



## BOTANY DEPARTMENT

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The department is largely concerned with plant physiology, seeking to understand the machinery responsible for plant growth that ultimately determines crop yields. Earlier studies of field crops attempted to correlate yields with climatic features, but pioneer work here showed that, in addition to final weighings, observations during the growth of the crop are required.

Growth analysis applied to many field crops here showed that the main difference between varieties is not in net assimilation rate. The techniques used required the interval between observations to be of the order of weeks to allow significant changes in growth conditions; further, the variability of our climate makes these changes in large part unpredictable. With such information, only generalisations encompassing relatively large variations could be formulated. To obtain more precise information, the growth of plants needs to be studied in controlled environments, which we now have and use to study some aspects of the growth of sugar beet and potatoes. Also, techniques are being developed, using radioactive isotopes, to measure individual metabolic processes such as photosynthesis, respiration and translocation in field crops. The use of very small amounts of radioactivity still permits a precision greater than that achievable by conventional chemical analysis, even for short periods of measurement. Initial experiments included studies with cereal and potato crops. The aim is to analyse further the conclusions reached by methods of growth analysis and to provide plant breeders with new criteria of selection for plant performance.

An alternative approach attempts to modify the growth of existing varieties by chemical treatments. Previous studies with growth retardants applied to cereals and potatoes have given promising but inconsistent results; more information is needed about their mode of action and new substances with potential use on arable crops are sought.

The department traditionally studies weed population of the classical experiments, but recent research has concentrated more on the life history of weed species difficult to kill with herbicides, e.g. perennial grass weeds, and less on weed population.

### Plant growth and environmental factors

**Effects of temperature and radiation at different stages of growth of sugar beet.** This experiment was described in last year's report (p. 97), but results were then incomplete. In it, sugar-beet plants growing outdoors were transferred for four weeks during April, June or August to growth rooms set at day and night temperatures corresponding to the expected mean temperature outdoors or 4°C warmer or cooler than this. Half the plants at each temperature received 740 J cm<sup>-2</sup> of visible radiation during a 16-hour photo-period (a total radiation equivalent to a fine August day), and half 370 J cm<sup>-2</sup>. After treatment, the plants were returned outdoors to complete their growth. Growth analyses and sugar estimations were made on samples of plants taken at the beginning and end of each treatment period and at intervals until the plants were harvested in September.

Plant growth was not affected by halving the daily radiation during the four weeks in April because the plants had barely emerged from the soil by the end of the treatment period; but halving it during June or August, when the plants were 8–12 and 20–24 weeks old respectively, decreased net assimilation rates (*E*) by 25%. However, in August, the

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decreased  $E$  in dim light was compensated by delayed leaf senescence, so that plant weights hardly differed at the end of this period. Only plants given different light intensities during June differed in weight at the end of treatment (45 g compared with 28 g dry weight) but neither the number nor area of the leaves was altered. The difference in plant weight at the end of the treatment disappeared soon after the plants were returned outdoors. Thus, the control plants apparently increased  $E$  compared with the treated plants.

The effect of temperature on growth depended on the period of treatment. Plants at the warmest temperature in April emerged soonest and grew fastest, weighing, at the end of treatment, 67 mg compared with 12 and 3 mg for plants grown at the normal and cooler temperatures. Treatment during June, when plants had ten leaves, 3.6 dm<sup>2</sup> of leaf area and weighed 1.9 g dry, resulted at the end of treatment in plants weighing 57, 37 and 21 g for warmer, normal and cooler temperatures respectively. Warmth increased the rate at which leaves were produced and expanded so that at the end of treatment, plants from the warmer conditions had a mean leaf area of 38 dm<sup>2</sup> (21 leaves), compared with 22 dm<sup>2</sup> (18 leaves) and 10 dm<sup>2</sup> (15 leaves) from the normal and cooler conditions respectively. Unfortunately the actual outdoor June temperatures exceeded those expected and were in fact nearer to the 'warm' temperature conditions within the growth rooms, not the 'normal' temperature as intended.

At harvest in September, plants grown in warmer, normal and cooler temperatures in April weighed 339, 263 and 247 g respectively (roots 232, 184 and 162 g) and those treated during June, 276, 216 and 162 g (roots 170, 129 and 101 g). Plants grown continuously outdoors weighed 285 g and the roots 181 g.

The differences in plant weights in September were caused more by differences in growth after treatment than growth during treatment, and more to changes in leaf area duration ( $D$ ) than in  $E$ . Values of  $D$  for the period after treatment for plants grown in warmer, normal and cooler conditions in April were 7.2, 6.0 and 5.6 m<sup>2</sup> weeks ( $\pm 0.28$ ) respectively and for  $E$  73, 78 and 80 g m<sup>-2</sup> wk<sup>-1</sup> ( $\pm 3.6$ ).

The differences in  $D$  arose partly because warmth increased the rate at which leaves were produced during the treatment periods and this advantage was retained throughout later growth outdoors. But warmth at these times also modified the morphogenesis of developing leaves so that sizes to which they eventually grew, some 4–6 weeks later, were 40% greater than leaves produced under normal or cool temperatures.

Both warmth and smaller daily radiation during August decreased sugar per cent fresh weight in the roots at the end of treatment, mainly by increasing the water content of the roots. However, at the September harvest the difference had disappeared. (Milford and Thorne)

**Effect of late season conditions on yield and sugar content.** Cold nights followed by bright days towards the end of growth are necessary and commonly thought to 'ripen' the crop and increase the sugar content of the roots. This idea was not confirmed by the experiment described above, or in a similar experiment (Thorne, Ford and Watson, *Annals of Botany* (1967) **31**, 71–101), when mature plants were little affected by large changes in temperature and radiation. The effect of late season conditions was re-examined using an inbred line of beet grown in larger containers to ensure that growth was not limited by soil volume or nutrient supply. Plants were subjected to all combinations of day temperatures 12.5° and 18.5°C, night temperatures 8.0° and 14.0°C and daily visible radiations of 320 J cm<sup>-2</sup> and 640 J cm<sup>-2</sup> per 12-hour day for the final four weeks of growth in September.

Outdoor conditions at this time of year approximate to a day temperature of 15.5°C, night temperature 11.0°C and daily visible radiation of 475 J cm<sup>-2</sup> per 12-hour day.

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The plants were grown outdoors until September and when put into the growth rooms weighed 96 g dry and had 34 leaves with an area of 34.5 dm<sup>2</sup>.

The warmer day or night temperature produced quantitatively similar effects on growth. The number of leaves was increased from 38 to 43, leaf area was increased from 37 to 40 dm<sup>2</sup> and plant moisture content increased from 4.5 to 5.1 g water per g of dry matter, but neither the dry weight of the whole plant, nor its parts, was affected. Doubling the amount of daily radiation increased final plant dry weight from 168 to 191 g mainly because it increased root weight from 80 to 97 g, but it decreased the moisture contents of the tops and left leaf development unaltered. Sugar concentrations within the roots were unaffected by the daily radiation but were increased from 15.4 to 15.9% fresh weight by cooler days and from 14.8 to 16.3% fresh weight by cooler nights. These changes were wholly attributable to changes in the water content of the roots, sugar per cent dry matter increasing with warmer day and night temperatures. The yield of sugar was consequently only marginally increased from 62 to 67 g by warmer day or night temperatures but significantly increased from 58 to 71 g by doubling the daily radiation. A general conclusion from both experiments is that the sugar concentration of the root may be related to factors internal to the root as well as to the photosynthetic activity of the leaves of the mature plant. (Milford and Thorne)

**Effect of seedling treatment on growth and yield of sugar beet.** This experiment gave inconclusive results in 1970 and was repeated.

Sugar-beet seeds, variety Klein E, were sown in Japanese paper-pots containing sterilised potting compost on 13 April and placed in controlled environment rooms at either 20° or 25°C with 16-hour photoperiod, 430 J cm<sup>-2</sup>. They were transferred on 5 May to an unheated glasshouse and transplanted into the field on 10/11 May. The growth of the transplants was compared with that of seed drilled in the normal way on 2 April and thinned to the same spacing during the latter half of May.

Plants raised at 25°C were larger initially than those raised at 20°C or directly drilled in the field, but by the middle of June those raised at 20°C became the largest and remained so subsequently. At the final harvest in October, the roots of plants raised at 20°C were 17% larger in fresh weight (51.2 tonnes/ha) than the drilled plants (43.7 tonnes/ha) and those raised at 25°C were 10% larger (47.7 tonnes/ha). A greater leaf area, leaf area duration and net assimilation rate of the leaves of the transplants all contributed to their greater root weight.

The experiment also tested the effect of 'Ethrel' (2-chloroethyl phosphonic acid) on the growth of sugar beet, the object being to slow top growth so that a greater proportion of photosynthate from the leaf might be transferred to the root. Unfortunately by an error, twice as much was applied as intended, and the effect in mid-July, when the leaf canopy covered the ground, was to hasten the senescence of leaves receiving the spray. This effect was greater on the drilled plants than transplants. By the beginning of September there were 20–30% more leaves on sprayed plants, and the new leaves were smaller and their net assimilation rate slightly greater than the others. The 'Ethrel' spray decreased the root yield of transplants least; the decrease was for 20°C plants 8%, for 25°C 9% and for drilled plants 21%. (Humphries)

**Effect of defoliation on the growth of sugar beet.** In an experiment in 1968 removing the individual leaves of sugar beet two weeks after each leaf attained maximum area increased new leaf area added and net assimilation rate, but decreased root weight, suggesting that the respiratory loss from the later formed leaves exceeds their photosynthetic contributions.

The experiment was repeated using Klein E plants raised in growth cabinets in 16-hour photoperiod at 20° or 25°C. A further treatment in which leaves 6–20 were retained,

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all others being removed, was included because previous work suggested that these leaves were the greatest contributors to the accumulation of dry matter in the sugar-beet root. Whereas removing all leaves after a period at maximum leaf area decreased root dry weight by 33%, retaining leaves 6–20 increased root dry weight by 15% compared to controls. A full analysis of the results is not yet completed. (Humphries)

**Effect of temperature on grain growth in wheat.** Warmth (i.e. 20° compared with 15°C) during grain growth of wheat caused the ears to grow faster initially. Photosynthesis of the flag leaf, and so probably the total supply of carbohydrate, was unaffected. Warmth presumably increased the amount of carbohydrate that moved to the ear from the rest of the plant. Warmth also hastened senescence of the leaves, ultimately decreasing the carbohydrate supply so that the final ear weight was less at 20° than at 15°C (*Rothamsted Report for 1968*, Part 1, 92; for 1970, Part 1, 94). The present experiment was designed to test whether increased translocation to the ear was caused by the warmer temperature of the developing grains or by an effect on the whole plant. Wheat plants, variety Kolibri, were grown outdoors and seven days after anthesis were transferred to controlled environment rooms with visible radiation of 674 J cm<sup>-2</sup> during a 16-hour day and a temperature of either 15° or 20°C. In each room 18 pots had the ears uncovered or in perspex boxes so that the temperatures around the ears and the rest of the plant could be controlled independently. The control treatment showed that enclosing the ears in a perspex box without change of temperature had no effect.

As previously, when plants and ears were both at 20°C initially ears grew faster and stems more slowly than when plants were at 15°C. Later the ears grew more slowly because leaves died sooner and the final ear weight was 15% less. Net photosynthesis of flag leaves was unaffected by temperature but warmth decreased the net uptake of CO<sub>2</sub> by the stems in the light and increased their respiration in the dark. Hence the smaller stem weight in the warm was probably a consequence of greater respiration by the stems and of greater translocation to the ear. Warming the ear only, but not the rest of the plant, had similar but smaller effects. After 14 days of treatment warm ears weighed about 2 g (10%) more than cool ones and their stems about 2 g less. CO<sub>2</sub> exchange of flag leaves and stems was unaffected by ear temperature indicating that increased translocation to warm ears accounted for the decrease in stem weight.

Later, warm ears lost their green colour sooner than cool ones and leaves on shoots with warmed ears died sooner, so that warm ears had a smaller supply of carbohydrate and hence 8% less final dry weight.

Movement of carbohydrate to the developing grain was increased by warming ears; it seemed to be increased still more by warming the whole plant but this was not proven. Leaves died sooner when the whole shoot, rather than the ears alone, was warmed. This effect of sink capacity on the longevity of leaves supplying the sink has been observed before, but the cause is uncertain. (Thorne)

**Root growth of wheat varieties.** Previous experiments studied the effects of fertilisers and of shading on the root growth of barley and compared root growth of winter wheat, spring wheat and oats. This year's experiment was the second studying the root development of six winter wheat varieties, made in collaboration with Dr. F. G. H. Lupton of the Plant Breeding Institute, Cambridge, who measured top growth and grain yield and Dr. F. B. Ellis of the A.R.C. Letcombe Laboratory, who studied nutrient absorbing activity.

Three dwarf winter wheat selections bred by the Plant Breeding Institute, TL 363/30, TL 365a/34, TL 365a/37 (all derived from Norin 10) and the varieties Cappelle Desprez, Maris Ranger and Maris Nimrod were sown at 202 kg/ha on 22 October 1970. The new variety Maris Nimrod replaced TL 365a/25 grown last year which proved susceptible to

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leaf diseases. Before sowing, 40 kg/ha N, 87 kg/ha P<sub>2</sub>O<sub>5</sub>, 176 kg/ha K<sub>2</sub>O and 100 kg/ha MgO were applied and 126 kg/ha N on 2 April 1971.

On 15 December 1970, 16 March 1971, 28 April 1971 and 15 June 1971, the tops were cut at ground level from sample areas 0.5 m wide across the middle six rows of each plot, for Dr. Lupton to make growth measurements. From within the same sampling areas, soil cores approximately 7 cm diameter were taken, four within the rows and four within the inter-row spaces to determine root length and dry weight by techniques described earlier (*Rothamsted Report for 1966*, 84 and *for 1967*, 94). At the first sampling the cores were 50 cm deep, at the second 75 cm and at later ones 100 cm. The cores were cut into layers at 15 cm then every 10 cm to 75 cm and at 100 cm, correcting for soil compaction as described in *Rothamsted Report for 1970*, Part 1, 96. Cores from rows and from spaces were kept separate on 15 December and 16 March, but were bulked together on 28 April and 15 June. The roots were washed and separated using techniques described previously.

Between 15 December and 16 March dry weight of both roots and shoots increased and the mean root : shoot ratio doubled from 0.57 to 1.16 (Table 1). On 28 April this ratio was 0.69 and it decreased to 0.16 on 15 June (Table 1). These results confirm those of 1970 and show that, whereas during winter roots grow faster than shoots, the reverse is true later. Between 15 December and 16 March both root dry weight and length increased about eight times, but after 16 March the dry weight growth rate increased whereas length growth rate did not.

The mean shoot and root dry weights and mean root length of the dwarf varieties did not differ significantly from the corresponding means for the conventional varieties until 15 June, when the mean root dry weight and length of roots of the commercial varieties was 121 ( $\pm 6.2$ ) g/m<sup>2</sup> and 16.4 ( $\pm 0.56$ ) km/m<sup>2</sup> and of the dwarf varieties 132 ( $\pm 6.2$ ) g/m<sup>2</sup> and 16.3 ( $\pm 0.56$ ) km/m<sup>2</sup>.

On 16 March TL 365a/37 had only 70% of the root length and weight of most other varieties (except Maris Nimrod) in the top 25 cm soil layer. This confirmed the indication in 1970 that roots of TL 365a/37 developed more slowly than the other varieties. Maris Nimrod had a dry weight of roots similar to TL 365a/37 on 16 March but a much greater root length, so it apparently had thinner roots than other varieties; its large root length : weight ratio persisted on 28 April. Although differences between varieties were not significant at later dates or lower depths, the root dry weight and length of TL 365a/37 were still among the smallest on 15 June.

TABLE 1

*Dry weights of roots and shoots, root : shoot ratio, and length of roots; means of all varieties*

Sampling date	15 December	16 March	28 April	15 June
Depth, cm	Dry weight, g/m <sup>2</sup>			
0- 15	3.44	22.0	39.2	88.9
15- 25	1.05	6.4	7.9	13.6
25- 35	0.43	1.8	2.5	4.6
35- 45	0.04	1.0	2.2	4.1
45- 55	—	1.0	2.0	4.1
55- 65	—	0.7	1.6	3.6
65- 75	—	—	1.1	3.1
75-100	—	—	0.8	4.8
Total	4.96	32.9	57.3	126.8
Shoot dry weight g/m <sup>2</sup>	8.7	28.3	82.8	777.5
Root : shoot dry weight ratio	0.57	1.16	0.69	0.16
Total length km/m <sup>2</sup>	0.9	7.6	10.9	16.3

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The average proportion of roots in the top soil layer changed very little between sampling dates, indicating that growth of roots in the top layer accompanied extension of roots into the deeper soil layers (Table 1). On 15 December 1970, 69% of the roots were in the top 15 cm although some penetrated to 45 cm. By 16 March 1971 the roots had penetrated to 65 cm but the proportion in the top 15 cm was still 67%. Although roots penetrated to 85 cm on 28 April and 100 cm by 15 June the proportions of roots in the top layer remained at 69% and 70% respectively. Root length was distributed between the different layers in the same proportions as dry weight. On the first two sampling occasions there were fewer roots in the spaces than in the rows in the top 25 cm although the differences were smaller on 16 March than 15 December. Below 25 cm there was no significant difference between rows and spaces on either date.

Final grain yields (85% dry matter content) were in tonnes/ha: Cappelle Desprez 5.91, Maris Ranger 5.97, Maris Nimrod 5.62, 363/30 7.34, 365a/34 7.18, 365a/37 6.35. (Welbank)

**Growth and yield of cereals on different sites.** These experiments on winter wheat and barley each grown at Rothamsted and Broom's Barn are described in the Report of the Chemistry Department (p. 60). This account deals with the development of the crops before harvest.

It was not usually possible to sample crops on both sites on the same day; dates of sampling at both sites are given for each occasion, with the Rothamsted date *first*.

**Winter wheat.** There was little difference between the top growth of wheat on the two sites on 15/16 December 1970, but on 26/25 March 1971 the wheat at Rothamsted had 43.7 g dry weight of tops/m<sup>2</sup>, 1494 shoots/m<sup>2</sup> and a leaf area index of 0.92 and at Broom's Barn 27.3 g/m<sup>2</sup>, 894 shoots/m<sup>2</sup> and 0.48. The crop was thus nearly twice as vigorous at Rothamsted as at Broom's Barn and continued so until the end of May. Nevertheless, ears were initiated at about the same time at both sites: double ridges were found at Rothamsted on 3 April and at Broom's Barn on 6 April. When ears emerged on 24/22 June wheat at Rothamsted had about 30% more shoots and leaf area than at Broom's Barn and about 25% greater shoot dry weight. These advantages in shoot number and leaf area persisted during the grain-filling period and were more than enough to account for the greater yield at Rothamsted.

Nitrogen fertiliser in April affected wheat little before 26/28 May, nor did it affect maximum shoot numbers. It increased the proportion of shoots that survived to produce ears and this effect was clear at Broom's Barn by 28 May and at Rothamsted by 24 June. Shoot dry weights and leaf areas largely reflected the response in shoot number. The responses to nitrogen of all these quantities were slightly greater at Broom's Barn than at Rothamsted, e.g. increasing nitrogen from 31 to 186 kg/ha increased leaf area index on 6 July from 4.5 to 7.5 at Broom's Barn and from 9.2 to 11.2 at Rothamsted, suggesting that lack of nitrogen might have limited growth at Broom's Barn.

Irrigation was applied to both experiments when necessary between 11 May and 7 June. It had no effect on sample yields before 22 June, but later at Broom's Barn allowed more shoots to survive (510, cf. 430 m<sup>-2</sup>) and increased dry weight and leaf area. This effect persisted until the final harvest. Irrigation had no effect at Rothamsted. Thus lack of soil moisture partly accounted for the smaller growth and yield at Broom's Barn. The nitrogen-response curves for shoot number and leaf area did not extend above their respective maxima at Rothamsted; had they done so it might have become clear whether shoot growth at Broom's Barn could equal that at Rothamsted, given irrigation and enough nitrogen.

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**Barley.** Barley had a smaller shoot dry weight and leaf area at Broom's Barn than at Rothamsted at the first sampling, but the same number of shoots, so it is possible that much of the difference between sites on this occasion may have been caused by earlier sampling at Broom's Barn (13, cf. 17 May). On 7/9 June the leaf area was greater at Rothamsted than at Broom's Barn only on unirrigated plots, but by 1 July/29 June Rothamsted barley had more shoots surviving ( $950 \text{ m}^{-2}$ ), greater shoot dry weight ( $887 \text{ g m}^{-2}$ ) and a larger leaf area index (9.3) than Broom's Barn (793 shoots  $\text{m}^{-2}$ ,  $802 \text{ g m}^{-2}$  and 7.2). The mean differences between sites were similar on 13 July, but there was then less effect of irrigation.

Nitrogen fertiliser increased growth and leaf area of barley more than of wheat, and at the first sampling (17/13 May) more at Rothamsted than at Broom's Barn. Later, responses to nitrogen were similar at both sites, e.g. on 1 July/29 June increasing nitrogen from 31 to 186 kg/ha increased leaf area index from 5.7 to 12.5 at Rothamsted and from 4.3 to 9.4 at Broom's Barn. Lack of nitrogen seemed not to be the factor causing smaller yields of barley grown without irrigation at Broom's Barn.

Irrigation had no consistent effect at Rothamsted, but at Broom's Barn it increased the number of surviving shoots, their dry weight and leaf area. On 29 June it increased mean shoot number from 730 to 860 per  $\text{m}^2$ , dry weight from 760 to  $840 \text{ g m}^{-2}$  and leaf area index from 6.3 to 8.0. There were small yield differences between irrigated plots at the two sites at the final harvest, but water was not applied after 8 June, so differences in moisture stress developing later than this may have affected grain yields. (Welbank with Widdowson, Chemistry Department)

### Growth and metabolism

**Growth of short and tall spring wheat varieties.** In 1967 and 1969 short spring wheat derived from the Japanese variety Norin 10 yielded similarly to the taller European variety Klokka. In 1967 the short varieties had less leaf area than Klokka suggesting that their leaves were more efficient in producing grain. The relatively good performance of the short varieties might have been related to the good weather of 1967 and 1969. In 1971 a further experiment included measurements of the distribution of dry matter and of grain yield, leaf area and light absorption. The short variety Penjamo 62 was compared with the standard variety Kolibri, sown at two rates approximately 30% above and below the standard, and with 50, 125 or 200 kg/ha nitrogen. Populations obtained for Kolibri and for Penjamo 62 were 164 and 364, 118 and 277 plants per ha respectively.

In contrast with the two previous experiments, Penjamo 62 yielded less (2.72 t/ha of dry grain) than Kolibri (3.86 t/ha). Penjamo 62 had the same number of ears as Kolibri but they weighed less because they had fewer spikelets. The varieties did not differ in number of grains per spikelet, grain size or the proportion of spikelets containing grain. In the earlier experiments the short varieties also had fewer spikelets but compensated by having more grains per spikelet. The fewer spikelets of Penjamo 62 did not result from faster development; ears were initiated by Penjamo within a few days of Kolibri and flowering was five days earlier.

Nitrogen had no effect on grain yield but increased shoot dry weight and leaf area. Doubling the plant population increased grain yield of Kolibri by 19%, but decreased that of Penjamo 62, and increased ear number of Kolibri by 35% and Penjamo 62 by 28% (much more than in 1969). The decrease in grain weight per ear was greater for Penjamo 62 than for Kolibri, thus accounting for the difference between the varieties in response to sowing rate. Shoot dry weight and leaf area of both varieties were increased by doubling the plant population. It is not clear why increasing maximum leaf area index from 5 to 7 by denser sowing increased grain yield proportionately, whereas grain yield



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was unaffected by a similar increase in leaf area index caused by additional nitrogen. Moreover, the large response in grain dry matter of Kolibri to increased sowing rate was unusual. (Thorne)

**Measurement of photosynthetic activity in the field using radioactive carbon dioxide.** In the experiment described in the preceding paragraph, photosynthetic rates were measured by exposing parts of leaves to radioactive carbon dioxide. The apparatus used was based on that described by Austen and Longden (*Annals of Botany* (1967) **31**, 122). The flow of normal air over the leaf was interrupted for a period of 15 seconds during which period part of the leaf was enclosed in a chamber through which air containing  $^{14}\text{CO}_2$  was passed. The total concentration of carbon dioxide in the air passing over the leaf was varied and the light intensity falling on the chamber could be decreased by a set of optically neutral filters. Immediately after the leaf was removed from the chamber, samples were taken and placed in a vacuum flask containing solid carbon dioxide and returned to the laboratory for analysis. Radioactivity was determined either in the dried leaf specimen or as carbon dioxide produced during total combustion of the sample.

Photosynthesis in both wheat varieties was independent of radiation when total radiation exceeded  $140 \text{ W m}^{-2}$ ; the light response curves were similar. When the concentration of carbon dioxide was increased in the chamber to three times that in the surrounding air the rate of photosynthesis was increased but possibly more in Kolibri than in Penjamo 62. The compounds that became radioactive were determined by extracting the leaf with alcohol and separating the concentrated extract using two-dimensional thin layer chromatography. The proportion of radioactivity appearing in sucrose was increased by exposing leaves to concentrations of carbon dioxide greater than normal. In normal air much of the radioactivity was in serine and glycerate, with less in glycine, so in the field these compounds are significant products of photosynthesis. There was no evidence of significant differences in the distribution of radioactivity between different compounds in the two varieties of wheat examined. These results are based on a single season's observations and require confirmation. (Whittingham)

**Metabolism of glycine, serine and glycerate in leaves.** Leaves excised from wheat plants were supplied with  $^{14}\text{C}$ -labelled glycine, serine or glycerate. Synthesis of sucrose from these compounds in the light was almost completely prevented by removing carbon dioxide from the atmosphere surrounding the leaves, a concentration of 200 ppm giving maximum synthesis of sucrose. The absence of carbon dioxide from the atmosphere permitted the conversion of glycine to serine but prevented the conversion of serine to glycerate and of glycerate to sucrose. The rate of uptake of labelled substrates was not greatly affected by carbon dioxide concentration in the atmosphere. In atmospheres containing 300 ppm of carbon dioxide, the synthesis of sucrose from glycine or serine was greater in 2% oxygen than in 21% oxygen; under anaerobic conditions, sucrose synthesis was slowed to 30% of the rate in 2% oxygen. Thus in leaves, sucrose synthesis from intermediates of the glycollate pathway depends both on photosynthesis and on a process occurring faster in 2% than in 0 or 21% oxygen. (Waidyanatha)

**Enzyme system responsible for photorespiration.** Conversion of two molecules of glycine to one molecule each of carbon dioxide, ammonia and serine, is thought to be an important reaction in the metabolic pathway responsible for photorespiration. The reaction is catalysed by an enzyme system that is firmly bound to particles in leaves. Differential and isopycnic density gradient centrifugation were used to fractionate particles from tobacco leaves. The catalytic activity was associated with fractions containing mitochondria. Mitochondria from etiolated leaves or from plant tissues without chlorophyll were less

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active than those from green leaves. The synthesis of serine from glycine catalysed by these preparations was slow in the absence of oxygen but proceeded at a maximum rate with 2% by volume of oxygen in the atmosphere. Approximately one atom of oxygen was used for each molecule of serine formed. The reaction was inhibited by Antimycin A, *o*-phenanthroline and cyanide, known inhibitors of electron transport in mitochondria. Furthermore the rate of reaction was increased by adding ADP (adenosine diphosphate). The added ADP was phosphorylated and phosphorylation was faster in the presence of glycine than in its absence. Isonicotinyl hydrazide, semicarbazide and sodium arsenite inhibited phosphorylation associated with serine synthesis from glycine more than that occurring in the absence of glycine. However, *trans*-aconitate slowed phosphorylation in the absence of glycine but had little effect on either serine synthesis or on the additional phosphorylation resulting from adding glycine. Conversion of two molecules of glycine to one of serine involves a large change in free energy ( $\Delta G_{298}^{\circ} = -42$  Kcal/mol) and could result in synthesis of ATP (adenosine triphosphate) in mitochondria in the light. The synthesis of ATP in the light, elsewhere than in the chloroplast, is a new observation suggesting a function for photorespiration. (Keys and Bird)

**Influence of water content on plant metabolism.** The influence of the water potential of the medium in which a plant grows must be by an effect on the water potential of plant tissues; this may change the rate and type of metabolism. Plants were grown either in soil, which had been allowed to dry out, or in culture solutions, in which the available water was artificially lessened by adding substances of high molecular weight; e.g. polyethylene glycol (PEG). In the first type of experiment sugar-beet plants of an inbred line provided by the Plant Breeding Institute, Cambridge, were grown in 15 kg of Geescroft soil containing 0, 1.4 or 3.2 kg added sodium chloride per pot, equivalent to soil sodium concentrations of 10, 50 and 100 ppm. The water content of the pots was maintained by weighing either at 23% or at 15% (equivalent to soil water potentials of  $-0.2$  and  $-2.0$  bars). Samples of the plants were taken for growth analysis and for measurements of  $\text{CO}_2$  exchange and of the water and osmotic potential and relative water content of the leaves. Under the growth conditions used, most of the plants showed symptoms of potassium deficiency. Nevertheless, a large effect of leaf water potential on carbon dioxide uptake was observed, a rate of  $10 \text{ mg dm}^{-2} \text{ h}^{-1}$  at  $-8$  bars falling to  $2 \text{ mg dm}^{-2} \text{ h}^{-1}$  at  $-20$  bars. Dark respiration was diminished also, from 2 to  $3 \text{ mg dm}^{-2} \text{ h}^{-1}$  at  $-10$  bars to 1 to  $2 \text{ mg dm}^{-2} \text{ h}^{-1}$  at  $-20$  bars. There was little evidence that the amount of sodium affected the decrease in photosynthesis resulting from water stress. In a further experiment, plants (Sharpe's Klein E monobeet) were grown in nutrient solutions with or without added sodium and at osmotic potentials of  $-0.4$ ,  $-3.0$  and  $-8.0$  bars produced by adding PEG. Corresponding leaf water potentials measured were  $-8$ ,  $-10$  and  $-12$  bars and leaf osmotic potentials were  $-9$ ,  $-11$  and  $-13$  bars. They were not affected by sodium. The small difference between the osmotic potential and the water potential indicates that the turgor pressure is very small; this agrees with field observation that sugar-beet plants readily show symptoms of wilting. The dry weight of the plant and the rate of transpiration and of carbon dioxide uptake were all decreased with greater water stress. A further experiment is required to show whether visible wilting in sugar-beet leaves is always accompanied by a significant decrease in photosynthesis and in growth.

In a similar experiment with wheat, variety Kolibri, grown in solutions containing PEG, the leaves of young and more mature plants grew fastest at  $-5$  bars osmotic potential,  $\psi$ , but growth was halved at  $-7$  bars and stopped at  $-12$  bars  $\psi$ . Stem and ear elongation decreased similarly but the ear grew better than the leaves at smaller solution osmotic potentials. Older leaves died sooner with decreasing water potential

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and during ear emergence four days stress at  $-16$  bars  $\psi$  almost halved the total dry weight of the leaves. The combined effect of accumulated leaf death and slower leaf expansion both decreased the total leaf area. The dry weight and size of the ears were 20% less after four days growth at  $-16$  bars  $\psi$ . Stem weight decreased by over 30% in four days at this water potential, suggesting that stored materials in the stem contributed to ear growth when the total dry weight was not increasing.

Transpiration of mature plants per unit leaf area was slowed to about 70% of the control rate at  $-6.5$  bars  $\psi$  and to 10% at  $-16$  bars, but carbon dioxide absorption (at 40 000 lux) decreased to 90% at  $-6.5$  bars  $\psi$  and 25% at  $-16$  bars  $\psi$ . Photosynthesis of leaves of young plants did not change with decreasing water potential between  $-5$  and  $-8$  bars but decreased almost to zero at about  $-14$  bars  $\psi$  at all light intensities.

The generation of carbon dioxide by wheat leaves in the light (photorespiration) was changed little by water stress up to  $-10$  bars, the compensation point rising from 60 ppm at  $-6$  bars  $\psi$  to only 75 ppm at  $-10$  bars  $\psi$ . After 15 minutes photosynthesis in air, leaves at  $-6$  bars  $\psi$  released carbon dioxide to carbon dioxide free air in the light and this was little changed at  $-10$  bars  $\psi$ . (Lawlor)

### Growth substances and growth regulators

**Growth substances in the wheat plant.** In a previous section the growth of the ear in relation to that of the plant was discussed in terms of the movement of carbohydrate from the rest of the plant to the ear. The movement of food substances between parts of the plant may not be related simply to supply of and demand for sugars, but may be controlled by plant growth substances present in small amounts. The gibberellin in the wheat plants in the experiment in which the ears were maintained at temperatures different from the remainder of the plant was assayed two weeks and three weeks after the ears had been placed at either  $15^\circ$  or  $20^\circ\text{C}$ , with the rest of the plant maintained independently either at  $15^\circ$  or  $20^\circ\text{C}$ :

TABLE 2

*Gibberellin content of wheat plants during growth*

Date harvested	Plants at Ears at	pg GA <sub>3</sub> equivalent per ear			
		15°C		20°C	
8 July (treatment commenced)			249		—
21 July		469	1725	791	3997
29 July		3614	7145	4471	5596

The amount of gibberellin per ear increased most in ears kept at  $20^\circ\text{C}$  on plants kept at  $15^\circ\text{C}$ . No significant difference was observed with ears at the same temperature on plants at different temperatures.

In a further experiment the biosynthetic ability of ears detached from wheat plants was examined. Ears were detached from field grown plants, variety Kolibri, at various dates after anthesis and the stems placed in 3% sucrose for four days. Either 100 ppm CCC (an inhibitor of gibberellin synthesis) or 1.0 ppm kinetin was added to the sucrose solution.  $10\ \mu\text{g}$  (-)-Kaurene (an immediate precursor of gibberellin) in 80% ethanol was applied to the top of the stems of some of the CCC-treated ears. Four days later the ears were extracted with ethanol and purified extracts were assayed using the barley endosperm test. Gibberellin was significantly less in ears after incubation at the first sample time, but increased greatly at the second sample time and the third sample so much before incubation that the differences between treatments were not significant.

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TABLE 3  
*Formation of gibberellins in detached wheat ears*

	pg GA <sub>3</sub> equivalent per ear		
	Date detached		
	12 July	19 July	26 July
No incubation	240	182	1626
Incubation in sucrose	72	550	1518
Incubation in sucrose + CCC	50	210	958
Incubation in sucrose + CCC + kaurene	58	2094	2094
Incubation in sucrose + kinetin	54	1626	2518

It is concluded that the ability to synthesise gibberellin develops in the wheat ear as the grain fills.

Last year we measured auxins, gibberellins and cytokinins in the ear during the development of the grain of Kloka spring wheat grown in the glasshouse. This year, plants were taken from the field. Cytokinins occurred at anthesis but later diminished; they were also detected in the exudates collected from cut stems before anthesis but not afterwards. Whereas the gibberellin and auxin contents of the grain progressively increase until three and four weeks respectively after anthesis, cytokinins decrease during development. The cytokinin content decreased less in ears of Kolibri wheat from which the stamens were removed before the anthers opened, as also did the gibberellin content but not the auxin.

The setting of grain by the upper florets of the wheat ear may be influenced by the earlier development of grains from the first flowers to reach anthesis. Hence, ears were divided into three equally long parts. At ear emergence, the upper third contained more cytokinin than the lower. As the grain developed the cytokinin concentration decreased most in the middle portion where grain development was most advanced. By contrast the gibberellin and auxin concentrations showed no change with position along the ear. (Radley and Wheeler)

#### Growth regulators applied in field trials

**Potatoes.** In 1970, dipping seed potatoes in solutions containing 'Ethrel' before planting both increased number and yield of tubers especially of the early variety Arran Pilot; the yield was increased more in less fertile plots. The experiment was repeated. Seed was soaked for 1 hour in water with 0 mg/l (E<sub>0</sub>), 60 mg/l (E<sub>1</sub>) or 120 mg/l (E<sub>2</sub>) of 'Ethrel' and planted in plots given three amounts of N, viz. 75, 150, 225 kg/ha N. Seven weeks after planting, plants treated with 'Ethrel' had a larger leaf area per plant, but four weeks later a smaller one, than the untreated plants. At the final harvest the more dilute 'Ethrel' had little effect on yield and the more concentrated increased it by 5%. There was an interaction with nitrogen, and plants given more 'Ethrel' and most nitrogen produced 17% more yield. This was in contrast to 1970 where the infertile plots yielded most with 'Ethrel' treatment.

**Cereals.** CCC shortens the straw and decreases lodging in wheat but in barley the effect persists only for a short period and is lost in the mature crop. A growth regulator that shortens barley and lessens lodging would be of practical value.

In experiments with barley in pots 'Ethrel' showed promise. Late spraying of cereal crops is not practicable so the chemical was applied to the soil surface as dust, to see whether it would persist. Barley in the field was treated with 'Ethrel' either as a spray (1.1 kg/ha) or as a dust ('Ethrel' mixed with fine sand) at 3.3 kg/ha. The dusts were

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applied when the plants had two leaves (17 April), four leaves (19 May) or six leaves (1 June) and the sprays on 7 June and 16 June. Dusts applied to the soil had no effect on plant height. Spraying shortened the stems by about 20%. Dusts did not affect yield but spraying decreased it by 16%, producing smaller grains and fewer grains per ear.

'Ethrel' had no significant effect on the yield of either winter wheat or spring wheat.

In 1970, CCC had no effect on yield of the semi-dwarf winter wheat Gaines. This year the variety Gaines at two seed rates (126 and 188 kg/ha) was compared with the variety Cappelle. Nitrogen was applied at 75, 150 or 300 kg/ha; CCC was sprayed at 1.1 or 2.2 kg/ha at the five-leaf stage. Lodging was slight and there was no effect of CCC on grain yield. Increasing the supply of N decreased grain yield of both varieties, mainly by making grains smaller.

The effect of CCC on dwarf spring wheat was again studied with the varieties Benoist 257 (now named Charles Peguy), VR.6/57 and Inia. Also the standard variety Kolibri was included. None of the varieties lodged. Treatment with CCC shortened Kolibri and VR by 20%, Inia by 18% and Benoist by 12%. Yield of all varieties was increased by CCC and by nitrogen because the number of ears per acre, the number of grains per ear, and the weight of the grain per ear were all increased. The variety Inia suffered a severe attack of mildew and the ears had an average of only nine grains per ear. (Humphries)

### Weed studies

**Broadbalk.** Annual weeds in *winter wheat* were very well controlled by terbutryne pre-emergence followed by a dicamba/mecoprop/MCPA mixture in May, but perennials remained a problem. Horsetail (*Equisetum arvense*) and couch (*Agropyron repens*) have now been joined by large patches of *Agrostis gigantea*. This grass was introduced to Rothamsted in the 1950s and first seen on Broadbalk in 1966. Creeping thistle (*Cirsium arvense*) and coltsfoot (*Tussilago farfara*) are less abundant now that most of the wheat is sprayed with herbicides.

On the unsprayed section 8, common vetch (*Vicia sativa*) was so abundant on plots receiving little or no nitrogen that it controlled the other weed species.

The chief weed in *spring beans*, where herbicide was not applied and weed control was by inter-row cultivation only, was knotgrass (*Polygonum aviculare*). This covered the ground on most plots by harvest, even where the crop was dense and tall; on plot 11 where the crop was very poor, the knotgrass overtopped the beans.

The main weed problem in *potatoes* was again horsetail (*Equisetum arvense*) which was unaffected by the pre-emergence spray with linuron/paraquat, which controlled all except very late-germinating annual weeds.

Volunteer potatoes are now among the common weeds (i.e. plants where they are not wanted), not only in the beans that follow them in the rotation, but also in the wheat after the beans. The spring herbicide applied to wheat defoliated the potatoes but they grew again and were plentiful (1.2 per m<sup>2</sup> approx.) in stubble on 22 plot-sections and present in smaller amounts on many more.

Small toadflax (*Chaenorhinum minus*, formerly *Linaria minor*) reappeared after many years' absence, still on plot 10 where it was formerly, but in spring beans (unsprayed).

Fluellen (now *Kickxia elatine*, formerly *Linaria elatine*) usually found in spring barley on Hoosfield (but not, shown in records previously, on Broadbalk) occurred on the unmanured plot 3 in beans on section 2 and in wheat after fallow on section 3.

Red Bartsia (now *Odontites verna*, formerly *Bartsia odontites*) occurred in beans on section 2, and the plants were larger and more vigorous than those in wheat. This is remarkable because on Broadbalk it has always been associated with wheat. (Thurston)

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**Park Grass.** Visual surveys of the vegetation were made before the plots were cut in June and September.

Whereas between 1965 and 1968 the number of species flowering on the recently limed, previously acid plots, trebled in June and doubled in the autumn surveys, there has been little subsequent change.

TABLE 4

Number of species seen flowering on section c of plots 1, 4<sup>2</sup>, 9, 10, 11<sup>1</sup>, 11<sup>2</sup> and 18 during the June and August or September surveys

	June survey							August/September survey						
	1965	1966	1967	1968	1969	1970	1971	1965	1966	1967	1968	1969	1970	1971
1c	6	6	8	13	17	17	19	1	4	4	10	8	8	9
4 <sup>2</sup> c	4	4	7	13	13	15	13	4	4	6	5	7	5	6
9c	3	6	7	11	14	11	12	2	4	3	5	6	5	4
10c	5	5	6	11	8	9	9	3	4	3	5	4	3	4
11 <sup>1</sup> c	2	3	7	9	8	7	9	1	1	1	1	3	2	2
11 <sup>2</sup> c	1	4	7	8	12	9	10	2	2	2	4	4	3	2
18c	5	5	8	12	14	14	16	4	5	4	9	7	9	9
Total	26	33	50	77	86	81	88	17	24	23	39	39	35	36

The changes in the botanical composition of these plots have been:

- (1) The occurrence of *Trifolium pratense* on all these plots; it is now well established on plot 9c, and to a lesser extent on plot 1c.
- (2) An increase in the amount of *Festuca* species on plots 1c, 4<sup>2</sup>c, 10c and 18c, i.e. on plots given the two smaller amounts of nitrogen and incomplete minerals.
- (3) The introduction, mainly since 1967, of *Arrhenatherum elatius*, *Dactylis glomerata*, *Alopecurus pratensis*, *Poa trivialis*, *Poa pratensis* and *Helictotrichon pubescens*, mainly into plots 11<sup>1</sup>c and 11<sup>2</sup>c, i.e. plots receiving most nitrogen and complete minerals. The first four species are now abundant on these two plots.
- (4) The invasion of *Lathyrus pratensis* from the edge of plot 14d to 1c.
- (5) The occurrence of *Taraxacum officinale* on all these plots. It is most obvious on plot 9c and is also plentiful on 1c and 11<sup>2</sup>c.
- (6) A general introduction of occasional plants of *Achillea millefolium*, *Conopodium majus*, *Hypochoeris radicata*, *Leontodon hispidus*, *Plantago lanceolata* and *Ranunculus acris*. *Anthriscus sylvestris* is now established on plots 9c, 11<sup>1</sup>c and 11<sup>2</sup>c.
- (7) A decrease in the amount of *Anthoxanthum odoratum* on plots 4<sup>2</sup>c, 9c and 10c and of *Holcus lanatus* on plots 11<sup>1</sup>c and 11<sup>2</sup>c.

The plots were cut later this summer than in the previous five years and during the wet June the appearance of some recently limed plots changed greatly. In particular, plots 11<sup>1</sup>c and 11<sup>2</sup>c, whose appearance during early June had in recent years become increasingly like the permanently limed ends of these plots, later appeared to be dominated by *Holcus*. Changes in the recently limed plots, therefore, include not only the introduction and increase from year to year of species previously absent, but also changes in the relative proportion of the indigenous and introduced species at different times of the year. (Williams)

**Weed competition in crop plants**

**Wild oats (*Avena fatua*).** In a previous experiment (*Rothamsted Report for 1969, Part 1, 120*) different wild oat populations were established by transplanting chitted seeds after drilling but before emergence of spring barley. Even 120 wild oat plants per m<sup>2</sup> produced

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little effect on the subsequent growth of barley. To avoid the setback from transplanting, whole plots were sown in early April with dry *Avena fatua* seeds giving 0, 77, 171 and 317 seedlings per m<sup>2</sup>. Sub-plots were drilled on the same day with spring wheat var. Rothwell Sprite or spring barley vars. Zephyr and Deba Abed, or left uncropped.

Wild oat seedlings emerged just after the crops, and were dominated by them throughout their growth. At the final harvest in July, just before the wild oat seeds shed and therefore before the crops were fully ripe, the mean yields were measured of the three crops with different wild oat infestations.

TABLE 5

*Growth of spring cereals in competition with wild oats*

Wild oats/m <sup>2</sup>	0	77	171	317
Dry weight tops per crop plant (g)	2.82	2.92	2.80	2.87
Average ears per crop plant	1.67	1.74	1.58	1.66

Although there was little effect of wild oat population on the growth of the crop, as in the previous experiment, crop competition greatly diminished growth of the wild oats.

TABLE 6

*Growth of wild oats in competition with spring cereals*

	None	Spring barley		Spring wheat Rothwell Sprite
		Deba	Zephyr	
Shoots per wild oat plant	3.51	1.04	1.07	1.34
Total dry weight shoots + ears (g) per wild oat plant	3.39	0.43	0.48	0.67

The wild oats also competed between themselves in the absence of a crop. At 317 plants/m<sup>2</sup> this effect was measurable at the first harvest (17 May) and by July there were clear differences in mean plant size between the different infestations.

TABLE 7

*Growth of wild oats in the absence of a crop*

Plants/m <sup>2</sup>	77	171	317
Shoots per plant	5.72	2.62	2.18
Dry weight tops (g) per plant	4.69	3.22	2.27

(Thurston)

*Agropyron repens*

*In cereals.* A similar experiment to the one with wild oats was made with *Agropyron*, although here the emphasis was on the effect of the crop on growth of seedlings of couch. Seeds of *Agropyron* were sown in rows of winter wheat (Joss Cambier), spring wheat (Kolibri) or spring barley (Julia), soon after crop-drilling. The cereals, sown at usual seed rate, were given either 75 kg/ha of nitrogen or none. The seedlings established poorly in winter wheat and herbicide was not applied in spring to control broad-leaved weeds. The few *Agropyron* seedlings that established were therefore competing with many other weeds.

In the spring cereals, drilled on 26 February, *Agropyron* seedlings were ringed as they emerged between early April and late May. Approximately 60% of the seeds sown produced seedlings. Samples of crops and seedlings were taken on three occasions (end

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of May, June and August) during the growing season. Nitrogen increased the weight of individual *Agropyron* seedlings from 3.8 to 11.4 ( $\pm 0.96$ ), 9.0 to 21.7 ( $\pm 2.4$ ) and 33 to 63 mg ( $\pm 6.1$ ), and the dry weight/m<sup>2</sup> of spring cereals from 167 to 324 ( $\pm 8.0$ ), 631 to 1015 ( $\pm 64.7$ ) and 869 to 1064 g at the three times of sampling. Cereals grew most between the first two samples, but *Agropyron* between the second and third samples, as the cereals became less competitive after ear emergence. More growth was made by *Agropyron* seedlings in spring wheat than in spring barley with, but not without, added nitrogen. Without nitrogen, barley and wheat had a similar leaf area index, whereas with nitrogen, barley had a much larger leaf area index than wheat, making it more competitive to the seedlings.

TABLE 8

*Dry weight (mg) of Agropyron seedlings*

	26 June			26 August		
	Spring wheat	Spring barley	S.E.	Spring wheat	Spring barley	S.E.
—	10.3	7.7	} 2.4	28	38	} 8.7
+N	27.3	16.2		77	50	
S.E.	3.4			10.8		

Except for one seedling, which had rhizomes at the first sampling, *Agropyron* seedlings did not have rhizomes until after the second sampling, i.e. until the crop started ripening. About 15% of the seedlings that established produced rhizomes and these were the ones that emerged before mid-April. Errors were large for rhizome weights but there was some evidence, as for shoot weights, that the response of seedlings to nitrogen was greater in spring wheat than in spring barley.

In winter wheat, seedlings of both nitrogen treatments had produced only 13 mg dry weight by early May and by harvest they had increased to 24 mg without nitrogen and 70 mg with. None of the seedlings in winter wheat produced rhizomes.

The final grain yields (85% dry matter content) were in tonnes/ha with and without added nitrogen: spring wheat 4.1 and 5.3; spring barley 5.8 and 5.8 and winter wheat (severely damaged by birds) 2.6 and 4.3.

***Spring barley and spring beans not undersown or undersown with ryegrass or clover.***

One hundred viable seeds of *Agropyron* were sown on 1 April in two 1 ft square areas in plots of barley or beans drilled on 26 March with or without undersown ryegrass or clover, sown one week later. *Agropyron* seedlings were removed from all plots shortly before crop harvest (18 August for barley and 10 September for beans).

The mean number of seedlings recovered from the areas in barley were 42 and 27, and nine when the crop was undersown with nothing, ryegrass, or clover respectively; in beans, 67, 20 and 5 respectively. At harvest the dry weight of *Agropyron* shoots was 0.41 in barley not undersown, and 0.16 and 0.07 g when undersown with ryegrass or clover. Rhizomes were not produced in barley. In the equivalent treatments in beans 15.9, 2.4 and 0.4 g shoot weight and 4.9, 0.9 and 0.04 g of rhizome was produced and the length of rhizome in these areas was 5.4, 1.1 and 0.1 m. In bean plots not undersown, *Agropyron* seedlings had 2.6 tillers and about 1.6 in undersown ryegrass and clover. (Williams)

**Biology of weed species**

**Blackgrass (*Alopecurus myosuroides*)**

**Effect of fertilisers.** Previous observations on Broadbalk suggested that dry weight of blackgrass increased more with PK, and less with the larger dressings of N, than the



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winter wheat in which it was growing. However, as reported last year (*Rothamsted Report for 1970*, Part 1, 108) there was a linear response in final dry weight per plant of blackgrass grown in pots without competing wheat over the range of N treatments given, but little increase with added P and K by the end of the growing season. This year, four blackgrass plants were grown per pot of 4.3 kg of Geescroft soil, with or without additional P or K, at two amounts of nitrogen; the most used in 1970 (N2) and double that amount.

[K = 232 ppm; P = 232 ppm; N2 = 87 ppm; N4 = 174 ppm]

Samples were taken: (1) in early April when well-established young plants were transferred from a cold glasshouse to a cage; (2) mid-June at maximum vegetative growth, when ear-emergence was just beginning and no lower leaves had died; (3) late August when the straw was completely ripe.

In early growth the biggest increase in dry weight of shoots was with added P ( $-P = 0.17$  g,  $+P = 0.52$  g). There was little effect of added nitrogen or potassium.

As plants reached maximum vegetative growth, the effect of added N became obvious, but plants without additional P receiving added N were retarded, as shown by time of ear-emergence and by their remaining green after the leaves and stalks of plants with P had begun to ripen and turn yellow. At the final harvest the biggest increase in dry weight came from added N (mean straw weights for  $-N$ ,  $+N2$  and  $+N4$  being 9, 21 and 27 g). Responses to added P ( $-P = 18$  g,  $+P = 21$  g) and K ( $-K = 20$  g,  $+K = 19$  g) were small.

As in 1970, plants grown without added fertilisers were not the poorest; they produced 11 g dry weight of straw compared with only 8 g for K alone and 9 g for P alone. N2 alone nearly doubled the straw yield (to 19 g) and N4 alone increased it to 26 g. The heaviest straw yield was from treatment  $+N4 + P - K$  (30 g).

The increased early growth with added P would favour blackgrass in competition with winter wheat, but the diminishing returns from larger dressings of N, especially with added P and K, would allow the wheat to overtop the blackgrass, as on Broadbalk. (Thurston)

### *Periodicity of germination*

(a) *Effect of fertilisers applied to parent plant.* Ripe seeds were collected from each pot in the experiment described in the preceding paragraph. Random samples of 100 seeds were sown in pans of sterilised Rothamsted soil so that their germination can be examined during a two-year period. Germination in the first month (mid-October to mid-November 1971) was maximal (32.7%) for seeds from plants with  $+N4 - P + K$  and minimal (20.2%) for seed from  $-N - P - K$ . Supplying N without K to the parent plants increased germination of seeds by 5%, but added P had no effect.

(b) *Effect of site collection.* In 1969 ten plants collected from each of six localities were grown in pots and their ripe seeds collected (*Rothamsted Report for 1969*, Part 1, 122). No attempt was made to control cross-pollination. Random samples of 100 seeds from each plant were sown in pans of sterilised soil in a cool glasshouse in autumn 1969. Seedlings were removed and the soil cultivated once a month. By November 1971, only 12 of the 60 pans had produced seedlings within the preceding year. These were kept, and the others discarded.

Most of the seedlings had emerged during the first 12 weeks, up to mid-February 1970, and there was then a pause of a few weeks to a few months before the next seedlings appeared. The number of seedlings emerging after week 12 was expressed as a percentage of the total seedlings recorded to week 101 (end of November 1971), providing an approximate estimate of dormant seeds. The mean per cent dormant seeds per ten plants

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differed little between localities (Nottinghamshire 4%, Wiltshire and Kent 5%, Huntingdonshire 6%, Sussex 7%, Cambridgeshire 9%) with approximately 10% dormant seeds for germination of blackgrass from Broadbalk soil. There was considerable variation between the different plants collected from the same site.

Dormant seeds are responsible for infestations after the use of control-measures. The results suggest the possibility that the variation in proportion of dormant seeds in the progeny of single plants may be genetic in origin. If so, intermittent use of herbicides might select for strains of blackgrass with above average proportions of dormant seeds. (Thurston)

### Variation in the growth of *Agropyron repens*

**Clones derived from seedlings.** Last year the growth of *Agropyron* seedlings from seeds obtained in 1969 from different areas (selections) was compared.

Ten clones were established in autumn 1970 from two seedlings from five of the selections and their growth and development compared during 1971. Enough plants were established from 1-node rhizome fragments to enable six replicates of each clone to be sampled on three occasions (March, mid-May and end of August).

One month from planting there were significant differences in the number and length of shoots produced by clones from different areas, confirming the observations in 1970, and these differences persisted throughout the experiment. Later, differences occurred in the total number of shoots produced by clones from seedlings from a given area. The number of primary shoots (those arising from the main shoot) and secondary shoots (those arising from upturned rhizomes) and their relative proportions also varied between clones from both within and between areas. Clones differed in both the amount of shoot and rhizome growth made; in August dry weight of shoots ranged from 33 to 56 g ( $\pm 1.7$ ) per plant and that of rhizomes from 29 to 94 g ( $\pm 4.0$ ) for clones from different areas. Clones from the area that produced the lightest shoot dry weight had the heaviest rhizomes but the opposite was not true. Within areas there was an inverse relation between shoot and rhizome weight; in each area the clone that had the lighter shoots had the heavier rhizomes. The results suggest that the relative size of rhizomes differs between genotypes, is probably heritable and is not simply a physiological consequence of a large growth of shoots. Spike number ranged between clones in 1971 from 17 to 65 ( $\pm 2.5$ ) and clones with least rhizomes tended to have most dry weight of spikes.

**Seedlings derived from a cross of two clones.** To try to decrease some of the variation from genetic differences, seeds from a cross of two clones of *Agropyron* were used in previous experiments. Large differences remained between replicates. In 1971 the amount of variation occurring between seedlings from a cross of the same two clones was estimated when seedlings from uniform-sized seeds were grown on an NIAE-type capillary irrigation bench. Sixty-four seedlings were established on 24 February; half were sampled on 5 May and the remainder on 9 June. By May the number of shoots per plant ranged from 4 to 19 (mean 11.1), rhizomes from 0 to 6 (mean 2.1), shoot dry weight from 0.3 to 0.8 g (mean 0.5) and rhizome weight from 0 to 0.086 g (mean 0.021). At this date plants with fewest shoots had most rhizomes and those with most shoots, fewest rhizomes. Seedlings of the two crosses did not differ at this date. By 9 June plants from the two reciprocal crosses differed in the number and weight of shoots and rhizomes per seedling and the cross that produced more and heavier rhizomes had fewer, slightly lighter shoots. One cross had a mean of 18 rhizomes and 2.9 g rhizome per seedling and the other ten and 1.6 g; the variation within the first was from nine to 26 and 1.3 to 4.2 g and within the second from three to 24 and 0.2 to 2.9 g. Within each

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cross there was no obvious relationship between shoot and rhizome weight. The results indicate a large amount of genetic variation within a cross of two clones. (Williams)

### Staff and visiting workers

Dr. J. A. Spence returned to the University of the West Indies, Trinidad and Dr. W. Fischer joined the department for six months from the Agricultural Extension Service, State of California, U.S.A.

C. J. Taylor was appointed in October 1971 to study the physiology of the potato crop, financed by a research grant from the Potato Marketing Board and Vivienne Frier joined the Department as a Scholar of the Potato Marketing Board. W. Bond left and A. C. Kendall arrived.

U. P. de S. Waidyanatha transferred from Imperial College, to continue his investigations on the physiology of the wheat leaf. Rosemary Cox left after completing two years of study for a Higher Degree of London University.

Sandwich students who worked in the department were D. Page, D. Banfield, B. Corless and Marion Smith.

Joan M. Thurston attended a symposium at Ochrid, organised by the Yugoslav Academy of Science and Arts, and gave a paper on grass weeds.

E. C. Humphries contributed to a symposium on Growth and Morphogenesis at Liège University, Belgium.

C. P. Whittingham and A. J. Keys gave papers at the 2nd International Conference on Photosynthesis at Stresa, Italy.