears photosynthesized more than did those of Plumage Archer. Increased total photosynthesis by the ears could result from an increase in their photosynthetic capacity, in their photosynthetic efficiency or both. Assuming that photosynthetic capacity is correlated with the size and weight of the parts of the ear other than the grain, any increase in it, without change in total dry weight of the crop at ear emergence, implies an increase in the ear : shoot dry-weight ratio. There was evidence of such a difference between varieties in ear : shoot ratio in the field at harvests after ear emergence, but this was complicated by differences in growth of the grain associated with varietal differences in time the ear emerged. To avoid this complication the ear : shoot ratio for the different varieties should be measured not on the same date, but at comparable stages of development and when the weight of grain is negligible, viz., at the time when the ears are beginning to emerge, or at anthesis. Such measurements have now been made on the main stem and first two tillers of plants grown in pot culture.

When ears start to emerge and at anthesis, the ear : shoot dry-weight ratios for Proctor and Herta were consistently slightly less

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

than for Plumage Archer, although at maturity this difference was reversed and the ratio was higher for Herta and Proctor, as in the field experiment. This suggests that the greater dry-matter production by the ears, which seems to be responsible for the superior grain yield of Proctor and Herta, is not attributable to greater photo-synthetic capacity of the ears, though the survival of a higher proportion of shoots of Proctor and Herta than of Plumage Archer to form mature ears may produce more photosynthetic tissue in the ears on unit area of land.

The reversal of the varietal difference in ear : shoot ratio between anthesis and maturity implies that the increment in ear dry weight in this interval per unit dry weight of ear at anthesis was greater for Proctor and Herta than for Plumage Archer. If dry weight at anthesis is a valid measure of the photosynthetic capacity of an ear, this result suggests that ears of Proctor and Herta have a higher photosynthetic efficiency than those of Plumage Archer. (French and Watson.)

Weed Studies

Previous lines of work on weed problems have been continued, and work has been started on the nature and intensity of competition between crop and weeds.

Wild Oats

Survival of seeds under temporary ley and in cultivated land. On plots ploughed in autumn 1957 after three years under grass in the experiment at Rothamsted on survival of seeds of *Avena fatua* in land under temporary ley (*Rep. Rothamst. exp. Sta. for 1956*, p. 80 and *1957*, p. 92) only 1·2 wild oats seedlings per sq. yd. were counted in spring 1958, compared with 3·9 per sq. yd. in 1957 on plots ploughed after two years under grass. This may not indicate a decrease in viable seeds, because grass regenerated on the newly ploughed plots, so that it was difficult to distinguish the wild oats seedlings, and some may have been missed. Also, the grass may have partly suppressed the germination of wild oats. Fortunately, this can be tested in 1959, after the plots ploughed in autumn 1957 are reploughed; any seeds held dormant under the grasses should then germinate.

From soil samples taken from the field in Northamptonshire with a mixed infestation of *A. fatua* and *A. ludoviciana* that has been under ley for 4½ years, wild oats seeds were recovered by washing through sieves in numbers representing over 4 million/acre; there was no apparent change since 1957. The husks of these seeds were so decayed that the species could not be identified. Previous experience indicates that recognizable seeds in this condition and of this age are still viable, and some germinated during the handling of the soil samples. The viability of the remaining seeds will be tested on samples to be taken in 1959.

In the field at Bishop's Stortford where stubble-burning in autumn 1957 stimulated germination of a small part of the popula- of wild oats, mainly *A. fatua* (*Rep. Rothamst. exp. Sta. for 1957*, p. 93), peas were sown after several spring cultivations, but became so thickly infested with wild oats that the crop was cut green for silage before the wild oats shed seed. This treatment greatly decreased the number of wild oats seeds in the soil; in October 1958, the top 6 inches of soil contained 24 seeds/sq. ft., only 3 per cent of the number present a year earlier. Subsoil samples from 10-inch depth had as many seeds as the surface soil. The husks of the remaining seeds were too badly rotted to identify the species; their viability is being tested, and some have already germinated.

Types from other countries. Samples of wild oats were received for identification from widely separated places, and some have been grown to see how they compare with the British ones. They included four types of *A. fatua* from Canada, one of *A. ludoviciana* from Greece and four sorts not found in Britain—*A. sterilis* var. *maxima* from Algeria, *A. sterilis* var. *scabriuscula* from Malta, *A. sterilis* subsp. *trichophylla* var. *calvescens* from Arabia and *A. barbata* from Malta. Seven British types of *A. fatua* and six of *A. ludoviciana* were also grown. Chitted seeds were planted in pots in the glasshouse at the end of December.

The Greek *A. ludoviciana* was less prostrate in the early stages of growth than its British counterpart, but the Canadian *A. fatua* were like the British ones in vegetative growth. *A. barbata* had a very prostrate habit, even after ear emergence. The Arabian variety of *A. sterilis* differed from all the others in having very short stems and many more ears per plant.

Ear emergence of *A. sterilis* began in early April and was completed in all but one of the foreign sorts by the end of the month; in one of the Canadian sorts of *A. fatua* it did not start until mid-May. In the British sorts it occurred between mid-May and early June. The early date for the Mediterranean types probably represents their normal time of flowering—the wild oats seeds from Malta were collected in the field in May, but Canadian wheat-lands are still frozen in April, when our plants grown from Canadian seed were flowering. Canadian conditions have apparently selected types with a short growth period, and this is evidently independent of whether the growth period includes the short days of an English winter or the long days of Canadian summer. The Canadian types of *A. fatua* produced about the same number of seeds as the similar types found in Britain, but many fewer than the commonest British types, which were not represented in the Canadian samples.

Seeds produced by the British and Canadian types of *A. fatua* showed a similar degree of dormancy, with about 10 per cent germination by late November. The germination behaviour of seeds of *A. sterilis* was similar to that of *A. ludoviciana*; most of the first seeds of spikelets could germinate soon after harvest, but second and subsequent seeds had a progressively higher percentage of dormancy and started to germinate later. (Thurston.)

Effect of combine-harvester on distribution of weed seeds

Samples of wheat grain, weed seeds and rubbish were taken from the three delivery spouts of the combine-harvester during harvest of selected plots of Broadbalk field. Samples of the straw and chaff thrown out by the combine on the plots were collected on a cloth drawn behind the machine. On other parts of the plots where straw and chaff were allowed to fall on the ground and were subsequently picked up by a baler in the usual way, samples were taken of the material recovered by the baler. These samples made it possible to estimate the proportions of seeds of different weed species that are bagged up and carted off the field, either as rubbish or with the grain, or removed in the baled straw and, by difference, the proportion that remains on the ground after passage of the baler. The same samples are being used by the Chemistry Department to determine the amount of chaff left behind on the plots. Separation of the weed seeds from the samples is not yet finished.

The samples take no account of weed seeds shed directly on the soil before harvest, and the amount of this is likely to be different for harvest by combine and by binder, because with a combine the crop is cut at a later stage of maturity. Analyses of *Vicia sativa* seeds in the grain fraction, undertaken to see whether grain yield can be recorded with sufficient accuracy as the weight of the grain fraction or whether cleaning or sampling for purity is essential, show that it is not necessarily the plots with the heaviest infestation of *Vicia* that give the highest proportion of *Vicia* seeds in the harvested grain, because the amount of seed shed before harvest also depends on when the *Vicia* plants mature. (Thurston.)

Weeds of Broadbalk

A survey was made as usual of the weeds present on Broadbalk in May and after harvest. A detailed study of the poppies (*Papaver* spp.) in June, when they were flowering and had a few seed-pods, showed that *P. rhoeas* and *P. argemone* were abundant, but no *P. dubium* was found. This agrees with observations in recent years, but conflicts with an earlier report * that though *P. rhoeas* is the commonest poppy " a certain number of other species occur, chiefly *P. dubium*. *P. argemone* is also known to occur occasionally on the field ". *P. dubium* has not been found on Broadbalk or elsewhere on the Rothamsted farm in the past 15 years.

The records for the past 30 years show that the amount of *Alopecurus agrestis* (black bent) present in the crop at harvest tends to increase when the crop is sown early, before about 23 October, whereas sowing at the end of October or in early November maintains the infestation at its previous level, and later November sowing decreases it. This is presumably because *Alopecurus* finishes germinating for the season in about the second week of November, but as yet there are no field data to confirm this. In pans of field soil brought into the glasshouse the species germinates chiefly in autumn.

A special survey was made of Section 1a, where continuous cropping with wheat has been resumed and weeds are controlled by herbicides, to compare with Section 1b which remains in the fallowing cycle, and soil samples were again taken to measure changes in the weed-seed population. The herbicide (CMPP) was especially effective on plots 3 and 5, which receive no nitrogenous fertilizer and are heavily infested with *Vicia sativa* (vetch) and *Medicago lupulina* (black medic). Elimination of competition by these weeds nearly doubled the yield of wheat, but over a period of years

* Brenchley, W. E. & Warington, K. (1930). *J. Ecol.* **18**, 235.

eradication of leguminous weeds may impoverish the soil in nitrogen and make yields decline. (Thurston.)

Competition between crop and weeds

Survey of competitive effects of common weed species. A series of pot experiments is projected to compare the effects of common annual weeds on the growth of crop plants. In the first of these, plants of kale or sugar beet were grown in pots alone or with *Chenopodium album* (fat hen), *Stellaria media* (chickweed) or *Capsella bursa-pastoris* (shepherd's purse). Crop and weed seeds were sown on the same day in May, and the seedlings were thinned to one crop plant and 16 weeds per pot (about 1 per 2·5 sq. in.). Pots were also set up with the same number of weeds but no crop plant, and two rates of nitrogen supply were tested with each combination of crop and weed. At harvest 10–11 weeks after sowing, fresh and dry weights were determined for both crop and weeds, and also the leaf area of the crop.

Of the three weed species, *Chenopodium* decreased crop growth most; its effect on the relative growth rate of sugar beet was three to four times that of *Stellaria* or *Capsella*. Kale was much less susceptible than sugar beet to competition from *Chenopodium* or *Stellaria*, but there was little difference between crops in the effect of *Capsella*. Conversely, kale depressed the growth of weeds more than sugar beet did, and the effects of both crops on *Chenopodium* was less than on *Stellaria* or *Capsella*.

It was hoped that the interactions between weed effects and nitrogen supply would throw light on the causes of competition, but most of these interactions were not statistically significant. Leaf growth of sugar beet was depressed by *Chenopodium* or *Stellaria* more at the higher rate of nitrogen supply, suggesting that competition depended on factors other than nitrogen. The water content of kale leaves was unaffected by weed competition, but that of sugar-beet leaves was decreased by *Stellaria* and still more by *Chenopodium*, so that in spite of liberal watering, there may at times have been competition for water between sugar beet and weeds.

The presence of *Chenopodium* decreased the total nitrogen content of sugar beet to about one-tenth of that of plants without competition; *Stellaria* and *Capsella* approximately halved it, at both rates of nitrogen supply. A positive correlation was found between mean log. total nitrogen content of sugar beet and mean log. dry weight of roots for different treatments within each rate of nitrogen supply, but increased nitrogen without weed competitors *decreased* the root dry weight, although it increased the total nitrogen content of the plants. A possible interpretation is that the effects of competition were the result of changes in root growth which determined the differences in nitrogen uptake, and were not wholly due to depletion in nitrogen supply. Similar results could not be got with kale, because the roots could not be separated from weed roots in the mixed cultures. The total yields of dry matter per pot in mixed cultures of kale or sugar beet with weeds was increased by higher nitrogen supply relatively more than those of crops or weeds growing alone. This indicates that some direct competition for nitrogen was involved. (Welbank.)

Competitive effects of Agropyron repens. A more detailed study was made of the effects of *Agropyron repens* (couch grass) on the growth of young sugar-beet plants, and their dependence on nitrogen and potassium supply. If *Agropyron* competes for these nutrients and so lowers the amounts available to the crop, the effects on the crop should be less when the supply of nutrients is high than when it is deficient. To test this, sugar-beet seedlings at the four-leaf stage were transferred without disturbing their roots into pot cultures of *Agropyron* grown from rhizome sections of a single clone, and comparable cultures of sugar beet alone or *Agropyron* alone were also set up. All three types of culture were then treated with all combinations of three rates of nitrogen and three rates of potassium supply. Plants were harvested at the time of transplanting, and 2 weeks later; fresh and dry weights and leaf areas were determined for growth analysis, and nitrogen, phosphorus and potassium contents are being determined. Statistical analysis of the results are not yet complete; preliminary inspection suggests that competition for nitrogen or potassium affected the test plants only when the other nutrient was present in excess. (Welbank.)

Production of toxic substances by Agropyron repens. Since Osvald * showed that extracts of dried roots and rhizomes of *Agropyron repens* (couch grass) inhibit germination of rape and oats, many people have held that the competitive effects of *Agropyron* partly come from toxic substances produced in the soil. However, in experiments at Cambridge no evidence of toxic action was found. Inhibiting effects of dried and ground material may have little bearing on production of toxins *in vivo*, and experiments were therefore done to test directly whether living roots and rhizomes produce substances that inhibit germination and growth.

Wheat, barley, kale and tomato plants were grown in nutrient solutions, and during the experimental period were transferred on alternate days from this solution either to a leachate of *Agropyron* roots and rhizomes, or to distilled water as control. The leachates were prepared from *Agropyron* plants grown in nutrient solution by placing the plants with their roots and rhizomes in a shallow tank of distilled water, after washing to remove nutrient solution.

The leachate had no effect on wheat or barley after treatment for 3 weeks, and after 4 weeks it *increased* the dry weight and leaf area of kale and tomato plants. This was thought to come from leaching of nutrients from the grass roots and rhizomes, and in subsequent experiments nutrient solution was added both to the leachate as prepared previously and to the distilled water controls in the same concentration, and the solutions were renewed daily. After treatment for 4 weeks, there were no significant effects on tomato, but again the leachate increased dry weight and leaf area of kale. The explanation of this growth-promoting action is not known. Certainly no evidence of any toxic effect was found in these conditions, but in soil a toxin might be produced by action of micro-organisms on exudate from *Agropyron* roots. To test this, leachate prepared as above was watered daily on to pot cultures of kale plants in a fertile or an infertile Rothamsted soil, or in Woburn soil. After 4 weeks, the leachate had no significant

* OSVALD, H. (1947). *Växtodling*, **2**, 288–303.

effects; the dry weight of plants grown in the poor Rothamsted soil was slightly decreased, but not in the others.

In another series of experiments, when chitted seeds of turnip or rape were placed on filter-paper held in contact with attached *Agropyron* roots kept moist with distilled water, the length of the radicle of turnip was increased by 30 per cent, and of rape by 15 per cent, compared with those of control seeds in similar conditions without *Agropyron* roots. Radicle growth might be stimulated by diffusion of ions out of the free space of the roots, or by secretion of elaborated organic compounds. The fact that replacement of water around the roots by a nutrient solution decreased the stimulation of radicle growth favours the former explanation, but chemical and spectrographic tests have so far shown only that sodium concentration was higher in the controls. *Agropyron* roots slightly inhibited hypocotyl growth, which appeared to increase with increasing strength of the nutrient solution.

The absence of any marked inhibitory effect of *Agropyron* roots or root leachates in these experiments indicates that the secretion of a toxin probably plays little part in the competitive effect of this species. Experiments are being made to see whether a toxin is produced when *Agropyron* decays in the soil. (Welbank.)

Effect of competition with Agrostis gigantea *on response of wheat to nitrogenous fertilizer.* Observations on a field experiment on winter wheat at Woburn in 1956 suggested that late nitrogenous top-dressing was less effective than early because an infestation of *Agrostis gigantea* harmed the crop more when the nitrogen supply was delayed. A pot experiment in 1957 did not wholly support this explanation (*Rep. Rothamst. exp. Sta. for 1957*, p. 93). Another pot experiment in 1958 compared spring wheat grown alone in Woburn soil with wheat grown in presence of *Agrostis* raised from rhizome cuttings, without nitrogenous fertilizer, or with nitrogen applied at two rates at the time of sowing or 7 weeks later. Comparable cultures of *Agrostis* without wheat were also grown. The main object was to test whether the interaction of weed competition and nitrogen supply on wheat can be explained wholly in terms of change in nitrogen uptake by the wheat, but this is not yet possible because the nitrogen analyses are unfinished.

The yield results suggest that *Agrostis* appropriated a greater proportion of nitrogen applied late to a mixed culture than nitrogen applied early, and so depleted the nitrogen supply to wheat more. In support of this, late nitrogen increased growth of *Agrostis* rhizomes more, though not shoots, than early nitrogen. Without *Agrostis*, the response in yield of wheat grain to nitrogen applied at sowing was about three times that of the later application; this effect of time of application was much greater than was found in the field at Woburn. In spite of this, the loss of wheat yield caused by competition with *Agrostis* was as great when nitrogen was given late as when given early, and the percentage loss was much greater with the late nitrogen application. Loss of yield from competition with *Agrostis* was greatly decreased by increase in early nitrogen application, as would be expected if *Agrostis* affected the wheat by depriving it of part of its nitrogen supply. On the other hand, the loss was independent of the rate of late nitrogen application, possibly because any effect of additional nitrogen in making good depletion of the nitrogen supply by *Agrostis* was counteracted by increased growth and competition of the *Agrostis* rhizomes. (Witts.)

PHYSIOLOGICAL EFFECTS OF VIRUS INFECTION

Effect of infection with yellow-net virus on sugar content of sugar-beet leaves

Analyses of sugar-beet leaves from experiments done in the Plant Pathology Department (p. 99 below) showed that infection with yellow-net virus decreased the content of both sucrose and reducing sugar per cent of dry matter, especially in leaves that had well-developed yellow-net symptoms. This effect is the opposite of that produced by infection with beet yellows virus. (French.)