Report for 1972 - Part 1

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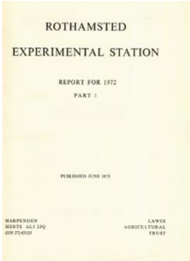
ROTHAMSTED
EXPERIMENTAL STATION
REPORT FOR 1972
PART 1

Botany Department

C. P. Whittingham

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BOTANY DEPARTMENT

C. P. WHITTINGHAM

Introduction

Work began on the study of the effect of aerial pollution on plant growth. In earlier years observations had been made at Woburn which indicated the possibility of damage by pollutants to cereal crops. The first objective is to obtain a quantitative estimate of the yield loss which may occur under conditions where the level of pollutants in the atmosphere is too small to produce obvious visual symptoms. The work is a natural extension of the long-term interests of the department in the study of the growth of cereal plants.

The effect of growth substances on crops had been largely investigated in the past by empirical studies in the field. The variability of the results obtained, e.g. most recently with sugar beet in many N. European countries, indicates that such studies need to be continued for many years before definitive results are obtained; yet they are very time-consuming and labour-intensive. For this reason further laboratory studies, particularly in connection with sugar beet have been initiated in an attempt to devise a laboratory test system which could be used in preliminary screening of potential growth substances.

The departmental glasshouse facilities have been extended with the erection of two 30-ft span aluminium houses on the vacant plot south of the Controlled Environment Building. One, a glass-roofed cage, has direct access to the facilities for growing plants in controlled environments; the other, is a conventional glasshouse for the raising of plant material. This has enabled us to make one of our glasshouses available as an immediate short-term help to the Soil Microbiology Department.

Studies of crop growth

Cereals

Growth and yield on different sites. Yields of winter wheat and barley are usually larger on the Clay-with-flints soils at Rothamsted than on the lighter soils at Woburn and Broom's Barn. A study of factors which may result in the lower yields on the lighter soils is in progress.

Duplicate experiments were set up at Broom's Barn and Rothamsted in 1971 and repeated in 1972 to study the growth, nutrient uptake and yield of winter wheat (var. Cappelle-Desprez) and barley (var. Julia). Nitrogen and water seemed the factors most likely to limit yields at Broom's Barn and so six equal increments of fertiliser nitrogen (from 31 kg/ha to 188 kg/ha) were tested both with and without irrigation. Irrigated plots were watered to bring the soil to field capacity whenever the soil moisture deficit reached 25 mm, up until mid-July. No water was needed before 2 June. The crops were sampled regularly throughout the growing season and measurements of dry weight, leaf area and nutrient content made together with final harvest yields. The dates of sampling at both sites are given with Rothamsted dates first. Top samples were cut from 0·5 m wide strips extending across the 11 middle rows of a 15 row drill-width (except where otherwise stated) to determine total dry weight, shoot numbers and leaf area indices of the crops. Plots of winter wheat were sampled on 18/14 April, 1/2 May, 30/31 May, 2/3 June, 19/20 June, 3/4 July (samples of 20 shoots only), 17/18 July, 31 July/1 August (samples of 20 shoots only) and 21/23 August (ripe crop). The crop was combine-harvested on 24 August. On 16/17 December and 16/17 March, before any treatments were applied,

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smaller numbers of samples were taken to study crop growth during the winter. Barley plots were sampled on 15/16 May, 5/6 June, 26/27 June, 10/11 July (sample of 20 shoots only), 25/24 July (sample of 20 shoots only), 10/14 August (ripe crop). The barley was combine-harvested on 11/23 August.

The chief weather differences between the two sites during the growing season were that air temperatures averaged about 0·5 to 1·0°C warmer at Broom's Barn than at Rothamsted from May onwards and Broom's Barn had about 24 mm less rainfall than Rothamsted. Rainfall was 11 mm more at Rothamsted during April and 14 mm more at Broom's Barn during July. Daily radiation was about 7% greater at Rothamsted than at Broom's Barn from mid-May to mid-June, but about 6% less from mid-June to mid-July.

Soil moisture contents to a depth of 120 cm were measured weekly between 24 March and 16 August on the winter wheat and between 26 April and 3 August for the barley, using a neutron probe. Access tubes for the probe were situated on each wheat plot given 125 kg/ha N and on each barley plot given 94 kg/ha N; these amounts of nitrogen were expected to produce maximum growth (and water use) without causing lodging.

Root growth with selected nitrogen treatments was studied using methods described in *Rothamsted Report for 1966*, 84 and *for 1967*, 94. Winter wheat roots were sampled from plots given 31 or 125 kg/ha N following the top sampling on 1/2 May. Barley roots were sampled from plots given 31 or 94 kg/ha N following the top sampling on 5/6 June. From each plot eight soil cores approximately 7 cm in diameter were taken, four within the rows and four in the spaces, at random positions in the half metre strips from which the tops had been cut. The soil cores were cut into layers at 25, 50, 75 and 100 cm and the corresponding layers of the eight cores from each plot bulked. The roots were washed and cleaned (*Rothamsted Report for 1970*, Part 1, 96) and subsamples photographed to estimate length (using an image analysing computer). They were then dried and weighed.

The following is an account of the results obtained so far. Further information also appears in the report of the Chemistry Department (p. 48).

Winter wheat. On 18/14 April there was a larger shoot dry weight at Rothamsted (69·4 g/m²) than at Broom's Barn (49·1 g/m²) but leaf area indices and shoot numbers were little different (1·07 and 880/m² at Rothamsted, cf. 0·95 and 900/m² at Broom's Barn). By 19/20 June the leaf area index at Rothamsted ranged from 8 to 12 but at Broom's Barn only from 6 to 10 and this difference persisted until 17/18 July. By 20 June water was possibly becoming a limiting factor at Broom's Barn because on most irrigated plots leaf area was 5% greater than on non-irrigated plots; the difference increased to about 40% by 18 July. There was no consistent effect of irrigation at Rothamsted until 17 July. Irrigation did not clearly alter numbers of shoots surviving or total dry weight of shoots, but it delayed leaf senescence.

Nitrogen had no appreciable effect until 30/31 May when at Rothamsted it increased shoot dry weight from 530 g/m² with 31 kg/ha N to 640 g/m² with 188 kg/ha N, surviving shoot number from 580/m² to 790/m² and leaf area index from 6·7 to 9·8. At Broom's Barn the effects of N were similar; it increased shoot dry weight from 496 g/m² with 31 kg/ha N to 656 g/m² with 188 kg/ha N, shoot number from 530/m² to 760/m² and leaf area index from 5·7 to 9·3. These effects persisted to the end of the season.

Barley. Shoot numbers, dry weight and leaf areas at Rothamsted were all less than at Broom's Barn on 15/16 May, but at later samplings only shoot dry weights were much greater at Broom's Barn. Between 15/16 May and 5/6 June shoot numbers at Broom's Barn decreased from 1690 to 1400/m² but at Rothamsted they remained relatively

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constant at about 1370/m²; leaf area index increased from 2·0 to 9·0 at Rothamsted and from 3·6 to 10·2 at Broom's Barn. By 26/27 June leaf area index was greater at Rothamsted than at Broom's Barn and remained on average 35% greater until the last leaf area estimation on 24/25 July. During this period total dry matter production was more rapid at Rothamsted than at Broom's Barn so that at the final harvest Rothamsted yielded slightly more straw and 17% more grain than Broom's Barn.

Nitrogen affected barley growth earlier than winter wheat. At all samplings until 24/25 July on both sites, increasing nitrogen from 31 kg/ha to 186 kg/ha increased shoot number by up to 40%, shoot dry weight by 50% and leaf area index by 100%. Irrigation also had a greater effect on vegetative growth of barley than of winter wheat; on 26/27 June it increased the numbers of surviving shoots by 10% at Broom's Barn. Irrigation increased leaf area index by 10% at Rothamsted, while at Broom's Barn, although irrigation had no effect on leaf area index with 31 kg/ha N, the response to irrigation increased with increasing N until with 186 kg/ha irrigation increased leaf area index from 9·4 to 14, suggesting that as nitrogen supply became non-limiting, water stress was increased and tended to restrict growth.

Neither abundant nitrogen nor irrigation completely eliminated the difference in growth between Rothamsted and Broom's Barn either for wheat or for barley. Leaf area and dry matter production of both crops at both sites responded similarly to N. Leaf area of both crops was increased by irrigation at Broom's Barn, but only of wheat at Rothamsted. It therefore appears that the Broom's Barn soils could not supply enough moisture for optimum growth of either crop, whereas Rothamsted soils supplied enough for barley but not for wheat. Whether the nitrogen and water factors alone can account for all the differences between sites cannot be determined until more of the results have been analysed. (Welbank and P. J. Taylor)

Plant water relations. On 4, 11, 14, 17 and 26 July plant water potentials of wheat at Rothamsted were measured using a pressure bomb. On each occasion ten ears and ten leaves were sampled from one irrigated and one non-irrigated plot given 125 kg/ha nitrogen.

Water potentials of both ears and leaves were less (more negative) on the non-irrigated than on the irrigated plot and the water potential of leaves was less than that of ears. On the non-irrigated plot the ear water potential decreased from −6·4 bar on 4 July to −10·8 on 14 July and then increased to −7·3 bar on 17 July and −8·2 bar on 26 July. The corresponding leaf water potential was −8·8 bar on 4 July, −16·8 bar on 14 July and increased to −13·5 bar on 17 July and −16·8 bar on 26 July. On the irrigated plot water potentials of the ears decreased by a smaller amount between 4 and 14 July, from −5·5 to −7·6 bar and increased to −5·6 bar on 17 July and −5·2 bar on 26 July. Similarly the leaf water potentials decreased by a smaller amount from −8·9 to −12·2 bar increasing to −10·8 bar on 17 July and decreasing again to −13·7 bar on 26 July. The plant water potentials experienced on 14 to 26 July were sufficiently negative to affect growth and the smaller leaf water potentials on non-irrigated than on irrigated plots could account for the increased rate of leaf senescence. (Lawlor)

Response of spring wheat to large amounts of nitrogen. Extra nitrogen does not increase grain yield of modern stiff-strawed varieties of wheat (that do not lodge) as much as might have been expected from studies with older varieties. The efficiency of the leaf area in grain production seems to decrease with increasing nitrogen, i.e. amounts of nitrogen that still increase leaf area give proportionately less increase in grain yield. The physiological factors limiting the response of wheat to nitrogen was investigated with Kleiber spring wheat at Rothamsted. Treatments were all combinations of nine nitrogen

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levels (0–200 kg/ha N) and two sowing rates (which produced 213 and 512 $\pm$ 8 plants/m^2). Observations on tillering, dry weight, leaf area, and nutrient content were made and also measurements of light penetration into the canopy, and changes in moisture content of the soil. The rate of photosynthesis of the top leaves, the nature of the immediate products of photosynthesis and the distribution of photosynthate were all investigated using radio-active carbon dioxide. Such observations should help determine whether the lack of response to nitrogen is because leaf area is above the optimum or because of some change in metabolic balance within the plant. (Thorne)

CCC on dwarf spring wheat. Studies were continued on the effect of CCC (0, 1·1, 2·2, 3·3 kg/ha CCC) and nitrogen (75, 150, 225 and 300 kg/ha N) on growth and yield of four varieties of dwarf spring wheats.

Charles Peguy (formerly called Benoist 257) yielded best (mean 5·28 t/ha) followed by Tobari 4·84, 6WUK4 4·72 and 6WUK3 2·53 t/ha. Increasing nitrogen increased yield in all varieties except Charles Peguy where it decreased yield, but CCC increased yield only in 6WUK3 and 4. There was no lodging. Nitrogen had little effect on straw height, but CCC decreased height up to 17% with increasing amounts in all varieties.

6WUK3 had most ear-bearing shoots per unit area. Nitrogen increased ear number in all varieties and CCC decreased ear number. Charles Peguy had most grains per ear, but they were the smallest and 6WUK3 least. Tobari had the largest grains. Both nitrogen and CCC decreased grain size but not to any great extent. The small number (6·4) of grains per ear in 6WUK3 compared with 10 to 14 in the other varieties undoubtedly contributed to its low yield in spite of the fact that it had most ears. Grain number per ear was obviously correlated with fertile spikelet number, which however was not greatly affected by nitrogen or CCC.

Comparing the performance of the same variety (Charles Peguy) in the two years 1971 and 1972, while straw yielded about the same, grain yields were 20% better in 1972 chiefly because there were more ears. Nitrogen increased the number of ears in each year but the effect of CCC was opposite in that it decreased ear number in 1972. There were more grains per ear in 1972 than in 1971, nitrogen decreased their number while CCC slightly increased grain number, but grains were smaller and both CCC and nitrogen further decreased their size. (French)

Effect of temperature on grain growth. Previous experiments in which either the whole of the plant or just the ears were warmed indicated that warming the ears alone increased the proportion of assimilate that moved to them (*Rothamsted Report for 1971*, Part 1, 104). However, the grain yield was not increased because the increase in ear weight was only small and did not persist; warmed ears matured faster than cool ones and yielded less grain. The smallness of the effect may have been related to the small temperature difference imposed (5°C), and to continuation of treatment throughout grain growth resulting in a shortening of the growth period. In a similar experiment in 1972 wheat plants, variety Kolibri, were grown outdoors until seven days after anthesis and then transferred to growth rooms with visible radiation of 645 J cm^{-2} during a 16-hour day and a temperature of 15°C. The ears alone were enclosed in transparent boxes through which air at 15, 20 or 25°C was passed.

Compared with ears kept at 15°C, warming to 25°C increased ear weight by 20% after ten days of treatment, by 7% after 20 days and decreased it by 27% at maturity after 60 days. Stem weight was decreased at ten and 20 days and increased at 60 days. Warming ears to 20°C had intermediate effects. These responses to differences in ear temperature can be understood best by considering the three intervals between samplings separately. During the first ten days of treatment the increase in ear weight was 40% greater (211

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mg/ear) at 25°C than at 15°C. Stems increased 215 mg less with ears at 25°C so ear temperature did not affect the change in total dry weight. During the second ten-day period ears were growing slightly faster than during the first period—at 70–80 mg/day—but warming ears had negligible effects on the growth rate of ears or stems. During the last period, which extended for 33 days, ears at 25°C increased in weight by only 288 mg and those at 15°C by 1274 mg. Stems of warmed ears lost 652 mg less dry weight than those of cool ones. Consequently, at maturity ears weighed less and stems weighed more when ears were at 25°C than when kept at 15°C, although the reverse had been true earlier.

Warming seemed to increase the storage capacity of the ears early, so that assimilates moved to the ear rather than accumulating in the stem, but hastened maturity so that later assimilates accumulated in the stem. Earlier maturity of the ears was also shown by early fading of the green colour at the end of the second period. Warming ears had no effect on senescence of leaves and stems until the last 20 days when leaves died more slowly on shoots with warmed ears. The effect of ear temperature on maturity seemed to have started during the first ten days of treatment; later growth and final dry weight of ears transferred from 25 to 15°C after ten days treatment were intermediate between those of ears continuously at either temperature. Ears transferred after 20 days treatment grew slower than those transferred earlier and faster than those continuously at 25°C. Their final dry weight was also intermediate.

Information of the changes in gibberellin content of the ears, the distribution of ^{14}C applied to the flag leaf at ten and 20 days, and the diurnal changes in sugar content of the flag leaf was also obtained. These analyses are as yet incomplete. (Thorne)

Effects of aerial pollutants on plant growth. Woburn farm lies 2 km to the south of the Bedfordshire brickfields and previous observations have suggested the possibility that the growth of cereal crops might be affected by air pollutants (*Rothamsted Report for 1969*, Part 1, 174–175). In the present season pot plants of 16 indicator species known to be sensitive to either fluoride or sulphur dioxide were grown at Rothamsted and Woburn. At neither place was there evidence of sulphur dioxide damage but there were indications of some effect probably due to fluorides at Woburn. Sweet corn showed marked chlorosis on the leaf tip and analysis showed this portion of the leaf to have high fluoride content. There was only a small but probably significant difference in total percentage sulphur in leaf samples in crops at Woburn and at Rothamsted. When leaves from hawthorn hedges were collected at progressive distances from the brickworks there was a marked reduction in percentage total sulphur with distance from the brickworks; obvious leaf damage was only observed very close to the brickworks.

Measurements of leaf injury on gladioli leaves again showed the probability of damage resulting from atmospheric fluorides at sites near to the brickworks. In future work the growth of a cereal crop will be investigated within polythene growing houses which contain either unfiltered air or air filtered through a particulate filter and a chemical filter to remove major air pollutants. (Hoskin and Dawson)

Potatoes

Physiology of the potato in relation to yield. There is evidence that the rate of photosynthesis of the potato leaf may be dependent on the activity of the tubers attached to the plant, since, when the products of photosynthesis are allowed to accumulate in leaf tissue, net assimilation rate is reduced. It follows that tuber initiation should produce detectable changes in photosynthetic rate and possibly also in the nature of assimilates and in their pattern of distribution in the plant as a whole. Potatoes, var. King Edward, were grown in controlled environments to investigate this relationship. Light intensity,

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photoperiod and nitrogen were varied to modify tuber initiation times and tuber growth rates. The results showed that tuberisation could be successfully regulated, but the treatment interactions were complex. Plants were grown under eight-hour days (SD) or eight-hour plus a 20 minute night break (NB) with each photoperiod at two radiation levels (370 J cm^{-2} and 185 J cm^{-2}). The introduction of a night break delayed tuber initiation by one week at the higher light intensity and by three weeks in the dim treatment. Changes in net assimilation rate and photosynthesis were observed, but contrary to expectation, the changes were not correlated with tuber initiation times.

Related investigations are being undertaken to assess the influence of water shortage on the relationship between the growth and metabolism of leaves and tubers of potato plants under field conditions. Standard irrigation practice was compared with non-irrigated plots. $1\frac{1}{4}$ to $1\frac{1}{2}$ in. of water was applied when a $1\frac{1}{4}$ to $1\frac{1}{2}$ in. soil deficit was obtained. Growth analysis harvests were made at regular intervals to determine tuber and foliage development. Data on photosynthetic rate and carbon metabolism were obtained using $^{14}CO_2$. An apparatus modified from earlier designs was used to feed an individual leaflet with CO_2 at 330 ppm total and 3·35 mCi/$mmol^{-1}$ specific activity for a 15-second period. Preliminary determinations of leaf water potential were made. Irrigation increased yield from 44 to 58 t ha^{-1} and this was probably related to two effects; an increase in leaf area resulting in a greater leaf area duration, and the maintenance of a high photosynthetic rate. Plants on non-irrigated plots showed a considerable depression in photosynthesis as the soil water deficit reached 6·5 in. Leaf water potential measurements taken in August when the soil water deficit exceeded 5·0 in. showed the irrigated plots (—4·32 bar) to be at just over half the value of the control plots (—7·77 bar) between 1000 and 1100 hours. From noon to late afternoon the values decreased to —10·42 bar in the control plots and —6·72 bar in the irrigated treatment. Mean rates of photosynthesis taken between 1430 and 1600 hours were $4{\cdot}19 \times 10^3$ and $9{\cdot}16 \times 10^3$ cpm respectively. In future it is planned to study in detail the diurnal as well as seasonal fluctuations in photosynthesis and their influence on tuber growth. (C. J. Taylor)

Sugar beet

Sugar content of sugar beet. Sugar stored in the roots of sugar beet has often been regarded as the excess of photosynthate over that needed for the growth of the plant. Experiments in which photosynthesis has been decreased by halving the amount of radiation received by the plant, either by shading field grown crops (*Rothamsted Report for 1968*, Part 1, 97) or by altering light intensities in controlled environment rooms (*Rothamsted Report for 1971*, Part 1, 102) have shown that although the *amount* of photosynthate entering the root was determined by the photosynthetic capacity of the plant, its partition between root growth and sugar storage was controlled by factors within the root itself. A previous study of the effect of nitrogen fertilisers on sugar concentration in the root indicated the importance of average cell size within the roots in determining the average sugar concentration (*Rothamsted Report for 1969*, Part 1, 110). A further study has been made of varietal, plant spacing and site differences on root sugar concentrations.

For the variety × site study, roots of four commercial varieties, Sharpe's Klein Polybeet (SKP), Bush Monobeet, Hilleshog Monotri and Amono, were obtained from the trials of the National Institute of Agricultural Botany at Bury (sandy loam) and at Ely (black fen peat). Roots used to examine the effects of plant density were from the variety Sharpe's Klein E grown at densities of 7·5, 15, 30 and 50 thousand plants/acre at Broom's Barn Experimental Station.

Both root weights and sugar concentrations varied considerably between individual roots. SKP and Bush Mono produced heavier roots (1·13 kg) with smaller sugar con-

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centrations (14·8%) than Monotri and Amono (0·95 kg and 16·7% sugar), but all four varieties yielded similar amounts of sugar per root (150 g). Averaged over all varieties, plants grown at Bury produced larger roots than plants grown at Ely (1·12 kg compared with 1·00 kg) but with smaller sugar concentrations (15·3% compared with 16·3%); roots from Bury yielded 170 g of sugar per root, 20 g less than at Ely. Plants grown at populations of 7·5, 15, 30 and 50 thousand/acre produced roots weighing 1·76, 1·32, 0·74 and 0·54 kg respectively, with sugar concentrations of 13·1, 14·4, 16·1 and 16·8%.

Transverse sections were cut from each root 1 cm beneath the lowest leaf scar and the areas of the alternating zones of vascular meristematic tissue and parenchyma tissue within the concentric peripheral rings measured. Duplicate samples of tissue (42·4 mm^3) were taken from both tissue zones of the five innermost rings, and the sugar content and the number and mean cell size determined. The number of cells within the whole root was calculated as the total of cells within the vascular and parenchyma zones of the five rings sampled and the mean cell size of the root calculated as the weighted mean size of these cells. The amounts of sugar per cell were calculated and the quadratic regression of sugar per cell on cell volume calculated for each root using the ten values obtained from the two tissue zones of each of the five peripheral rings.

Differences in root size within and between the four varieties grown at Ely and Bury were more closely associated with differences in cell size than in number of cells. The regression of root weight on number of cells within the root over all varieties and both sites accounted for 42% of the variation in root size. A similar regression on the mean size of the root cells accounted for only 5% of the variation in root size, but this was partly obscured by a negative relation between the numbers and sizes of the cells in the roots, so the multiple regression on both parameters accounted for nearly 60% of the variation in root weight. However, differences in root weight caused by increasing plant density were associated more or less equally with differences in both the number and size of the root cells. Regressions of root weight on the number of root cells and on their mean size individually accounted for 40% of the variation in root size, and the multiple regression including both parameters accounted for 80%.

The differences in sugar concentration within and between varieties grown on different sites and those caused by increasing plant density were mainly associated with change in average cell size. In both cases the negative regression of sugar concentration in the root on the mean size of the root cells accounted for 55% of the variation and this was not improved by adding the specific sugar per cell in the multiple regression.

The conclusion is that selection for high sugar yield should take account of both cell size and cell number in the root because large roots consisting of many smaller cells are to be preferred to those with fewer large cells. (Milford)

Defoliation effects upon growth and yield. Experiments were continued to study the effects of removing certain leaves on the growth of sugar beet in pots.

The data has not yet been fully analysed but retention of leaves 6–20 only resulted in a small (1%) decrease (unlike last year) in the mean yield of fresh root. Unwanted leaves in this treatment were removed (by scissors) when large enough to handle. When the growing point was treated with an amino acid to retard or stop its growth, the effect soon disappeared; also, when the growing point was excised by cork borer no further main leaves were produced, but both these treatments encouraged production of axillary leaves and the net yield was decreased 13%. When leaves 6–20 were removed yield was 36% of the undefoliated controls.

A second experiment attempted to measure the contribution to yield of groups of five leaves up to the twentieth. Groups were *removed*, leaving all others to function as they were produced, or *retained* when all others were removed as they appeared. Axillary

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leaves were also removed in all plants to avoid complications by their presence. Preliminary analysis of the results indicate that leaves 1–5 contributed about 6%, 6–10 17%, 11–15 22%, 16–20 26% and all those above 20 up to 50 or 60 the remaining 30% of the total dry weight of the plant. (French)

Growth substances

Cereals. There is evidence that the relative abundance of growth substances may regulate the movement of carbohydrates in plants. Experiments are being carried out with wheat to examine the part played by growth substances in the development of the grain.

Jenner (*Australian Journal of Biological Sciences* (1968) **21**, 597) showed that wheat ears detached soon after anthesis continued to accumulate starch for several days when placed in sucrose solution. We have investigated how far growth substances modify this process. Ears of cv. Kleiber from field-grown plants were stood in 5% sucrose solution, changed every day for four days. Five spikelets were taken from one side of each ear at the beginning of the experiment and from the other side at the end. The difference in dry weight between the two groups of spikelets was 130 mg, an increase of 36%. Indoleacetic acid and gibberellic acid between 0·01 and 1·0 μg/ml had no effect, nor had 1·0 μg benzyl adenine applied to the stem. 1·0 μg/ml kinetin induced a significantly greater increase in dry weight, and so did 10 μg (-)-kaurene (a precursor of gibberellin) applied to the stem; the two treatments combined had no greater effect.

When ears were incubated with ^{14}C-sucrose for 48 hours after 24 hours in non-radioactive sucrose, (-)-kaurene caused a significant increase in radio-activity in both the aqueous ethanol soluble compounds and the starch of the grain. Application of (-)-kaurene, kinetin and indoleacetic acid combined also increased radio-activity in the aqueous ethanol soluble fraction, but the increase in the starch fraction was not significant; nor was that in the aqueous ethanol soluble fraction when kinetin alone was used.

Last year it was shown that kinetin and (-)-kaurene can both induce an increase in the endogenous gibberellin concentration in detached ears of Kolibri. In a similar experiment this year with Kleiber a greater increase in gibberellins was found in the final spikelet samples after four days incubation when the ears were treated with (-)-kaurene or benzyl adenine, but kinetin gave a variable response. An increase in endogenous gibberellin appears to be associated with a greater accumulation of starch, but some treatments increase one factor without affecting the other. The lack of response to applied gibberellic acid is not necessarily inconsistent with this effect since a concentration gradient within the ear may be required.

Semi-dwarf wheat cultivars derived from Norin 10 do not respond to applied gibberellins by increased vegetative growth. Also, many of these cultivars contain high levels of endogenous gibberellin during growth up to ear emergence. The endogenous gibberellin content of ears of several dwarf cultivars at weekly intervals after anthesis was compared with that of the flag leaves and top internodes, using plants of the Japanese cv. Waijata No. 1, the Plant Breeding Institute cvs. TW 161 and TL 363/30 and, for comparison, Kolibri. The internodes were extracted by a centrifugal technique which is thought to remove substances in the vascular bundles. The gibberellin-like activity in the stems increased sharply approximately three weeks after anthesis (third harvest), in three cultivars, and showed a small but earlier increase in TW 161. The gibberellin-like activity in the ears tended to decrease somewhat at the second harvest, when the grains just reached full length but at the third harvest the gibberellin-like activity per ear had increased in all cultivars except Waijata No. 1. The gibberellin-like activity in the flag leaves fluctuated, being lower at the middle harvest in Waijata and TW 161, but showing

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a marked decrease at the final harvest in Kolibri and TL 363/30, probably in the latter cases accompanying the onset of senescence. Apart from these two samples the amount of gibberellin-like activity per g fresh weight was higher in the leaves than the ears in three cultivars, but relatively lower in the leaves of TW 161. All three cultivars derived from Norin 10 did not show a gibberellin distribution distinctly different from Kolibri.

The effects of growth substances on dry weight increase in detached ears of these cultivars was also examined. Three samples of ears were taken at different times after anthesis and treated as already described for Kleiber. No consistent responses to growth substances were found from this material during four days incubation although the increases in dry weight were at least as great in detached ears as in ears remaining on the plants.

Interaction between leaves and ears. Ears and leaves were removed from the main stem of wheat plants (cv. Kolibri) at several stages of growth to test the possibility that the ears and leaves compete for growth substances. Tillers were removed from the plants as they appeared. Samples of ears and flag leaves were extracted at later stages and their contents of cytokinin, gibberellin, auxin, tryptophane and chlorophyll were estimated.

Removing ears before anthesis shortened the uppermost stem internode; later removal of ears or of leaves was less effective. Factors essential for stem elongation may be produced in the ear or the ears may compete with the stem for substances produced elsewhere. Excising ears before anthesis at first had little effect on the leaves, but later the flag leaves became heavier and contained less gibberellin and chlorophyll, but more tryptophane, per unit fresh weight of leaf. Thus, flag leaves senesce earlier when the ears are removed. The auxin and cytokinin contents of the flag leaves were unaffected by removing ears.

When flag leaves were removed before anthesis the chlorophyll and tryptophane contents of the ears were unaffected but their content of auxin, gibberellin and cytokinin increased, possibly because of lack of competition from flag leaves. Although removing all the leaves from stems before anthesis increased the cytokinin content of the ears, as previously, their gibberellin content decreased. (Radley and Wheeler)

Sugar beet. The growth studies of sugar beet reported in the previous section suggest that the accumulation of sugar in the root may be related to the number of cells present. This would be expected to relate to the presence of hormonal substances and this year a study of the hormone physiology of the beet plant has begun.

Work is in progress to investigate the endogenous growth substances present in different parts of the plant at different stages of development and to correlate their occurrence with processes of growth and development. Ethanolic extracts of the tops and roots of young plants with 3–4 true leaves contained at least two gibberellin-like substances, and the amount in the roots was greater than in the tops when expressed on a unit fresh weight basis. Extracts from plants with 8–9 true leaves contained similar substances but amounts were lower than in the younger plants, and there was more activity in the tops than the roots. At the later stage there is a higher proportion of non-meristematic tissue in the root, so that the gibberellin concentration is higher in immature tissue.

Gibberellin-like substances have been extracted from the vascular elements of petioles by centrifugation but more were obtained by subsequent extraction with ethanol. Gibberellic acid may be present both in the vascular stream and in the non-conducting tissue. The centrifugal extracts also contained an auxin-like substance similar to IAA, and two cytokinin-like substances. However, attempts to demonstrate the presence of these substances in ethanolic extracts of tops and roots have been unsuccessful, although traces of auxin-like activity were found in the tops. Probably the alcoholic extracts also contain inhibitory substances which affect the bioassay.

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The effect of gibberellic acid and kinetin applied either to the leaves or roots was studied using young plants growing in sand culture in a glasshouse. 10 μg/ml GA_3 gave a significant increase in root size six weeks after the commencement of the experiment, and the effect was greater when applied to the root system. Kinetin at 0·1 μg/ml appeared to be without effect on root size and neither GA_3 nor kinetin had any significant effect on concentration of sugar in the root. The promotion of root size by GA_3 was due to an increase in the expansion of the concentric ring structure, since in the treated roots an average of five rings had begun to expand, whereas this number was only four in control plants. The synthetic cytokinin, 6-benzylamino-9-(tetrahydropyran-2-yl)-9H purine (SD 8339), had an inhibitory effect on root and shoot growth at 0·01 μg/ml.

Other experiments are in progress using rooted single sugar-beet leaves but here the variability of the plant material is great. (Garrod, Radley and Wheeler)

Metabolism and plant growth

Measurement of photosynthetic activity in the field. The experiments which were initiated last year to determine photosynthetic rates in the field by exposing parts of leaves to radio-active carbon dioxide (*Rothamsted Report for 1971*, Part 1, 108) were extended.

Last year observations were confined to one type of apparatus based on the design of Austin and Longden (*Annals of Botany* (1967) **31**, 122) but this year studies have been made also with an apparatus based on the design of Shimshi (*Journal of Experimental Botany* (1969) **20**, 381). The methods differ in the design of the leaf chamber and the rate of air flow through it. The relationship between the observed rate of photosynthesis and incident light intensity was not the same for the two methods. Further investigations with plants growing in controlled environments were undertaken to show whether the difference has a biological significance.

These measurements will be related to measurements of carbon dioxide exchange using the infra-red gas analyser and longer term measurements of dry weight increase. Published rates of photosynthesis of single leaves or small plants of sugar beet and barley are similar although sugar beet is consistently observed to have a greater net assimilation rate than barley. On five occasions the gas exchange of four sugar beet and four barley plants growing in solution culture was measured continuously for six days with the infra-red gas analyser and the change in dry weight and leaf areas also determined. For both species the increase in dry weight calculated from the carbon dioxide exchange (assuming conversion to hexose) agreed closely with the observed figure. Net assimilation rate of barley was half that of sugar beet because photosynthesis was half. There was little difference between the dark respiration rates. Initial dry weights and leaf areas were: sugar beet 0·13 g and 0·20 dm^2; barley 0·14 g and 0·29 dm^2. Final dry weights and leaf areas were: sugar beet 0·87 g and 1·32 dm^2; barley 0·61 g and 1·29 dm^2. Thus with plants of this size grown in a constant environment at 20°C with 16 hours of visible radiation at 103 W m^{-2} intensity the net assimilation rate of sugar beet is greater than that of barley. Further experiments will correlate these measurements with observations of the rate of uptake of carbon dioxide using radio-active carbon dioxide. (Whittingham, Thorne, Ford and Kendall)

Water stress and carbon dioxide assimilation. Carbon dioxide exchange was measured with 0·03% carbon dioxide in the mature flag leaf or second leaf of Kolibri wheat grown in polyethylene glycol solutions (*Rothamsted Report for 1970*, Part 1, 100 and *for 1971*, Part 1, 109). The compensation point in 21% oxygen increased from 60 ppm carbon dioxide to 90 ppm at −18 bar ψ (leaf water potential) and, at more severe stress, increased to over 300 ppm. Apparent photosynthesis with 160 W m^{-2} visible radiation

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and 25°C decreased from 30 mg dm^{-2} h^{-1} at −5 bar ψ to zero at −18 bar ψ and at greater stress there was a net loss of carbon dioxide from the leaf.

Photorespiration was estimated by measuring carbon dioxide release into carbon dioxide free air in the light and dark. Carbon dioxide release into carbon dioxide free air with 21% oxygen in the light was 6 mg dm^{-2} h^{-1} at −5 bar ψ. The peak carbon dioxide release in the dark immediately following illumination was about 9 mg dm^{-2} h^{-1} and steady dark respiration 2 to 3 mg dm^{-2} h^{-1}. Increasing water stress decreased the carbon dioxide released progressively and at −18 bar ψ, 1 to 2 mg dm^{-2} h^{-1} of carbon dioxide was released in the light compared to a dark respiration of 4 mg dm^{-2} h^{-1} with increasing stress. Dark respiration showed some increase but carbon dioxide released in the light and that released immediately upon turning off the lights were both decreased. Thus, water stress does not increase photorespiration relative to apparent photosynthesis but as photosynthesis decreases so does photorespiration.

To confirm this the effects of oxygen partial pressures were studied. At −5 bar ψ apparent photosynthesis increased from 24 mg dm^{-2} h^{-1} to about 35 mg dm^{-2} h^{-1} when 21% oxygen was replaced by 2% oxygen; at −17·5 bar ψ apparent photosynthesis was 0·5 mg dm^{-2} h^{-1} and 0·8 mg dm^{-2} h^{-1} in 21% and 2% oxygen respectively. Lower oxygen concentrations decreased the release of carbon dioxide into carbon dioxide free gas in the light from 7·5 mg dm^{-2} h^{-1} at 21% to 0·6 mg dm^{-2} h^{-1} in 2% oxygen. With a stress of −17·5 ψ bar the carbon dioxide released to a carbon dioxide free gas stream with 2% oxygen decreased to 1·4 mg dm^{-2} h^{-1} from 1·6 mg dm^{-2} h^{-1} at 21%. Dark respiration was not affected by change in oxygen concentration.

Compensation point decreased from 50 to 60 ppm in 21% oxygen to about 8 ppm in 1% to 2% oxygen with ψ of −5 bar. Increasing oxygen concentration to 30% increased compensation point approximately linearly to 80 ppm even at −14 bar ψ. With severe stress of about −20 bar ψ, the compensation point (70 to 100 ppm) was not dependent upon oxygen concentration. However, attainment of equilibrium at these stress levels is slow and it was difficult to maintain constant oxygen levels at given water stresses to ensure complete equilibrium.

With increasing water stress the stomata close, approximately linearly, stomatal resistance r_s at −5 bar ψ ($\simeq$ 1 to 2 sec cm^{-1}) rising at −18 bar ψ to 20 sec cm^{-1}. As apparent photosynthesis decreases so does carbon dioxide release also. It is possible that increasing r_s allows re-cycling of photorespired carbon dioxide so that the estimate of photorespiration becomes proportionally smaller with stress. (Lawlor)

$^{14}CO_2$ feeding of water-stressed plants. The effect of water stress on distribution of carbon between different products of photosynthesis was studied by short-term feeding of radio-active carbon dioxide. Wheat was grown in polyethylene glycol solution of −0·4 (control), −5·0, −10·0 and −15·0 bar ψ. The flag or second leaf was fed 10 μCi of $^{14}CO_2$ in the presence of 300 ppm $^{12}CO_2$ for 15 seconds with 160 W m^{-2} visible radiation and at 25°C either 4, 24, 48 or 72 hours after application of the polyethylene glycol solutions. Samples were frozen in liquid nitrogen immediately after feeding and extracted in boiling ethanol. The concentrated extract was separated by two dimensional T.L.C. on cellulose layers. A reduction of 5% in total assimilation at −7 bar ψ, 36% at −12 bar ψ, and 96% at −17 bar ψ was observed compared to the −5 bar ψ control.

Almost 50% of the total ^{14}C assimilated was found in phosphoglyceric acid and this was more or less constant with time and degree of stress. Fifteen per cent of the radio-activity incorporated was observed in sucrose but this decreased linearly with increasing stress to about 5% at −18 bar solution osmotic potential. Seven per cent radio-activity was in alanine with an indication that the percentage increased with stress; glycerate also increased from 4 or 5% at −5 bar ψ to about 9% at −18 bar ψ. Glycine remained more

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or less constant from −5 to −12 bar ψ but incorporation increased markedly to 9% at −18 bar ψ. Serine also increased with increasing water stress. A similar change in products of photosynthesis has been observed with potato plants growing in the field under conditions of water stress. (Lawlor)

Enzymes associated with photorespiration. Serine synthesis from glycine has been shown to be catalysed by mitochondria from wheat leaves; it is accompanied by electron transfer along the mitochondrial electron transport chain. The process was shown to be accompanied by phosphorylation of ADP. The electron transfer to oxygen has three constituent parts each of which can be coupled to phosphorylation. Ferricyanide can substitute for oxygen as a terminal electron acceptor but accepts electrons between coupling sites II and III. The amount of ADP phosphorylated was then halved whilst the rate of serine synthesis was slightly increased. Amytal, a powerful inhibitor of electron transport between coupling sites I and II, inhibited synthesis of serine from glycine only slightly. Therefore, coupling site I and reduction of the internal pool of NAD in the mitochondria are not involved. Antimycin A which inhibits transfer of electrons in the region of coupling site II strongly inhibited serine synthesis. Hence, the oxidation of glycine to serine must transfer electrons to the electron transport chain at a site between coupling sites I and II. Therefore, with oxygen as terminal electron acceptor, a maximum of two molecules of ATP may be formed for each molecule of serine synthesised.

Purification of mitochondria from leaves without loss of their ability to catalyse serine synthesis was difficult to achieve consistently. Density gradient centrifugation using sucrose solutions was accompanied by considerable loss of activity; when caesium chloride replaced sucrose greater activity was obtained but the method was unreliable. The variability observed may be as much a function of the source of leaf material as of the media used for grinding and resuspension of the particles. Young leaves from the top of mature tobacco plants gave preparations that rapidly lost the ability to catalyse synthesis of serine from glycine. Particles having the greatest and most stable catalytic activity were obtained from fully expanded but not yet senescent leaves.

Improved media were sought for the preparation of mitochondria from leaves that catalysed rapid synthesis of serine from glycine. The main constituents required were shown to be citrate and bovine serum albumin with sucrose, sorbitol or mannitol to provide the correct osmotic strength. There was a disadvantage in using media of high ionic concentration especially in the absence of sucrose. For example, particles extracted in the presence of 0·2*M* KCl or 0·2*M* Tris-HCl and resuspended in fresh medium with the same salt concentration had little or no activity. Addition of ATP and magnesium had little effect. Media with high ionic strength extracted substances which could be separated by dialysis into high and low molecular weight components; both were needed together to conserve the catalytic activity.

Typical rates of CO_2 evolution by photorespiration *in vivo* range from 10 to 75 μmol h^{-1} g^{-1} fr. wt. Our most active preparation catalysed the formation of one molecule each of serine and CO_2 from two molecules of glycine at a rate of 43 μmol h^{-1} g^{-1} fr. wt. Much of the CO_2 evolved in photorespiration could therefore be accounted for by this reaction.

Measurements were made of the rate of serine synthesis catalysed by preparations from leaves of wheat plants growing in the field. Flag leaves were harvested from 0530 to 1930 hours at one- or two-hourly intervals, homogenised and the ability of the preparations to catalyse synthesis of serine from glycine measured. At 0530 leaf preparations catalysed the reaction at rates equivalent to 43·1 μmol h^{-1} g^{-1} fr. wt. but for the rest of the day the rate was between 34·1 and 37·1 μmol h^{-1} g^{-1} fr. wt. Flag leaves from wheat receiving large applications of nitrogenous fertiliser gave extracts that converted glycine to serine

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more rapidly (42·5 μmol h^{-1} g^{-1} fr. wt.) than leaves from wheat receiving little nitrogenous fertiliser (34·8 μmol h^{-1} g^{-1} fr. wt.). Extracts of flag leaves of wheat from the field catalysed serine synthesis from glycine three-to four-fold faster than extracts of pea leaves grown at low light intensities and 18°C in a growth room.

Preliminary experiments have sought those enzymes in leaves responsible for the further metabolism of serine to sucrose. Glycine or serine were converted to D-glycerate in reaction mixtures containing a suspension of particles including mitochondria and peroxisomes, chloroplasts capable of CO_2 fixation, an extract containing soluble protein, glyoxylate and $NADH_2$. Whilst some PGA and sugar phosphates were formed, their synthesis was not entirely dependent on the presence of intact chloroplasts, and in none of the experiments was there evidence of sucrose synthesis. (Keys, Bird and Cornelius)

Weed biology

Park Grass. No increase was seen in the number of species occurring on the recently limed sections (c) of the previously acid plots nor did the relative abundance of the species already present differ greatly from 1971. The botanical compositions of section (b) of plots which have received lime since 1965 have not changed.

One change resulting from the addition of lime to a previously unlimed plot has been an increase in the amount of *Holcus lanatus* on plot 9c. This change is unexpected since *Holcus* is most abundant on the very acid end of plots receiving the largest amount of ammonium sulphate and complete minerals. In the past *Holcus* was abundant on the unlimed half of plot 9 but more recently *Anthoxanthum odoratum* has been the dominant species. This is still so on plot 9d, i.e. there has been no increase in *Holcus* on the unlimed plot.

In the mid 1960s some *Agrostis* became established in the N.W. corner of plot 11^2d and subsequently the area has greatly increased; the area was measured this year so that future changes can be quantified. This year, more *Trifolium pratense* occurred on plot 8d than on 7d throughout the year; in most seasons more *Trifolium pratense* occurs on the unlimed section of plot 7 (PKNaMg) than on plot 8 (PNaMg).

These changes show that, in addition to the now well-known differences in botanical composition between the plots of Park Grass caused by different fertiliser treatments, more subtle differences are occurring with time in response to changing selection pressures within plots. (Williams)

Broadbalk. Section 8 (wheat, no herbicides), last fallowed in 1963, was fallowed again in 1972 because it had become very weedy (*Rothamsted Report for 1971*, Part 1, 112).

At harvest, the wheat sections with herbicides were remarkably free of weeds, some plot-sections having fewer than five weed plants. The main species in 1972 were all perennials. *Convolvulus arvensis* was more abundant, lush and darker green than usual. *Equisetum* was dense and extensive on some low-N plots. Large patches of *Agrostis gigantea* have developed on five plots, mainly on section 9 (continuous wheat since 1958, with herbicides) with smaller clumps or isolated plants on six others. *Agropyron repens*, although still present, has not spread and is a little less extensive and dense than in recent years on some plots. This probably results from applying aminotriazole to the stubble as a spot-treatment in several seasons and over the whole of the herbicide-treated sections in autumn 1971.

The potatoes (section 4) were also free of weeds. They were not severely infested with *Equisetum*, although it was present on several plots.

Beans (section 7) were infested with *Polygonum aviculare* as in previous years (*Rothamsted Reports for 1968*, Part 1, 110; *for 1970*, Part 1, 106, and *for 1971*, Part 1, 112), and

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Polygonum convolvulus was abundant, especially on the dung plots. *Atriplex patula* was dominant on the no-K plots and was so abundant that it obliterated other species on plot 12 (PNa only). Eleven out of 19 plots had large, dense patches of *Equisetum*, i.e. it was more prevalent this year in beans than in potatoes, but it was on section 7 that the potatoes were so badly infested in 1968. Position on the field therefore affects density of *Equisetum*, as well as the cropping regime (*Rothamsted Report for 1970*, Part 1, 106).

Kickxia elatine occurred again in wheat on the unmanured plot 3 (*Rothamsted Report for 1971*, Part 1, 112). (Thurston)

Hoosfield. Continuous detailed records for Hoosfield have not been taken since 1948 when routine spraying with herbicides began, but the plots have been inspected for major weed-problems since the new cropping-regime was introduced in 1968.

The barley stubble in 1972 was very free of weeds, except on the no-N quarter-plots, which stood out as green rectangles in the predominantly straw-coloured field. The green was mainly leaves of *Tripleurospermum maritimum* ssp. *inodorum*, with *Equisetum* on several plots in the S.E. corner of the experiment, where it was also recorded in 1971. *Polygonum aviculare* was much less prevalent than in recent years, probably because a herbicide containing dicamba, effective against *Polygonum* at Rothamsted, was used in 1972.

Although cruciferous weeds were abundant on Hoosfield in the 1940s, *Brassica sinapis* and *Raphanus raphanistrum* were not seen in 1972 and only one plant of *Thlaspi arvense* occurred. On the other hand two Scrophulariaceae also common in the 1940s, *Chaenorhinum minus* (formerly *Linaria minor*) and *Kickxia elatine* (formerly *Linaria elatine*), were more abundant than they have been for years.

Tussilago farfara is no longer a problem on Hoosfield and *Agropyron repens*, also previously prevalent on some plots, was not seen in 1972. Both have been controlled by the use of appropriate herbicides (2,4-D ester and aminotriazole) in recent years. *Agrostis gigantea* occurs sporadically over the field.

The potato plots of the rotation were almost weed-free, although small plants of *Senecio vulgaris* were beginning to infest P only plots where the potato haulms were nearly dead.

The bean plots were moderately weed-infested, chiefly with *Polygonum aviculare*, *P. convolvulus* and *Tripleurospermum*, but on one plot (P only) *Chaenorhinum* was making bush plants about 1 ft high, especially on the N2 sub-plot, in contrast to the plants 6 in. high with only a few branches in the wheat. (Thurston)

Biology of annual grasses

Avena fatua (Wild oats)

Competition between* A. fatua *and spring cereals. The experiment on *A. fatua* freshly sown in plots drilled with either barley (Deba Abed or Zephyr) or spring wheat (Rothwell Sprite) (*Rothamsted Report for 1971*, Part 1, 113–114) was repeated in 1972 with the same treatments on the same plots, relying on the dormant seeds sown in 1971 to provide the weed infestation. The mean populations of *A. fatua* at harvest were only 35, 53 and 71 per m^2, i.e. about one-third of those in 1971.

Although the *A. fatua* seeds were chitting when the crops were sown, and emerged simultaneously with the wheat and barley, the crops again dominated the wild oats and were unaffected by them. It is possible that a high proportion of the population of wild oats came from smaller, more dormant seeds, giving rise to below-average sized seedlings.

As before, spring wheat depressed wild oats slightly less than did either of the barleys, which were equally competitive. The mean dry weights per plant of the three crops and

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the wild oats in July were similar to 1971, crops averaging 2·5 g and the wild oats in them 1·1 g.

The greatest density of wild oats/m² in 1972 was comparable to the least in 1971 (97 and 77 plants/m²). Comparing density of population with mean dry weight per plant of wild oats on the uncropped plots in 1971 and 1972, a population increase from 50 to 100 plants/m² decreased mean dry weight per plant from 25 g to 5 g approximately, whereas increasing population to 300 plants/m² decreased dry weight only to 2·5 g. It seems remarkable that such intense competition between the weeds grown alone has no parallel effect on the crop, and that the crop in this experiment succeeded in dominating the wild oats. The large size of wild oat plants often seen projecting above non-experimental crops suggests that this result is not typical of commercial farming. (Thurston)

Viability of wild oats in grain stored on farms. For the past two years (1970, 1971) the S.W. Region of ADAS has sampled stocks of grain held in various methods of storage on farms and determined the proportion of wild oat seeds. These seeds were tested for viability at Rothamsted during 1972. Although no samples of wild oats before storage were available for comparison the results seem to warrant a further investigation of propionic acid storage for grain infested with wild oats. In both years, retention of viability was outstandingly less where propionic acid had been used than in any other method of storage, including rolled grain. (Thurston)

***Alopecurus myosuroides* (Blackgrass)**

Dormancy and periodicity of germination. The experiment to determine the response of *Alopecurus* to NPK fertilisers (*Rothamsted Report for 1970*, Part 1, 108) is now approaching completion. The average percentage of viable seeds for each level of fertiliser was 60–70% and 85–90% of them germinated in the first autumn. There were no consistent differences between treatments. The greatest N applied was too little to give maximum growth of *Alopecurus* in pots. Germination is continuing in the pans set up with seeds from a subsequent experiment including a larger amount of N (*Rothamsted Report for 1971*, Part 1, 116) and pans are being started with seeds from the 1972 experiment (see below). (Thurston)

Effect of fertilisers and crop-competition. Following on the experiments described in *Rothamsted Report for 1970*, Part 1, 108, and *for 1971*, Part 1, 115–116, eight plants of *Alopecurus* or of spring wheat cv. Kolibri, or four plants of each spaced alternately round the pot, were sown on 10 March 1972 in pots containing 4·3 kg Geescroft soil. Fertiliser treatments were P0 (none added) or P2 (4·49 g $Ca(H_2PO_4)_2H_2O$ per pot) and three rates of N (N0 = none added, N2 = 1·03 g and N4 = 2·06 g NH_4NO_3 per pot) in all combinations. No K was added because in previous experiments it was slightly detrimental to *Alopecurus*. Three replicate pots of each treatment were harvested at each of three growth-stages: (1) well-established young plants in late April, when the remainder were transferred from a cold glasshouse to a cage; (2) in early June at maximum vegetative growth, when flowering was about to begin and no lower leaves were dead; and (3) in mid-September when the wheat and the first formed inflorescences of *Alopecurus* were ripe, although in some pots the blackgrass was still producing small green ears.

Alopecurus seeds were collected as they ripened from all pots before the final harvest-date, air-dried and stored in the laboratory until duplicate sets of 100 could be sown in pans of soil in a cool glasshouse for viability and dormancy tests.

The response to fertilisers of *Alopecurus* alone resembled that in 1971, with an early increase from added P overtaken by a later and larger increase from added N. Wheat responded similarly, but wheat plants were always heavier than the corresponding

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TABLE 1

Response to fertilisers of Alopecurus *and wheat alone and in competition*

Date of harvest	Treatment	Mean dry weight of tops (g per plant): *Alopecurus* (A) competing — With A	With W	Wheat (W) competing — With W	With A
24 April	P0 N0	0·05	0·03	0·21	0·18
	P0 N2	0·05	0·02	0·15	0·17
	P0 N4	0·03	0·02	0·12	0·12
	P2 N0	0·09	0·05	0·38	0·46
	P2 N2	0·07	0·09	0·44	0·58
	P2 N4	0·06	0·06	0·38	0·41
18 September	P0 N0	1·89	1·80	2·64	3·99
	P0 N2	4·98	4·53	5·13	6·46
	P0 N4	5·15	7·09	7·07	6·51
	P2 N0	1·66	1·55	3·18	5·06
	P2 N2	4·65	2·70	7·46	13·02
	P2 N4	6·73	3·66	11·26	15·95

Alopecurus. At the first harvest, giving N without P was always detrimental, but with P only, N4 was detrimental to wheat and N2 increased its dry weight. During subsequent growth, P0 plants were retarded in development compared with P2 and were still green when the corresponding P2 plants were ripening; by continuing growth longer P0 finally attained the same weight as P2.

In April the *Alopecurus* dry weights were too small to show differences clearly, but there was already a tendency for plants competing with other *Alopecurus* to be larger than those competing with wheat.

With P2 wheat plants were larger when competing with *Alopecurus* than when competing among themselves. Thus although *Alopecurus* alone benefited from P, when applied to mixed stands in pots, the balance was shifted in favour of the crop and against the weed. The increase in dry weight of wheat given P2, alone or with *Alopecurus*, persisted to the end of the experiment.

By September, *Alopecurus* plants competing with wheat were consistently smaller than those competing with other *Alopecurus* (except in P0 N4), the differences being greater in P2 than in P0. Conversely, wheat plants were heavier when competing with *Alopecurus* than with other wheat (except in P0 N4).

The pots of four *Alopecurus* and four wheat plants outyielded the pots of eight wheat plants in final total dry weight of tops in four treatments, the differences being about 5–10%. However, in the two N4 treatments wheat outyielded the mixed stand by 56·6 to 54·4 g (4%) at P0 and 90·1 to 78·4 g (13%) at P2. Thus by the end of the growing season N4 had also shifted the balance in favour of the crop. This agrees with earlier observations on Broadbalk (*Rothamsted Report for 1968*, Part 2, 207). (Thurston)

Biology of perennial weeds

***Equisetum arvense* (Field Horsetail).** *Equisetum* has become troublesome on certain of the classical experiments at Rothamsted and Woburn (*Rothamsted Report for 1970*, Part 1, 106). Work on the biology and control of the weed began in 1971–72 with preliminary observations at Woburn. Land infested with *Equisetum* was divided into 11 plots (2·4 × 9·1 m). Ten soil cores (7 cm diameter) were taken to a depth of 1 m from

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each plot in early January to see how deep the rhizomes penetrate and at what depth tubers (which represent a short branch consisting of a single swollen internode, capable of giving rise to a new plant) occur. Fifty per cent rhizome weight occurred in the upper 25 cm, 23% between 25–50 cm, 15% between 50–75 cm and 12% between 75–100 cm. Some rhizomes probably penetrate much deeper than 1 m. Tubers also probably occur deeper than 1 m, but are most numerous between 50–75 cm. On average there were 300 tubers/m³ throughout the experimental area with a maximum of 1000/m³.

TABLE 2

Per cent of total numbers, total weight and weight per tuber of Equisetum *at various depths in Woburn soil*

Depth (cm)	% of total numbers	% weight	Weight per tuber (mg)
0–25	25	12	62
25–50	22	14	85
50–75	39	51	173
75–100	13	23	242

The seed bed was prepared as for cereals and shoots of *Equisetum* started emerging during early May continuing throughout the month and to a lesser extent throughout most of the summer. Sufficient *Equisetum* emerged on only seven of the plots to be included in the experiment, and the effect of chlorthiamid (applied at 11 kg a.i./ha on 19 May), N-phosphonomethyl-glycine (at 4·5 kg a.i./ha on 23 May) and aminotriazole (at 9 kg a.i./ha on 23 May) were compared; there were four control plots alternating with herbicide-treated plots.

The plot treated with chlorthiamid remained clear of *Equisetum* and other weeds throughout the season, whereas N-phosphonomethyl-glycine and aminotriazole only partly suppressed the growth of *Equisetum*.

Continuing the study of rhizome and tuber distribution a small number of larger, deeper soil cores will be taken from control plots in late autumn. The area will also be sown with a range of crops in 1973 to see whether there are any deleterious herbicide residues and to compare *Equisetum* growth on the untreated plots with those treated with herbicides in 1972. (Thurston, Williams and Welbank)

***Agropyron repens* and *Agrostis gigantea* seed dormancy and longevity.** The experiments on seed dormancy in *Agrostis* (*Rothamsted Report for 1970*, Part 1, 106) continued and between 1970 and 1972 a further 1% of seeds sown in 1967 and 1968 germinated; 1·5% more of seeds sown shallowly in 1968 in pots and transferred to pans in 1969 and 0·6% of those originally sown more deeply in the same experiment. In the investigation where *Agrostis* seeds were sown in soil in 1968 germination was 38% after one year, 51% after two years and 57% after four years when the soil was cultivated monthly; 30, 46 and 63% with cultivation twice a year and 10, 26 and 62% for zero cultivation for two years and then monthly.

The data suggests that *Agrostis* seeds are not innately dormant but that dormancy may be enforced by burial. They may therefore persist for long periods in the soil. To test this and also for *Agropyron*, seeds of both species were sown on the surface of the soil in September 1971. Plots were given one of three cultivation treatments, typical of control measures that might be used to control vegetative parts. (1) Ploughed 2 November and spring-tine cultivated 29 March 1972; (2) Chisel ploughed 24 September, ploughed 2 November and tine cultivated in March; (3) Chisel ploughed 24 September, 11 October and

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28 October, thus simulating no control in autumn followed by a cereal, control in autumn followed either by a spring or by a winter cereal respectively. Half plots were treated with paraquat before cultivation. Each plot was further split into two and each quarter-plot (2·4 × 1·2 m) was sown with either *Agrostis* or *Agropyron* seeds at approximately 2300 viable seeds/m^2.

In treatment (1) only 10% of the *Agropyron*, but 32% of *Agrostis* seeds germinated before ploughing. Only about one seedling per m^2 germinated over winter and two per m^2 after spring cultivations. In treatment (2) many more *Agropyron* seedlings (38%) but fewer *Agrostis* seedlings (5%) appeared in autumn, there was little winter germination, and 0·3% of *Agropyron* and 0·1% *Agrostis* germinated after spring cultivation. In treatment (3) 23% of *Agropyron* and 2% of *Agrostis* seeds gave emerged seedlings in autumn and about 5% (100 seedlings/m^2) more *Agropyron* and 1·5% *Agrostis* did so after the last cultivation. Paraquat decreased *Agropyron* germination in treatments (2) and (3) by 75% and by 30% in treatment (1); its effect on *Agrostis* was smaller and not consistent. The experiment is being continued to see how many seeds remain viable longer than a year. Soil cores have also been taken from one block and germination in these will be counted in the glasshouse to provide an independent estimate.

In a parallel investigation in the glasshouse, seeds were sown in Rothamsted and Woburn soils and given similar frequencies of soil disturbance as in the field. *Agropyron* germinated quickly in soil but when seeds were sown on the soil surface and not incorporated until late autumn germination was delayed until spring. *Agrostis* however germinated but on the surface and quicker in Woburn than in Rothamsted soil. In contrast to the field experiment after one year almost all the viable *Agropyron* seeds and 60–70% of the *Agrostis* seeds had germinated. (Williams)

***Agropyron repens* and *Agrostis gigantea* seedlings in cereal crops.** In 1971 the growth of *Agropyron* seedlings was studied in cereals with two amounts of nitrogen. The seeds were sown dry and seedling emergence was protracted and the amount of growth made by them depended on when they emerged. In 1972 the experiment was repeated with modifications, with the inclusion of *Agrostis* seedlings. Seedlings of *Agropyron* and *Agrostis* were raised in the glasshouse and transplanted at the one-leaf stage 23 cm apart into rows of spring wheat cv. Kolibri or spring barley cv. Julia, drilled on 24 March. Seedlings were transplanted when the cereals had one leaf (13 April) (E) or late (L) when they had two leaves (27 April). The cereals were given 40 units of N and sprayed with a hormone broad-leaved weed killer. Crop and weed seedlings were sampled on four occasions. Most of the weed seedlings survived, except for a quarter of the *Agrostis* seedlings planted late in barley.

Agropyron seedlings made most growth when planted early in wheat but only half as

TABLE 3

Total dry weight (g) of seedlings per 0·476 m^2

	Agropyron				*Agrostis*			
	Wheat		Barley		Wheat		Barley	
	E	L	E	L	E	L	E	L
22 May	0·86	0·34	0·73	0·31	0·58	0·13	0·55	0·11
19 June	2·88	1·00	1·38	0·81	1·95	0·61	1·78	0·28
17 July	4·15	1·69	2·19	1·29	3·08	1·07	2·80	0·45
24 Aug.	—	—	3·00	1·42	—	—	3·20	0·55
4 Sept.	5·60	2·59	—	—	4·11	1·96	—	—

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much when planted early in barley. Delaying planting more than halved the amount of growth made in wheat and almost halved it in barley. *Agrostis* seedlings planted early in wheat made 25% less growth than *Agropyron* but grew almost as much in barley as wheat. Delaying planting in barley had a larger effect on *Agrostis* than on *Agropyron*.

Agropyron seedlings planted early in wheat produced the greatest amount of rhizome and 15 seedlings from a sample area produced nine rhizomes which measured a total of 65 cm. *Agrostis* produced a smaller amount of rhizome than *Agropyron* in wheat but about the same in barley. Later planting of both weeds resulted in less rhizome.

TABLE 4

Rhizome dry weight (g) of seedlings per 0·476 m²

	Agropyron				*Agrostis*			
	Wheat		Barley		Wheat		Barley	
	E	L	E	L	E	L	E	L
19 June	0·157	0·002	0·003	0	0·034	0	0·040	0
17 July	0·305	0·017	0·037	0·001	0·094	0·008	0·061	0
24 Aug.	—	—	0·048	0·002	—	—	0·041	0
4 Sept.	0·783	0·064	—	—	0·161	0·010	—	—

Fewer barley than wheat plants emerged initially but when they tillered more and more shoots survived so that at the first, second and third samplings barley had 20, 40 and 60% respectively more shoots than wheat. During May and June, barley had a greater shoot dry weight per unit area than wheat and these characteristics must in part account for its greater competitive ability. Although between mid-June and mid-July barley had a leaf area index of 8 and wheat 5, only 3% more of the visible radiation penetrated the wheat than the barley canopy so differences in shading in mid-season probably cannot account for the different competitive abilities. Barley yielded 481 and wheat 453 g/m² dry weight of grain. (Williams)

Comparison of the growth of *Agropyron* and *Agrostis* from seed and from rhizome with or without a crop. The growth of *Agropyron* and *Agrostis* from seed and from one-node rhizome fragments was studied in the glasshouse with or without competition from spring wheat cv. Kolibri. When the weeds or crop were grown alone three plants were grown per pot but six (three of crop and three of weed) when the species were in competition. The pots contained 5 kg of Woburn soil given 2 g NH_4NO_3 + 2 g K_2HPO_4. Wheat had a large effect on the growth of the weeds but the weeds had less effect on the growth of the crop. Grain weight was decreased by 12–15% by the weeds growing from rhizomes, by 18% by *Agropyron* seedlings and not at all by *Agrostis* seedlings. With wheat *Agropyron* had less shoot weight (16–2 g), fewer shoots (18–9) and less rhizome weight (8–1 g). Similar results were obtained whether the *Agropyron* was grown from rhizomes or from seeds. Without wheat *Agrostis* plants from either rhizomes or seeds had a similar weight of shoot and rhizome. With wheat *Agrostis* seedlings had only 1·7 g shoots and 1·3 g rhizomes compared to 3·5 g shoot and 6·3 g rhizome for plants grown from rhizomes. *Agropyron* plants growing alone from seeds or rhizomes had a similar number of spikes (11) but in competition those from rhizomes had two and seedlings one. *Agrostis* seedlings produced no panicles, and plants from rhizomes very few.

Thus seedlings of both species are capable of producing as much total growth and rhizome as plants from one-node rhizome fragments but *Agrostis* seedlings which are very small initially are more susceptible to competition than plants from rhizomes. The

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results of this experiment, where crop and weed started growing simultaneously resulting in a small effect of the weed on the crop, contrast with those of an earlier experiment (*Rothamsted Report for 1968*, Part 1, 108) where the weed planted earlier than the crop resulted in a much larger decrease in crop growth. (Williams)

Staff and visiting workers

Dr. E. C. Humphries retired in March 1972 after 25 years at Rothamsted and Miss Margaret Ford left to take up an appointment at the Plant Breeding Institute, Cambridge.

New members of staff appointed were P. Hoskin and P. J. Dawson, who began work on the effects of air pollution on plant growth. Other new appointments were J. F. Garrod and J. R. Lenton to investigate the role of growth substances and I. Pearman, who is concerned with the maintenance and monitoring of the facilities for growth of plants in controlled environments.

Dr. J. H. Wilson, of the School of Agriculture, University of Melbourne, who formerly studied at Rothamsted, visited the Department for six weeks. S. Kumarasinghe from the University of Ceylon commenced investigations on the metabolism of the cereal leaf as a student of London University for a Higher Degree. Miss Rosemary R. Cox was awarded the M.Sc. degree of London University for work at Rothamsted on weed competition. C. P. Whittingham attended the 35th Winter Congress of the Institut International de Recherches Betteravieres in Brussels and took the chair at the seminar on physiology held in connection with the Congress. Gillian N. Thorne attended a symposium on the use of Phytotrons for Research in Environmental Physiology at Duke University. She also visited various laboratories in the U.S.A. which are conducting research in connection with the effects of aerial pollution on plant growth. In addition Dr. Thorne visited the Cereal Research Institute at Kromeriz, Czechoslovakia, to attend an International Symposium on Breeding and Productivity of Barley. Joan M. Thurston and E. D. Williams spoke at the 11th British Weed Control Conference at Brighton.

C. P. Whittingham and P. Hoskin visited Landesanstalt für Immissions und Bodennutzungsschutz, Essen, West Germany, and the Instituut voor Planten-Ziektenkundig Onderzoek, Wageningen, The Netherlands, preliminary to commencing work on aerial pollution at Rothamsted.

Sandwich students who worked in the Department were Elizabeth Burrows, S. Deeman, M. Duckham and Janet Munns.

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