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D. J. Watson

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BOTANY DEPARTMENT

D. J. WATSON

Gillian N. Thorne returned from Ottawa, where she spent fifteen months as a Post-Doctorate Fellow of the National Research Council of Canada. Dr. Waclawa Maciejewska-Potapczyk left at the end of August to visit other research institutes before returning to Poland. Miss A. V. Delap of East Malling Research Station came in May to spend six months in the department, and G. J. Leach, who holds a post-graduate scholarship from the Ministry of Agriculture, Fisheries and Food, joined us in October.

Joan M. Thurston was invited to speak at the meeting of the International Research Group for Weed Control at Stuttgart in March, and was asked to identify wild oats from the participating countries. She also attended the German Weed Control Conference that followed the international meeting. E. C. Humphries and D. J. Watson went to the IXth International Botanical Congress at Montreal and visited plant-physiological laboratories in Canada and U.S.A.

A new glasshouse for work on weeds, a covered floor for preparing soil for pot-culture experiment and a store for pots and other equipment were completed in October. Other additions were two thermostatically-controlled cabinets with artificial lighting for growing uniform test plants.

PHYSIOLOGY OF GROWTH

Much of the laboratory work was concerned with the physiology of leaf expansion, because previous work showed the importance of leaf area as a determinant of the yield of field crops. In particular, work on gibberellic acid (GA) has continued, both because it affects leaf size when applied externally to plants and because there is evidence that a gibberellin-like substance is a normal constituent of leaves and controls their growth. Effects of GA and other growth substances were studied in growing tissues other than leaves. Changes in phosphorus compounds and related enzymes were studied with the help of Dr. Potapczyk, a specialist in this subject. The new growth cabinets were used to find the best form of lighting for the controlled environment rooms being equipped in the West Building. This work showed some unexpected effects of light quality on growth, which were further studied.

Interaction of gibberellic acid and nitrogen supply

Previous work (*Rep. Rothamst. exp. Sta.* for 1958, p. 75) showed that spraying potato plants with solutions of GA increased their leaf area. Plants with a high initial nitrogen supply showed at first a corresponding increase in dry matter production, but later the photosynthetic efficiency of the leaves, measured by net assimilation rate (*E*), was depressed, and the final yield was similar to that of unsprayed plants. From the outset spraying with GA decreased the dry weight and *E* of plants poorly supplied with N.

Analysis of material from the 1958 experiment showed that spraying did not affect nitrogen uptake, so that increase in leaf area was accompanied by a decrease in nitrogen content per unit area of leaf and per cent of dry matter in the high-N plants whose dry weight was increased by spraying. There was little change with time in N per unit area of leaves of low-N plants, but there was a steady fall in high-N plants, so that ultimately leaves of sprayed high-N plants had nitrogen contents similar to those of unsprayed low-N plants. These results, and the chlorosis and accelerated senescence of leaves of sprayed plants, suggested that GA induced a deficiency of N that ultimately became severe enough to injure the photosynthetic mechanism.

If the decrease in *E* of plants sprayed with GA is caused by acute N deficiency, continuing to supply additional N should prevent or delay its onset and maintain the initial gain in dry-matter production. To test this, potato plants grown in pots with high-N supply, sprayed as previously with 50 p.p.m. GA in aqueous solution 2 or 6 times at weekly intervals, and unsprayed controls, were given additional nitrogen, either as ammonium nitrate applied to the soil or as urea solution sprayed on the leaves twice weekly during the latter part of the growth period; additional P and K was also supplied to all pots. As before, GA at first increased dry weight, but later the increase did not persist even in plants that received the extra sustained N supply. Leaf area was much increased by GA, but *E* was equally decreased by GA whether or not the additional N was given. The nitrogen contents of the plants have still to be determined, so it is affected leaf nitrogen content, but the results do not support the hypothesis that GA decreases *E* because it induces nitrogen deficiency. (Humphries and French.)

Leaf-growth substances

The procedure for assaying leaf-growth substances in plant extracts (*Rep. Rothamst. exp. Sta.* for 1958, p. 77) was modified and the red light previously used was replaced by a dim green light, produced by a filter that transmits mainly in the range 500–570 m μ . The difference in growth between disks of etiolated primary leaves of dwarf French bean kept in green light for 15 minutes and disks kept in darkness was only just detectable.

The disks grow less when floated with the abaxial instead of the adaxial surface in contact with the test solution. Similarly, vaseline smeared on the abaxial surface inhibited growth more than on the adaxial surface. As the abaxial surface of primary leaves of dwarf bean has more than seven times as many stomata as the adaxial surface, the solution or vaseline probably decreased growth by blocking the stomata and interfering with gas exchange. In support of this, orientation on the test solution affects the growth of bean-leaf disks much more than disks cut from the first foliage leaves of radish, which have fewer than twice as many stomata on the abaxial surface as on the adaxial surface.

The presence in extracts of cotyledons or primary leaves of dwarf French bean seedlings of an acidic leaf-growth promoting substance that moves on paper chromatograms at the same rate as GA was reported last year (*Rep. Rothamst. exp. Sta.* for 1958, p. 78). The

amounts of this substance in plants grown in a controlled environment at 25° C. were measured. Extracts made from cotyledons and leaves taken at intervals were assayed by the etiolated-bean-leaf-disk test, calibrated with serial dilutions of GA solution. The amount of the growth substance in the cotyledons increased to a maximum after 4 days' growth, whether in light or dark. In plants grown in light the maximum content in the primary leaves occurred later than in the cotyledons, and coincided with the time of maximum growth rate of the primary leaves. In darkness, the primary leaves did not expand and the growth substance did not accumulate in them. The correlation between content of leaf-growth substance and growth rate of the primary leaves suggests that the substance causes leaf growth. No neutral or basic substances that promoted leaf expansion were found in extracts of primary leaves.

The higher sensitivity to GA of disks cut from etiolated primary leaves of plants grown from lighter seeds, reported last year, prompted an examination of the leaf-growth-substance content of seeds of different weight grades, germinated for 1 or 3 days at 25° C. No differences in leaf-growth-substance content were found, but dry weight, leaf area and height were all greater in plants grown from the heavier seeds. The leaf-growth substance in cotyledons of dwarf bean disappeared when the seeds were washed for 24 hours in tap-water, and plants grown from these seeds were smaller than plants from seeds soaked by the standard procedure for only 1 hour before planting. Hence part of the leaf-growth substance that controls the growth of primary leaves may come from the cotyledons. (Wheeler.)

Mode of action of gibberellic acid, kinetin and light on leaf expansion

The method of estimating the number of cells in leaf tissue by digesting it with pectinase and the disodium salt of ethylenediamine-tetra-acetic acid (EDTA) to separate the cells so that they can be counted (*Rep. Rothamst. exp. Sta. for 1958, p. 78*) was further used to determine whether effects of GA, Kn (kinetin) and light on expansion of disks of etiolated bean leaf are attributable to changes in cell division or in cell extension (5.4).

GA and Kn increased cell size both in light and darkness; light decreased the effect of Kn but greatly increased that of GA. GA increased cell number only in darkness, and had no effect in light, whereas Kn had no effect in the dark but in the light decreased cell division, and this offset the increase in cell size. Consequently, leaf expansion was increased by Kn only in darkness, and GA increased it in the dark but still more in the light. Illumination increased leaf expansion partly by increasing cell number, but mainly by increasing cell size. The interactions of light with externally applied GA and Kn gave no clear evidence that light acts by influencing concentrations of GA or Kn in the leaf. (Humphries and Wheeler.)

Effects of light quality on plant growth

When the controlled environment cabinets were completed, tests were made to find whether fluorescent-tube lighting needs to be supplemented in the red, infra-red region by tungsten incandescent

lamps to give normal growth with the species we use. Kale, sugar beet, barley, tobacco, potato and radish plants were grown in a 16-hour photoperiod at 20° C. under white fluorescent tubes alone, or with varying proportions of additional incandescent light. The light intensity at 2 feet below the fluorescent tubes, measured by a selenium photocell, was 1,450 f.c.; it was not much increased by the incandescent light. However, the total radiation was increased from 6 mW./cm.² with the fluorescent tubes alone to 12 mW./cm.² with the full additional incandescent light.

After 33 days the dry weight of tobacco was increased by additional incandescent light, those of barley, sugar beet and potato were decreased, and those of kale and radish were unchanged. The total leaf area per plant was affected similarly to dry weight, except that the leaf area of sugar beet was unaltered, whereas that of kale was decreased. The incandescent light increased stem extension of potato, kale and tobacco, and decreased shoot number and leaf number of barley.

Similar tests were done with tall and dwarf varieties of garden pea (*Pisum sativum*), broad bean (*Vicia faba*) and French bean (*Phaseolus vulgaris*), and with runner bean (*Phaseolus multiflorus*); in these tests light intensity was also varied. The supplementary incandescent lighting usually increased weight and height, but those of tall pea and tall broad-bean and height of runner bean were unaffected, and weight and height of dwarf broad bean were decreased. Dry weight decreased with lower light intensity, but height was unaffected. Evidently, to obtain optimal growth the form of lighting must be adjusted to the species or even variety of plant.

The area of the primary leaves of the French and runner bean plants was unaffected by the incandescent light or by variation in light intensity. However, the first trifoliolate leaves of the French and runner beans were larger on plants that had incandescent light, possibly because increased internode extension under incandescent lighting brought the trifoliolate leaves closer to the lights. (Humphries and Wheeler.)

Experiments were done to find whether the increased extension of dwarf-bean stems caused by supplementary incandescent light is associated with changes in growth-substance content. The mean height of dwarf French-bean plants after 12 days' growth in fluorescent light (720 f.c.) was 180 mm.; with additional incandescent light it was 326 mm. Most of this increase occurred in the three internodes above the epicotyl. Extracts of these internodes were separated on chromatograms, and zones corresponding to GA and indolylacetic acid marker spots were assayed by the etiolated-bean-leaf-disk test and the wheat-coleoptile test respectively. The longer internodes of the plants that received additional incandescent light had a higher auxin content than those grown in fluorescent light alone, and their gibberellin content was apparently also higher, but not significantly.

The incandescent light did not affect the area of the primary leaves of 7-day-old plants, nor did it alter the amounts of growth substance in the leaves. This work will be repeated with the larger numbers of plants and higher light intensities possible in the new controlled environment cabinets.

No difference was found between dwarf bean plants grown in darkness and plants grown in light in amounts of auxin or gibberellin-like growth substance in hypocotyls or epicotyls, although the etiolated stems were more than twice as long as those of plants grown in light. (Wheeler.)

Formation of adventitious roots

When hypocotyls of young dwarf French-bean plants, severed a few cm. below the cotyledonary node, are kept with their base in nutrient solution, adventitious roots form on the hypocotyl and sometimes on the epicotyl. This process was greatly stimulated when the hypocotyls were pretreated for some hours with a solution of indolylacetic acid (IAA) or naphthalene acetic acid (NAA) before transfer to the culture solution. Similarly, adventitious roots formed at the cut end of petioles of detached dwarf French bean leaves kept in nutrient solution, and pretreatment with IAA or NAA caused roots to form along the length of the petiole and not only at or near the cut end. Addition of 0.5–1 p.p.m. kinetin (Kn) to the nutrient solution inhibited root growth in untreated hypocotyls or petioles, and greatly restricted it in hypocotyls or petioles pretreated with IAA. Although Kn prevented the differentiation of roots, it did not inhibit cell division; on the contrary, it induced the formation of a white callus 8–10 mm. in diameter at the cut end of the petiole. When the Kn treatment was maintained for several weeks the callus continued to grow, but after Kn was withheld roots began to emerge from the callus tissue. Little or no callus formed at the end of hypocotyls treated with Kn, but more was formed at cut surfaces of epicotyls. Pretreatment with NAA increased the dry weight of hypocotyls. Subsequent Kn treatment also increased the dry weight of untreated hypocotyls by up to 25%, but had no effect after pretreatment with NAA. (Humphries.)

Stimulating cell division and root formation in hypocotyls by treatment with NAA greatly increased total phosphorus content, e.g., from 200 to 500 g. P/hypocotyl, but Kn had no effect on total P content. Orthophosphate, acid-soluble bound P, lipid P, ribonucleic acid P (RNAP) and deoxyribonucleic acid P (DNAP), were all increased by pretreatment with NAA without Kn, but after Kn treatment, when root formation was inhibited, NAA increased only acid-soluble bound P and DNAP. Kn treatment increased acid-soluble bound P, lipid P (in absence of NAA) and DNAP, but decreased orthophosphate P and RNAP, i.e., it had opposite effects on DNAP and RNAP. The results suggest that Kn increased the rate at which orthophosphate was used. The large increase in RNAP caused by pretreatment with NAA may be associated with increased cell number. The total phosphorus content per cent of fresh weight of callus tissue formed on petioles by treatment with Kn was only 50–70% of that of the petiole tissue. (Humphries and Potapczyk.)

Kinetin and indolylacetic acid increased the activities of ribonuclease and deoxyribonuclease in extracts of dwarf French bean hypocotyls; gibberellic acid had no such effect (5.5). (Potapczyk.)

The effect of boron on formation of adventitious roots by severed hypocotyls of dwarf French bean (*Rep. Rothamst. exp. Sta. for 1957*, p. 84) varied with the quality of the light in which the plants

were grown. Hypocotyls from plants grown in light from fluorescent tubes alone, supplied with a nutrient solution without boron, produced about three times the weight of roots as when additional incandescent light was given, whereas when boron was supplied additional incandescent light nearly doubled the weight of roots. (Humphries.)

Phosphorus compounds in plant tumours

Crown-gall tumours produced by inoculating stems of *Datura stramonium* with *Agrobacterium tumefaciens* contain more phosphorus than normal stem tissue. The increase in total P is made up of increases in the amount of acid-soluble P, lipid P, ribonucleic acid P and deoxyribonucleic acid P. The activities of ribonuclease, deoxyribonuclease and glycerophosphatase were all considerably higher in tumours than in normal stems (5.6). These changes are similar to those found in some animal tumours. (Potapczyk.)

GROWTH ANALYSIS

Effect of soil water deficit on plant growth

In the Irrigation Experiment at Woburn (*Rep. Rothamst. exp. Sta.* for 1955, p. 77), when prolonged drought was broken by a little rain, sugar beet sometimes showed a spurt of growth. When plants on un-irrigated plots with a water deficit of 6 inches received less than 1 inch of rain, they temporarily had a higher relative leaf growth rate and net assimilation rate, and for a short period produced more dry matter, than the much larger irrigated plants that had never suffered from water stress. This effect has been reproduced in a sugar-beet crop grown on plots under a Dutch-light structure with the whole water supply under control, after two relatively unsuccessful attempts. (*Rep. Rothamst. exp. Sta.* for 1957, p. 89, 1958, p. 79). Its magnitude probably depends on the size of the plants when subjected to drought, the severity of the water stress and possibly on the prevailing weather.

Sugar-beet seedlings raised in soil blocks were transplanted to the glasshouse in early May, and received uniform watering (4.8 inches) until the beginning of June. The following treatments, similar to those used in 1958, were then applied to different replicated plots:

- (a) *Minimal water stress*, maintained by frequent watering.
- (b) *Early drought*. The plants were subjected to one drought cycle, compared with three in 1958. No water was given from 2 June until 30 June, when the water content throughout the top 12 inches of soil had fallen to permanent wilting point, and the deficit was $4\frac{1}{2}$ inches; $\frac{1}{2}$ inch of water was then applied, and water was again withheld for a fortnight, during which the deficit increased to $8\frac{1}{2}$ inches. Sufficient water was then applied in the next fortnight to restore the soil-water content to field capacity, and from late July onwards, the plot was watered as for (a).
- (c) *Late drought*. Water was supplied as for (a) until 25 June, and then no more was given.

The total amounts of water applied from the beginning of June to mid-September were: (a) 17.4 inches; (b) 14.0 inches; (c) 3.5 inches.

By the end of June, plants receiving treatment (b) had only half as much leaf area and two-thirds as much dry weight as the fully watered plants. In the period immediately after applying $\frac{1}{2}$ inch of water at the beginning of July, their net assimilation rate and relative leaf-growth rate increased to about double those of the fully watered plants, and this difference persisted during the next 14-day period while the soil water content returned to field capacity. The dry-matter increment during July was slightly, though not significantly, greater for treatment (b) than for the others. These results closely parallel those found in the field at Woburn in 1955. By the end of August dry-weight yield and leaf-area index were the same for treatments (a) and (b).

Treatment (c) had no detectable effect until early August, when the plants had less area and weight of leaves than those of treatment (a). At the final harvest in late September treatment (c) had decreased the total dry matter yield by only 9%, and its effect was nearly all on the leaves; the small difference in root dry weight between treatments (a) and (c) was not significant. This result suggests that, provided the sugar-beet crop has a full water supply during its establishment and early growth, irrigation in the later stages of growth is unlikely to be effective.

Drought and subsequent watering affected leaf area per plant mainly by affecting leaf expansion. After the plots of treatment (b) were brought back to field capacity in July the plants for a short time had more leaves than those on other plots, and at the end of the growth period there were fewer leaves per plant with treatment (c) than with treatment (a) or (b), but these differences in leaf number were small compared with those in leaf size.

Although there was much more sunshine in 1959 than in 1958, the dry weight yield was nearly the same in both years; a higher mean net assimilation rate in 1959 was offset by a lower leaf-area index. (Orchard.)

Measurement of leaf area

The scanning planimeter (*Rep. Rothamst. exp. Sta. for 1958, p. 81*) was used for routine leaf-area measurements for a full season. It proved reliable, as well as being quick and easy to operate, and gives results comparable to those obtained by more laborious methods. A planimeter based on the same principle, but adapted to measure areas of long, narrow leaves, like those of cereals and grasses, is being designed. (Orchard.)

Varietal differences in yield of barley and wheat

Previous work suggested that Proctor and Herta barleys give higher grain yields than the older variety Plumage Archer because their ears photosynthesise more. The greater photosynthesis by ears of Proctor and Herta cannot be attributed to relatively greater amounts of ear tissue; on the contrary, a pot experiment in 1958 showed that the ear : shoot dry-weight ratio at ear emergence was smaller for Proctor and Herta than for Plumage Archer, although

this difference was subsequently reversed by greater growth of the grains of Proctor and Herta (*Rep. Rothamst. exp. Sta.* for 1958, p. 82). The experiment was repeated with Proctor and Plumage Archer in 1959, but some ears were covered with opaque paper shades to prevent them photosynthesising, and samples of shaded and unshaded ears were taken at intervals between ear emergence and maturity. As before, the ear : shoot dry-weight ratio of Proctor was less at emergence and greater at maturity than that of Plumage Archer, but this was true for shaded as well as unshaded ears, showing that the reversal cannot be attributed solely to a difference between varieties in amount of photosynthesis by the ears.

Shaded and unshaded ears of Proctor both grew faster than those of Plumage Archer, and this was associated with a slightly greater loss in dry weight between ear emergence and maturity from shoots of Proctor than of Plumage Archer. Proctor ears may grow more rapidly because translocation from the shoots is greater. Leaves of Proctor survived longer than those of Plumage Archer, so that leaf-area duration between emergence and maturity was greater for Proctor, though not enough to account for the greater increase in ear dry weight. In this experiment, therefore, leaves of Proctor appeared to be more efficient in dry-matter production after ear emergence than those of Plumage Archer; no evidence of this was found previously. The experiment was unsatisfactory because the size and yield of grains and the effects of shading ears were all much smaller than usual, probably because the plants ripened prematurely in the exceptionally high glasshouse temperatures. Another variety, Brant, a Canadian six-rowed barley adapted to a short, hot growing season, was included in the experiment and was not adversely affected, but yielded as well as in previous pot experiments in Canada. Shading ears of Brant decreased their dry weight by 30%; this is more than for two-rowed barleys, presumably because the six-rowed ears are larger and so photosynthesise more, relative to leaves and stems.

Photosynthesis by ears during the period 4–5 weeks after emergence was measured directly with an infra-red gas analyser. In 18 comparisons between shoots cut from adjacent field plots of Proctor and Plumage Archer, apparent photosynthesis per ear did not differ significantly between varieties. Respiration rate per unit dry weight, measured at night, was similar for the two varieties, so respiration rate per ear was greater for the heavier ears of Plumage Archer. Consequently, true photosynthesis per ear was greater for Proctor. Apparent photosynthesis per unit surface area of ear, also, was greater for Proctor because it has smaller ears than Plumage Archer; the mean total assimilating surface of Proctor ears, including awns, was about 70% of that of the Plumage Archer ears. This confirms the conclusion reached previously for other reasons that Proctor ears have a higher net photosynthetic efficiency than Plumage Archer ears, and implies that the contribution to total grain yield made by photosynthesis in the ear is greater for Proctor because it produces more, though smaller, ears than Plumage Archer.

No differences in total shoot dry weight or in ear : shoot ratio were found between the spring wheats Fylgia I and Koga II,

although in the field Koga II has shorter straw and higher grain yield than Fylgia I. Comparisons between shaded and unshaded ears showed that in both varieties photosynthesis in the ears contributed about 20% of their dry weight. (Thorne.)

The nature and effects of competition within a crop

As is well known to exhibitors at agricultural shows, plants in a field crop are smaller than they would be if grown in isolation, because they compete with each other for factors that influence their growth. Increase in density of plant populations produces smaller individual plants, so that final yield per acre is nearly independent of variation in plant number over a wide range. Conversely, in thin patches of a crop, or at the edges where the plants are without neighbours on one side, the plants grow larger; "edge-effects" are often obvious in field experiments where the plots are separated by paths.

An experiment on competition in winter wheat sought the stage when competition becomes effective, what changes it induces in the plants and what environmental factors are involved in the competition. Plots were arranged with 9 rows spaced at the normal 7 inches, separated by single rows with 21-inch spacing; one set of plots was drilled with rows running east to west, and another with rows running north to south, to find whether growth of edge-rows was affected by differences in exposure to sunlight. Growth measurements were made throughout the season, and the results await analysis by the electronic computer. (French, Watson and Witts.)

Photosynthesis of leaves at different levels in a crop

A previous experiment, which measured the effects of removing increasing proportions of the foliage of plants in a kale crop on the dry weight increment in the following fortnight (*Rep. Rothamst. exp. Sta.* for 1957, p. 91) showed that the upper, younger leaves were much more effective in dry-matter production than the lower leaves. The four uppermost leaves out of an average of 11 per plant, together representing 30% of the total leaf area, produced 66% of the total dry-weight increment, and their net assimilation rate (E) was five times that of the four lowest leaves. If the vertical gradient in photosynthetic efficiency resulted from shading of the lower leaves, the difference between upper and lower leaves should be less when leaf area index (L) is smaller, and this was tested by removing alternate plants from some plots so as to halve L . The experiment was not precise enough to detect differences in effects of defoliation between thinned and unthinned plots, but the results suggested that decreasing L had similar effects on E of leaves at all levels, i.e., it did not much affect the gradient in E .

The experiment was therefore repeated with more replicates and a design expected to give more accurate estimates of dry-matter increment. Unfortunately, the results show some unexplained anomalies, but again the vertical gradient was no less on the plots with the smaller L .

E of sugar beet depends less on L than does E of kale, possibly because the morphology of the sugar-beet plant ensures more uniform illumination of the whole foliage with less severe shading of

the lower leaves than in kale. If this is correct, differences in E between upper and lower leaves should be smaller in sugar beet than in kale. However, an experiment similar to those on kale, but without the thinning treatment to vary L , showed gradients in E very like those found for kale; the 8 youngest leaves of sugar-beet plants with a mean of 23 leaves, representing 19% of the total leaf area, contributed 53% of the dry-matter increment, and E of these young leaves was about six times that of the 8 oldest leaves.

These results suggested that the gradient in E between the upper, young leaves and the lower, old leaves might reflect differences in age rather than in illumination, but direct measurements with an infra-red gas analyser made on detached leaves showed no consistent differences in rate of photosynthesis between leaves of different ages. (French, Thorne, Watson and Witts.)

WEED STUDIES

Wild oats

Survival of seeds under temporary ley. The decline in numbers of seeds of *Avena fatua* able to germinate after an increasing period under temporary ley in the experiment at Rothamsted (*Rep. Rothamst. exp. Sta.* for 1956, p. 80, 1957, p. 92, and 1958, p. 83) continued in 1959; on plots ploughed in Autumn 1958 after 4 years under grass only 0.6 seedlings/sq. yd. appeared, compared with 1.2/sq. yd. in 1958 on plots ploughed after 3 years. Although the decrease from 28.5 per sq. yd. at the beginning of the experiment to 0.6 per sq. yd. after 4 years under ley is big enough to be agriculturally useful, there are still about 2,500 viable seeds per acre, and ploughing up and cropping at this stage without control measures against wild oats would soon restore the original infestation. In this experiment, each ploughed-up plot is reploughed at the end of its first year and kept under observation for a further year. The seedlings found in the second season have remained nearly constant at about 1/sq. yd. for 1, 2 and 3 years under grass, suggesting that there may be a residue of heavily-dormant seeds that retain their viability longer than those that are easily induced to germinate.

Soil samples taken in spring from the field in Northamptonshire that has a mixed infestation of *A. fatua* and *A. ludoviciana* and has been under ley for 5½ years showed no significant decrease in numbers of apparently viable seeds since the previous year. The field still has nearly 5 million seeds/acre, and the number is not decreasing, unlike the lighter infestation at Rothamsted. To check that the seeds counted after recovery by washing on sieves are viable, germination tests on another set of soil samples are in progress in the glasshouse.

Wild oats from other countries. The germination behaviour of seeds of *A. sterilis* from Algeria, Malta, Greece and Arabia was studied. As with *A. ludoviciana*, the second and subsequent seeds of a spikelet were progressively more dormant and tended to germinate later than the first seed. Some seeds of Algerian *A. sterilis* took 4 years to germinate in pans in the glasshouse. The only British wild oats to stay dormant so long in these conditions were two selections of *A. ludoviciana*, type ID (probably var. *typica* sub. var. *hibernans* Malzew).

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A. barbata from Malta had a germination pattern similar to that of *A. sterilis* and *A. ludoviciana*, with 50% non-dormant seeds, and no germination between February and August. In this species the successive seeds, like those of *A. fatua*, are not distinguishable, as they are shed separately and each has an abscission scar.

As arranged at the meeting of the International Research Group for Weed Control at Stuttgart, samples of wild oats seeds were received for identification; 289 samples came from seven European countries. *A. fatua* predominated, and came from all countries. *A. ludoviciana* was only in samples from central and southern France, and the one sample of *A. barbata* came from the south of France. No other species were present. Different types of *A. fatua* vary in their geographical distribution; a sort with grey glabrous seeds and short hairs at the callus was characteristic of Scandinavia, and also occurred in samples from Holland but only rarely from Belgium, France or Germany; the type commonest in Britain, fA, was also abundant in France, Holland and Belgium but infrequent in Scandinavia. There is an odd discontinuity in the distribution of *A. ludoviciana*; it occurs in England and the southern half of France, but not in northern France. This may be because it is a recent chance introduction into England (it is thought to have arrived here in French wheat imported during the 1914–18 War) or because the winters in England are milder than in northern France.

Effect of gibberellic acid on germination. As gibberellic acid increases germination of seeds of some other species, its effect was tested on seeds of *A. ludoviciana*. First seeds of the spikelets were soaked for 24 hours at room temperature either in tap-water, with or without subsequent pricking of the seed coats with a needle, or in gibberellic acid solution (50 p.p.m.) and then put to germinate in incubators at different temperatures. At 7° C. 95% or more of the seeds germinated irrespective of treatment, but at higher temperatures more pricked than unpricked seeds germinated, and gibberellic acid treatment was nearly as effective as pricking in breaking temperature-induced dormancy, e.g., at 27° C. only 10% of unpricked seeds germinated, but pricking or treatment with gibberellic acid gave 50% germination. Gibberellic acid solution was less effective when the seeds were soaked in it for less than 20 hours; 25 p.p.m. were as effective as 50 p.p.m., but lower concentrations had less effect. (Thurston.)

Other weed species

A test set up 3 years ago has shown that seeds of corn marigold (*Chrysanthemum segetum*) germinate mainly in the period August to March, and not during the summer; 93% of seeds have now germinated, and a few seedlings continue to appear.

Seedlings of fat hen (*Chenopodium album*) and orache (*Atriplex patula*) are easily confused, but observations on seeds germinated in the glasshouse show that they can be distinguished by the colour of the backs of the cotyledons at emergence—mauve in *C. album* and green in *A. patula*. Seeds of *A. patula* germinated only in April and May, but *C. album* germinated throughout the summer until August,

though most seedlings appeared in spring. Only 40% of seeds of *A. patula* and 65% of *C. album* germinated in the first year. (Thurston.)

Weeds of Broadbalk

At the suggestion of F. T. Last (Insecticides and Fungicides Department), the records of occurrence of the semi-parasitic plant *Bartsia odontites* on Broadbalk were examined to compare with his observations on *Striga* attacking sorghum in the Sudan. Like *Striga*, *Bartsia* was less abundant on plots that receive nitrogenous fertiliser than where no nitrogen is given, probably because of increased competition from the crop rather than any direct effect of nitrogenous fertiliser on germination or establishment of *Bartsia* seedlings. *Bartsia* was slightly more abundant in the first wheat crop after fallow than in subsequent crops, and this suggests that germination may be stimulated by presence of the crop, but the crop is not essential because *Bartsia* seeds will germinate in isolation on filter-paper or in soil.

Soil samples were again taken from Section 1a of Broadbalk, which has reverted to continuous wheat with weed control by herbicidal sprays, and Section 1b, which continues in the fallow cycle without herbicides, to measure changes in the weed-seed population. Although the counts are not yet complete, three successive years of herbicide treatment have clearly lowered the numbers of dicotyledonous weed-seeds, but some species, including *Alchemilla arvensis*, *Papaver* spp. and *Veronica arvensis*, are still more abundant on Section 1a than on 1b. (Thurston.)

Competition between crop and weeds

Weed density and crop yield. Experiments were started to measure the losses of crop yield caused by different weed species and how they depend on the density of the weed population. Such information may make it possible to apply control measures more rationally, by deciding from knowledge of the nature and density of an infestation whether or not the increase of crop yield to be expected from eradicating the weeds would justify the cost.

In the first experiment on two fields of spring wheat, 90 small plots were selected so that their weed floras represented a wide range of densities of common weeds; the species present included *Atriplex patula* (orache), *Chenopodium album* (fat hen), *Polygonum convolvulus* (black bindweed), *P. aviculare* (knotgrass) and *Stellaria media* (chickweed). Another 20 plots were selected in a field of winter wheat infested with *Sinapis arvensis* (charlock), *Papaver rhoeas* (poppy) and *Ranunculus repens* (creeping buttercup). Each plot was halved, and one half chosen at random was covered with polyethylene sheet to protect it from herbicide when the whole field was sprayed. The uncovered, sprayed, half-plots acted as controls for the covered halves and the difference in crop yield between them measured the effect of the weed controlled by the spray.

The density of each of the common weed species on each plot was estimated by inspection at the time of spraying, and on about half the covered plots the seedlings were counted on sample areas, so that the density ratings could be calibrated in terms of plant

numbers. The crop on each plot was cut by hand just before the field was fit for combining, threshed and the weights of grain and straw determined. Partial regressions of decrease in yield on the density of each species are being calculated on the electronic computer, but inspection of the data suggests that the effects of the weeds may be small, possibly because of the unusually dry season. (Welbank.)

Survey of competitive effects of common weed species

The series of experiments to compare the effects of common annual weeds on the growth of crop plants (*Rep. Rothamst. exp. Sta.* for 1958, p. 86) was continued. Single plants of kale or wheat were grown in pots alone or with *Chenopodium album*, *Polygonum aviculare*, *P. persicaria* or *Atriplex patula*. There were 16 weed plants per pot, except with *Atriplex*, which germinated poorly, and pots were also planted with weeds alone. Two rates of nitrogen supply were tested. The above-ground parts were harvested after 8 weeks; the roots of crop and weeds could not be separated.

Chenopodium and the two *Polygonum* species affected crop plants similarly, but *Atriplex* had less effect, probably because of its lower density per pot. With low N supply, the weeds decreased leaf area and dry weight of both kale and wheat by about 40%. With high N supply all weeds had slightly less effect on kale than with low N supply, but had a much greater effect on wheat, decreasing leaf area and weight by 60%. Weeds usually affected stems less than leaves, except that with high N supply *Chenopodium* decreased stem dry weight of wheat more than leaf weight, so that in presence of *Chenopodium* the weight of wheat stems was less with high N than with low N supply. Competition with kale decreased the weights of weeds more than competition with wheat, and the effects of crop on weeds were similar at both rates of N supply.

The results suggest that, for kale, competition with weeds for nitrogen was important, but for wheat it was subsidiary to some other factor. Why *Chenopodium* behaved differently from the *Polygonum* species in its effect on wheat stems is not clear. The difference was associated with lower shoot number and leaf nitrogen content in wheat plants grown with *Chenopodium*. Shading may have been greater with *Chenopodium* than with the other weeds, and this may have decreased the capacity of the wheat plants to assimilate nitrogen. (Welbank.)

Competitive effects of Agropyron repens (couch grass)

The results of an experiment done in 1958 to find whether the harmful effects of *Agropyron repens* on crops can be explained by competition for nutrients in the soil (*Rep. Rothamst. exp. Sta.* for 1958, p. 87) were analysed. Young sugar beet transplanted singly into pots in which *Agropyron* was already growing, or into similar pots without *Agropyron*, received all combinations of three rates of nitrogen application and three rates of potash. Pots of *Agropyron* without sugar beet were set up with the same treatments to measure the effects of nutrient supply on the grass. The plants were harvested after 2 weeks, fresh and dry weights and leaf areas were

recorded, and the dried plant materials were analysed for N, P and K.

The relative growth rate of the sugar beet was increased by N and K treatment and decreased by competition with *Agropyron*. The mean response to N, but not to K, was greater with competition than without. Similarly, the effects of N on relative leaf growth rate and on percentage dry matter of leaves, stems and roots were all increased by competition, but those of K were not. Thus the yield data alone indicate that there was competition between sugar beet and *Agropyron* for N but not for K.

However, competition with *Agropyron* decreased uptake of both N and K by sugar beet; the effect on N uptake was the greater, and the decreases in both N and K were largest at the lowest rates of nutrient supply. All the effects of treatments on growth, including those of competition, could be related to differences in N and K uptake rates. Apparently competition was acting solely through its effects on these rates, with competition for N having more effect than competition for K. There was evidence, however, that competition may decrease uptake of a given nutrient in other ways than by diminishing the amount of it in the soil, e.g., by depleting another nutrient that interacts with it. (Welbank.)

Production of toxic substances by Agropyron repens

Previous work gave no support to the suggestion that the harmful effects of *Agropyron repens* on crops is partly caused by toxic substances secreted by the living roots or rhizomes (*Rep. Rothamst. exp. Sta.* for 1958, p. 87). The possibility that toxin production occurs during decay of *Agropyron* residues in the soil has now been tested.

Fresh roots and rhizomes were cut up and mixed with 40 parts by weight of Woburn soil to 1 part of dry weight of plant material. Water was added in varying amounts to give differences in oxygenation and the mixtures were incubated at 20° C. Soil alone was used as control. After 15 and 22 days the mixtures were extracted with water, making a total of 50 ml./g. of dried plant material, and the extracts clarified and sterilised by filtration and the pH adjusted to 5.8. Toxicity was tested by placing germinated rape seed in the extracts, and measuring radicle and hypocotyl lengths after 3 days. Germination tests also were done with rape.

Incubation with poor oxygenation (high water content) produced extracts highly inhibitory to extension growth of rape; radicle elongation was approximately halved by extracts of root preparations, and decreased to about one-third by rhizome preparations; hypocotyls were less affected. After 22 days' incubation, extracts were more toxic than after 15 days. One of the most potent rhizome-extracts lost its effect when diluted 16 times. Germination tests gave variable results, though many extracts were obviously inhibitory.

To check that toxicity was not caused by some soil mineral such as manganese dissolving at the low pH of many of the plant-soil mixtures, plant material was incubated with only a small inoculum of soil. It gave an extract nearly as toxic as when the large amount of soil was used. However, soil alone incubated with citrate buffer

at pH 5.1 was also slightly toxic, so it is still not clear whether acidity is responsible for the effect.

Extracts from preparations with better oxygenation (lower water content) during incubation had little or no effect on seedling growth.

Field observations suggest that the amounts of root and rhizomes present in land heavily infested with *Agropyron* are enough to affect crop growth by toxin production when they decay in suitable conditions, but there is no reason to suppose that this effect is specific to *Agropyron*, for other workers have found that extracts of other plant residues incubated with soil inhibit germination and respiration of tobacco. (Welbank.)