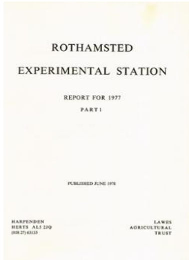
Report for 1977 - Part 1

Full Table of Content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EXPERIMENTAL STATION
REPORT FOR 1977
PART I

Botany Department

C. P. Whittingham

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Introduction

Cereal yields were higher than in the previous year, although the harvest was delayed. Hence all the results for this year's cereal experiments are not yet complete. The effect of the removal of aerial pollutants on the growth of barley at Woburn were significant but less than in the previous year with respect to total dry matter production and resulted in a smaller effect on grain yield. Also in 1977 increasing the concentration of carbodioxide in the atmosphere in which spring wheat was grown did not influence grain yield, although photosynthesis of the flag leaves was doubled. It appears that in our cereal experiments in 1977 grain yields were not restricted by the availability of carbohydrate. Again in 1977 halving ears had no effect on dry weight per grain in winter wheat var. Maris Huntsman. Studies of photorespiration have continued with special attention to the influence of water stress, which increases photorespiration relative to photosynthesis. Although several compounds were tested, none have proved satisfactory for the inhibition of photorespiration in cereals under field conditions.

Studies on the growth of sugar beet in controlled environments have continued. It is proposed in future to develop joint studies on the field crop with the staff at Broom's Barn, and at Rothamsted to investigate further in controlled environments those specific processes which have been shown to be of the greatest significance under field conditions.

New experiments have been undertaken this year with the potato crop to investigate how far photosynthesis and leaf metabolism regulates the tuber yield under different growth conditions.

Work on weed biology has now been restricted to studies relating to the classical experiments.

https://doi.org/10.23637/ERADOC-1-134

A decision is still awaited concerning the rebuilding of the glasshouse block. Progress is continuing on the building of additional facilities for growth of plants in controlled environments; these facilities are now used to the maximum extent because of the increased demand by the station as a whole.

Cereal crops

Precision seeding. Recent experiments elsewhere have indicated that with the best husbandry, precision sowing of cereals can give increased yields over conventionally-sown crops. In a preliminary experiment in 1975–76 at Rothamsted, hand-sown winter wheat at square spacing permitted smaller amounts of seed to be used without loss of yield. However, there was insufficient evidence to conclude that square spacing was superior to a similar plant population drilled in rows (*Rothamsted Report for 1976*, Part 1, 31–32).

We were unable to repeat this experiment in 1976–77 with winter wheat because of unfavourable drilling conditions in autumn. However, in the spring of 1977, barley, var. Ark Royal, was substituted for winter wheat and the crop was sown on 22 April. Two sowing rates (57 and 114 kg ha^{-1}) with two row spacings (10·5 and 21 cm) were tested with a Stanhay precision drill and a conventional Nordsten drill, at three levels of nitrogen fertiliser (75, 100 and 125 kg ha^{-1}) and with and without irrigation. These drills were compared with a conventional farm drill with approximately 18 cm rows at the higher sowing rate. Two patterns of hand sowing at the lower seed rate were also included; one a square spacing (7·25 cm) and the other 2·5 cm apart in 10·5 cm rows. Three extra 18 cm row plots were included, one receiving no nitrogen fertiliser, the others 150 and 175 kg ha^{-1} to determine the optimal amount of nitrogen for growth and yield. Irrigation was tested on all the treatments except the 18 cm row plots, using trickle equipment so that the crop could be watered until it reached maturity. Water could not be applied until 7 July (100 mm); a further 25 mm was applied on 26 July before abundant rain made further irrigation unnecessary. Soil water content was monitored using a neutron soil moisture probe on selected plots.

The seed bed had many stones and large clods which, together with the heavy tractor wheelings along the centre of the Nordsten and 18 cm row plots, prevented proper penetration of the soil by the drill coulters. Consequently despite harrowing after drilling there was less than 50% establishment on Nordsten and 18 cm row plots, compared to over 80% on Stanhay and hand-sown plots.

The maximum tiller number was reached on 4 July when Stanhay 10·5 cm high seed rate plots had the most shoots (1022 m^{-2}) and Stanhay 21 cm low seed rate the least (754 m^{-2}). The plots sown by the Nordsten and 18 cm row drills only partly compensated for the poor germination; the best from the Nordsten had 638 shoots m^{-2} and the 18 cm row plots 739 m^{-2} (both at high seed rate).

By 20 July (near anthesis) with Stanhay-drilled plots seed rate predictably had most effect, increasing shoots from 694 to 896 m^{-2} and shoot dry weight from 575 to 643 g m^{-2}, with a comparable increase in leaf area index (LAI) from 6·7 to 7·8. Close row spacing increased shoot numbers by a much smaller percentage, from 745 to 845 m^{-2}, and LAI from 6·6 to 7·8, although it had no significant effect on shoot dry weight. Irrigation increased LAI from 6·7 to 7·7 while nitrogen fertiliser had no significant effect.

Although hand-sown plots appeared very uniform and vigorous throughout the season, there was no indication that hand sowing increased tillering, LAI or dry matter yields up to anthesis.

Final combine grain yields showed differences between the drills, but these were largely attributed to the poor stands from the Nordsten and 18 cm row drills. The higher seed

https://doi.org/10.23637/ERADOC-1-134

rate increased yield, in the case of the Stanhay drill from 3·3 to 3·6 t ha^{-1}, but the effects of closer row spacing or irrigation were not significant. Yields with six nitrogen rates from 18 cm row plots indicated an optimum for grain yield of 75 to 100 kg N ha^{-1}. Plots with barley hand-sown in 10 cm rows had yields of 3·1 t ha^{-1}, no higher than comparable Stanhay-drilled plots. With crops hand-sown with square spacing, there was a suggestion that yield was increased about 0·3 t ha^{-1}.

There was little evidence from this experiment that closer rows, as between 20 and 10 cm, or irrigation were of great importance for yield and the precision drill was generally as good as hand sowing. Successful comparison with other drills must await a later experiment. The importance of seed rate was possibly a consequence of late sowing, but this experiment certainly did not suggest that normal rates were superoptimal for barley. The absence of irrigation benefit reflected the water holding capacity of Rothamsted soil and a season wet enough to keep it adequately replenished. The experiment also proved the feasibility of using trickle equipment with cereals with irrigation right through to ripeness. (Taylor, Welbank and Thorne, with Widdowson, Soils and Plant Nutrition Department)

Physiology of winter wheat

Distribution of photosynthate. In 1975 and 1976 the distribution of ^{14}C in winter wheat was studied after supplying $^{14}CO_2$ to leaves in the field either before or after anthesis (Paper 11). Post-anthesis applications were also investigated in spring wheat in 1972 to 1974 (Paper 13). When $^{14}CO_2$ was supplied to the leaf below the flag leaf after anthesis, or to either of the top two leaves before anthesis, a greater proportion of the total ^{14}C content of the shoot at maturity was found in the ear than had been expected from the previous work. To test whether our results were peculiar to the seasons concerned, the distribution of ^{14}C was studied in shoots on six of the highest-yielding plots on Broadbalk (plots 21, 22, 07, 08, 15, 16 after beans). In 1976 and 1977, flag leaves and the leaf below the flag leaf were exposed to $^{14}CO_2$ about 14 days before anthesis (at Feekes' growth stage 9·5, Zadoks' 42) and at 10 days after anthesis. At maturity the ^{14}C in the ear and the rest of the shoot was measured. In 1976, the percentages in the ear were similar to those found by Makunga *et al.* (1978) for the same variety (Cappelle–Desprez) in an adjacent experiment. When $^{14}CO_2$ had been supplied to either leaf before anthesis 40% was recovered in the ear. When supplied 10 days after anthesis, 92% of the ^{14}C from the flag leaf and 80% of that from the leaf below the flag leaf was in the ear. Distribution patterns for 1977 are not yet available. (Makunga and Thorne)

Sugar concentrations in different plant parts at dusk were studied in winter wheat in 1975. As in spring wheat (Paper 13) nitrogen tended to increase the concentration of both reducing sugars and non-reducing sugars in the glumes and rachis. Concentrations of these sugars in the top internode were also increased by nitrogen in winter wheat (from 37·4 mg g^{-1} fresh weight at 15 kg N ha^{-1}, to 53·1 mg g^{-1} fresh weight at 195 kg N ha^{-1}, SED 4·3), but concentrations in the flag laminae were not. There was no evidence that the slower respiration rates of the ears of Maris Fundin 18 days after anthesis were related to smaller concentrations of sugars in the grains or ear structures, compared with Maris Huntsman 15 days after anthesis. Nor were there any significant differences between the varieties in the sugar concentrations in the top internodes or flag laminae. Plants of Maris Huntsman were harvested at two stages during grain growth; 4 and 15 days after anthesis. This was to determine if sugars accumulated in any plant part early in grain growth when the small grains might not be able to absorb all of the carbohydrate produced in photosynthesis at this stage. No accumulation of sugars in any plant part at the earlier date was observed. The only significant difference was more glucose in the

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flag laminae at the later date (5·40 and 8·89 mg g^{-1} fresh weight, SED 0·94 at 4 and 15 days after anthesis respectively). (Thomas)

Carbon dioxide exchange. The dark respiration rate of the ears of the semi-dwarf varieties Maris Fundin and Hobbit were less than for ears of Maris Huntsman. The slower rate of Maris Fundin, but not Hobbit, might have been related to its earlier maturity (*Rothamsted Report for 1975*, Part 1, 36; and *for 1976*, Part 1, 36). Further comparisons were made in 1977, to see whether ears of semi-dwarf varieties generally had slower respiration rates. Comparable plants of the semi-dwarf Sportsman and of Maris Huntsman were dug from the field at Rothamsted and transferred to growth rooms at 16°C. During 11 to 15 days after anthesis the dark respiration rate of Sportsman was significantly less (8%) than that of Maris Huntsman. A similar difference was found between ears of Hobbit and Maris Huntsman collected from an Agricultural Development and Advisory Service (ADAS) trial. (Pearman and Thorne)

Calculations using these respiration rates, and short-term measurements in the field of gross photosynthesis, for the top two leaves of winter wheat, suggest that nitrogen fertiliser increased dark respiration of the ear relatively more than it increased photosynthetic production, and increased dark respiration of the rest of the shoot proportionately to photosynthesis (Paper 1). To study the relation between photosynthesis and respiration further, a field unit consisting of an infra-red CO_2 analyser, air pump, chilled water supply to cool the leaf chambers and a ten channel switching device was constructed. A data logger recorded CO_2 exchange, leaf and air temperature and solar radiation. Rectangular leaf chambers of Perspex were made having a 1-cm-thick layer of chilled water above the leaf which maintained leaf temperature within 2°C of air temperature, when this ranged from 15 to 25°C. Light intensity at the leaf surface was reduced 20% by the leaf chamber. Ears or shoots were sealed into uncooled cylindrical glass chambers by means of rubber bungs and silicone rubber for measurement of dark respiration. This apparatus was used for measuring net photosynthesis of the top two leaves and dark respiration of the stem plus leaves or ear of Maris Huntsman wheat that had received 30, 90, 150 or 210 kg N ha^{-1}. (Pearman, Thorne and Young)

Factors determining grain size. Removing the top half of ears of Kleiber spring wheat to increase the supply of carbohydrate per grain, resulted in faster growth in volume, fresh and dry weight of the grains until 23 days after anthesis, when volume was maximal; during the subsequent 47 days the grains doubled in dry weight in both control and treated plants (*Rothamsted Report for 1976*, Part 1, 35). To test whether the period before the time of maximum volume was most critical for determining grain size, another experiment was done in 1977 using Kleiber grown in the glasshouse. Treatments were halving ears before or after the time when maximum grain volume was attained, combined factorially with halving the light intensity by shading before or after this time, or throughout grain growth. Volume did not reach its maximum until 39 days after anthesis, only 8 days before the grains stopped increasing in dry weight, and none of the treatments applied at this time had any effect. Halving early increased, and shading early decreased, volume, water content and dry weight of the grain, and dry weight of the rest of the plant. Both treatments altered grain dry weight by about 25% and dry weight of the rest of the plant by 8%.

In the field in 1976 halving ears increased dry weight per grain in Hobbit but not in Maris Huntsman. In 1977 some ears of Huntsman in the field were halved 5 days after anthesis and at 30 days when grain volume was approximately maximal (grain weight was 64% of the final value). The correct time of this stage was difficult to determine because the smooth ontogenetic trend in grain volume was obscured by fluctuations

https://doi.org/10.23637/ERADOC-1-134

associated with rain. Dry weight per grain was unaffected by halving, as previously. Chaff dry weight was increased by early treatment and shoot dry weight by both treatments.

These experiments suggest that the time when maximum grain volume and water content occur is not necessarily early in grain growth, as was indicated in the data of Radley (*Journal of Experimental Botany* (1976), **27**, 1009–21), and may not represent a critical stage of grain growth. (Martinez–Carrasco)

Metabolism of water-stressed barley. Analysis of plant material from the 1976 irrigation experiment (*Rothamsted Report for 1976*, Part 1, 34 and 238) on spring barley (var. Julia) has continued with the aim of correlating yield and grain size with the water status of the crop and of understanding how the physiology and biochemstry of the plant are modified by water stress. Mature leaves were exposed to $^{14}CO_2$ for short periods and the ^{14}C content measured. In the unusual summer, radiation throughout the experiment and during feeding periods was relatively intense and constant. The highest rates of gross photosynthesis were observed in the continuously-irrigated treatment; the continuously-droughted plants photosynthesised *c.* 20% less. Leaves of plants, subjected to drying after early growth in well-watered soils, photosynthesised progressively less and finally had smaller rates than the long-term drought treatments. The large differences in leaf area caused by stress (the long-term dry treatment had only 40% of the leaf area of the wettest at the time of maximum leaf area) were sufficient to substantially decrease total photosynthesis. Where stress developed later, rates of leaf death were much greater even than in long-term stress so that total crop production was smaller.

Awns photosynthesised more than leaves in the main period of grain growth and filling. The rate of gross photosynthesis per unit area of awns was smaller in the dry treatments than in the controls but the late drying treatments decreased photosynthesis still further. Awns of rewatered plants had larger rates of photosynthesis than those of continuously-watered plants, probably because the greater area of awns in irrigated plants caused self-shading, but the smaller leaf area restricted the total photosynthesis. Rates of gross photosynthesis of about 20 ng CO_2 cm^{-2} s^{-1} in the controls were obtained at 620 W m^{-2} irradiance and 14 mg CO_2 cm^{-2} s^{-1} in the long-term drought treatment.

During the period of grain filling the awns yellowed much faster in the dry treatments than in the wet, so that the period over which photosynthesis was active was shorter. In the well-watered crop subject to late drought, the reduction in photosynthesis probably explains why 1000-grain mass was smaller than for plants subject to stress over longer periods. Grain number was also larger in the initially-watered crop so that with later drought competition for assimilate was of importance in regulating grain size.

Earlier work on water-stressed plants, spring wheat and sunflower, indicated that stress stimulated carbon flux through the glycollate pathway and consequently photorespiration relative to photosynthesis. Assimilation decreased because of stomatal closure and greater loss of fixed carbon. In new experiments leaves of barley were exposed to $^{14}CO_2$ for short periods and the ^{14}C distribution in assimilates measured. After short-term feeding (30 s–5 min) the proportion of ^{14}C in serine and glycine increased from 10 and 5% respectively in the continuously watered treatments to 20 and 15% in the long-term drought treatments. With late drying the serine was about 12% and glycine 4%. Alanine, an amino acid known to contain less ^{14}C under stress conditions, contained 26% in the wet, 8·8% in the dry and 12% in the recently dry treatment.

Because leaves died during the latter part of the season, the behaviour of the awns was studied. Awns from ears fed $^{14}CO_2$ for up to 5 min contained about 8% of the total ^{14}C in glycine, 10% in serine and 20% in alanine. There was no evidence of change with stress. A greater proportion of ^{14}C was present in sucrose in awns, after 2 min feeding,

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than in leaves. In both awns and leaves there was very little radioactivity in 3-phosphoglyceric acid (PGA).

Evidence from sunflower measured in low oxygen atmospheres which suppresses flux through the glycollate pathway, and maize, a C_4 plant with small rates of photorespiration, suggest that when glycine production is small alanine is increased. Hence the possibility exists that the pathways of carbon flux in barley awns may differ quantitatively from those in leaves, and may be important in stress physiology. (Lawlor, with Day and Legg, Physics Department)

Analysis of carbon flux in water-stressed plants. Previous reports have emphasised the role of water stress, an environmental factor of agricultural importance, in controlling carbon flux in plants. However, the quantitative analysis of flux is complicated by the changes in pool size of intermediates, and possible changes in biochemical pathways within the leaf. A model (Laing, Ogren and Hageman, *Plant Physiology* (1974), **54**, 678–685), based on the characteristics of ribulose bisphosphate (RuBP) carboxylase/oxygenase and the known stoichiometry of glycine decarboxylation (Bird *et al.*, *Phytochemistry* (1972), **11**, 1587–1594) has been developed to analyse the results of controlled experiments on ^{14}C flux in sunflower leaves suffering degrees of water stress. Using the enzyme characteristics measured for spinach by Badger and Andrews (*Biochemical and Biophysical Research Communications* (1974), **60**, 204–210), the gross photosynthesis and stomatal resistance, it is possible to predict the rates of photorespiration at water potentials between -4 and -16×10^5 Pa. With greater degrees of stress, damage to the photosynthetic mechanism and loss of carbon from non-glycollate pathway respiration occurs.

The model predicts that increasing stress will result in more carbon from storage being mobilised and used as substrate in photorespiration, as observed experimentally. Sucrose decreases in stressed leaves, and would in general be of low specific radioactivity, consistent with the low specific activity of CO_2 observed to be evolved in stressed leaves. From the specific radioactivity of the fed gas and the amounts of compounds in the tissue, the specific activity of products was calculated as a function of time to simulate the experimental data. Both the photorespired CO_2 and 3-PGA specific activities were calculated to increase much faster than measured, although the saturation values of specific activity were in good agreement with the experiment (with the exception of the most severe stress). By incorporating a time delay, which increased with stress, into the differential equations used to calculate the specific activity, the kinetics of carbon flux were reproduced. The experimental data showed that the specific activity of glycine was lower than that of the CO_2 photorespired, an impossible situation if glycine is the substrate, Hence the model postulates that more than one pool of glycine exists and that carbon flux between active and inactive pools occurs. Serine also probably occurs in two pools, one synthesised *via* glycine, the other from an alternate source, probably pyruvate. Alanine, an important early product of photosynthesis under some conditions, decreases with stress and at higher concentrations of CO_2; it may be an alternate product to serine and glycine. The model is being used to examine the interactions between photosynthesis, respiration and carbon fluxes in biochemical pathways in leaves subject to different oxygen, carbon dioxide and water stress conditions. (Lawlor, with Pearlman, Statistics Department)

Effect of various chemicals on photosynthesis and photorespiration. Various chemicals were supplied to segments from wheat leaves by methods similar to those of Waidyanatha, Keys and Whittingham (*Journal of Experimental Botany* (1975), **26**, 15–26). Sodium L-2-hydroxy-3-butynoate, previously used by Kumarasinghe (*Rothamsted Report for 1975*, Part 1, 37), did not completely inhibit in 20% oxygen metabolism of glycollate at

https://doi.org/10.23637/ERADOC-1-134

a concentration known to completely inhibit glycollate oxidase activity *in vitro* (Jewiss, Kerr and Whittaker, *FEBS Letters* (1975), **53**, 292–296). The inhibitor was fed to leaf segments in 2% oxygen and 0·1% carbon dioxide in an attempt to avoid competition between the inhibitor and accumulating glycollate. Incorporation of carbon into glycine and serine still occurred during photosynthesis so glycollate carbon was still metabolised to glycine. Also, isonicotinyl hydrazide, which inhibits conversion of glycine to serine, caused glycine accumulation even in the presence of L-2-hydroxy-3-butynoate. Riboflavin monophosphate (FMN) (2 mM) caused 60% inhibition of photosynthesis but had a less severe effect on photorespiration thus explaining the increased CO_2 compensation concentration for wheat leaves in the presence of FMN reported by Tregunna (*Science* (1966), **151**, 1239–1240). After 5 min photosynthesis by leaves in $^{14}CO_2$, there was no evidence of a specific effect of FMN on photorespiratory metabolism. Several sulphhydryl reagents were tested also because Giaquinta (*Plant Physiology* (1976), **57**, 872–875) reported that those usually excluded by biological membranes prevented transfer of sucrose from mesophyll cells into the cell-free space, and therefore vein loading. Sucrose is a major product of glycollate metabolism. Sulphhydryl reagents, e.g. p-chloromercuribenzoate (1 mM) and 5,5-ditho bis-2-nitrobenzoate (2 mM), decreased incorporation of carbon into sucrose relative to glycine and serine but also strongly inhibited photosynthesis and transpiration suggesting stomatal closure with a consequent decreased concentration of CO_2 in the intercellular spaces. When vacuum infiltrated, or used to soak the leaves, 2 mM p-chloromercuribenzoate had little effect on photosynthetic metabolism although it caused a 95% inhibition of the conversion of glycine to serine catalysed by leaf mitochondria *in vitro*. Phosphate buffer (20 mM) inhibited photosynthesis by 30% and caused relatively more carbon to be incorporated into phosphate esters and serine; buffer solution made with N-2-hydroxyethylpiperazine-N^1-2-ethane sulphonic acid (5 mM) caused a 90% inhibition of photosynthesis with decreased incorporation of carbon into sucrose and an increase in glycine and serine, whilst N-tris(hydroxymethyl) methyl glycine (tricine) buffer had the reverse effects causing a maximum stimulation of photosynthesis at 2·5 mM. With leaves grown later in the year the effect of tricine was not reproduced. Other substances supplied to leaf segments, 4,4,4-trifluoro-1-(2-thienyl)-butane-1,3-dione (1 mM), ethirimol (1 mM) and L-methionine-DL-sulphoximine (0·5 mM) were without significant effects on photosynthesis or photorespiration. To avoid complications caused by effects of stomata, preliminary attempts have been made to use isolated protoplasts instead of leaf segments to test potential inhibitors of photosynthesis. (Keys and Generowicz)

RuBP carboxylase from wheat leaves. A method for preparing a freeze-dried powder containing RuBP carboxylase from wheat leaves, free from major contamination by other proteins, has been devised. The specific activity of the preparation is 0·25 μmol mg^{-1} protein h^{-1}. Evidence obtained by Hall (*Ph.D. Thesis, University of Bradford* (1977)) at Rothamsted, shows that the enzyme in young flag leaves has a specific activity approaching 11 μmol mg^{-1} protein h^{-1}. The freeze-dried powder was used to test extracts from wheat leaves for their ability to activate the enzyme. One fraction that caused an increase of up to 50% in the activity contains the enzyme carbonic anhydrase (E.C. 4.2.1.1.). A purified animal carbonic anhydrase also slightly stimulated RuBP carboxylase activity of the freeze-dried powder. Leaf carbonic anhydrases are unstable and attempts to test the effect of purified samples on the activity of the RuBP carboxylase have proved difficult. (Cornelius)

Photosynthetic mechanism of *Camellia sinensis* L. Leaves of the tea plant, *Camellia sinensis* L., were studied to show whether the mechanism of photosynthesis was C_3 or C_4

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type. Plants were obtained from K. N. Wickramsinghe (Soils and Plant Nutrition Department). Leaves from these plants photosynthesised slowly in July and August (2–5 mg CO_2 dm^{-2} h^{-1}). After transplanting into bigger pots, and further growth in a heated glasshouse with a high humidity, rates improved to 12 mg dm^{-2} h^{-1}. The CO_2 compensation concentration at 25°C in 21% O_2 ranged from 60 to 70 vpm. Rates of photorespiration, measured as efflux of CO_2 into CO_2-free air and by extrapolation of photosynthetic rate to zero CO_2 ranged from 2 to 4 mg CO_2 dm^{-2} h^{-1}. Increasing the oxygen concentration from 21 to 55% increased the rate of photorespiration and the CO_2 compensation concentration and decreased net photosynthesis; lowering the oxygen to 2% increased the rate of photosynthesis by 40% and decreased both the rate of photorespiration and the CO_2 compensation point. Using the same methods sugar-cane leaves (C_4-mechanism of photosynthesis) showed a CO_2 compensation concentration of zero, did not release CO_2 into CO_2-free air and showed only small effects of oxygen concentration on photosynthetic rate. Wheat leaves (C_3-mechanism of photosynthesis) showed a CO_2 compensation concentration of 35 to 45 vpm and photorespired at 2·0–2·5 mg dm^{-2} h^{-1} with photosynthetic rates of 18 to 22 mg CO_2 dm^{-2} h^{-1}. When photosynthesis in $^{14}CO_2$ was followed by a period in $^{12}CO_2$, leaves of tea contained most ^{14}C initially in phosphoglycerate with subsequent rapid appearance in sucrose, glycine and serine. This is similar to the sequence in wheat leaves and unlike that in sugar cane where malate and aspartate are initially the most strongly radioactive intermediates following photosynthesis in $^{14}CO_2$. A preliminary study of leaf structure showed no evidence of a bundle sheath cells densely packed with chloroplasts round the vascular bundles. Therefore, gas exchange measurements, early products of CO_2 assimilation and leaf structure are consistent with tea having the C_3-mechanism of photosynthesis. (Roberts)

C_4-photosynthesis in *Spartina townsendii*. The salt marsh grass *Spartina townsendii* provides the opportunity to study C_4-photosynthesis in a temperate climate. Analyses of the metabolism of $^{14}CO_2$ at mid-day in August (25°C, 1000 μE m^{-2} s^{-1}, photosynthetically-active radiation) have been completed and the results can be compared with those obtained previously at a cooler temperature (10°C in May) (*Rothamsted Report for 1976*, Part 1, 40). The transfer of radioactivity observed is consistent with the operation of the C_4-pathway of photosynthesis at both temperatures, but there were some differences. When leaves were harvested immediately after a 5 or 10 s pulse of $^{14}CO_2$, 80% of the radioactivity was found in malate and aspartate at both temperatures, and the rest in PGA and its derivatives. When the leaves were left in normal air the radioactivity moved more slowly from the organic acids into PGA, glycine, serine and alanine at the lower temperature, but the transfer of label into sugar phosphates and sugars was the same at both temperatures. Over 40% of the label remained in malate until 30 s after transfer to normal air at low temperature, whereas at 25°C only 25% of the label remained in malate at this time. A similar slower transfer of label from malate has been observed in other cold-adapted C_4 species (Caldwell, Osmond and Nott, *Plant Physiology* (1977), **60**, 157–164). Its role in the adaptation of C_4 plants to cool temperatures is difficult to assess without further study of the location of C_4-acid pools. (Thomas)

Carbon dioxide enrichment—its effect on growth and yield in spring wheat. Enrichment of glasshouse atmospheres with CO_2 is an established technique for increasing the yield of horticultural crops. However, few studies have examined the effect of increased concentrations of CO_2 on arable crops. High levels of CO_2 should both inhibit photorespiration and increase photosynthesis. We examined the effect on growth and yield of wheat grown in air enriched to 1000 vpm CO_2 compared with a control crop grown in normal air (320 vpm CO_2 concentration). Ample nutrients and water were supplied so neither of

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these limited yield. A preliminary experiment in 1976 showed that the experimental conditions were capable of providing good yields, so only small changes needed to be made for the 1977 experiment.

The crop was grown outside, in a glass-roofed cage, with natural daylight and at ambient temperature. Spring wheat (var. Kleiber) was sown in rows 12·5 cm apart into a mixture of 50% Kettering loam, 50% peat contained in 18 capillary-watered beds, size 1·0 × 1·2 m. The seedlings were thinned to 38 m^{-1} of row and the soil covered with polythene granules to reduce evaporation. Polythene sheet was erected around pairs of beds, forming open-topped enclosures, and a network of pierced, small-bore plastic tubing was supported just above plant height in each enclosure. To half the beds, CO_2 from cylinders was supplied and to half, ambient air was pumped through at a similar rate. CO_2 concentration was maintained at 1000 vpm using Gasomat conductiometric analyser/ controllers. Both CO_2 and pumped air were supplied from 7·00 h to 19·00 h. Enrichment started 2 weeks after emergence and continued until senescence was advanced. As the crop grew the plastic feed tubes and the polythene sides were raised.

Weekly counts of shoot numbers were made, a 30 shoot sample was harvested at anthesis and a final harvest sample of 0·9 m^2 taken. Measurements of gross and net photosynthesis and CO_2 release into CO_2-free air were made weekly from about 2 weeks before until 4 weeks after anthesis. Measurements of leaf diffusive resistance and light intensity were made at the same time.

Only the results of the growth and yield measurements have so far been analysed. Increased CO_2 significantly increased maximum shoot number (2030 shoots m^{-2} compared with control 1860 shoots m^{-2}, SED = 87). However by anthesis there was no significant difference in shoot numbers, though CO_2 had significantly increased ear numbers (796 ears m^{-2} compared with 749 ears m^{-2}, SED = 17). Other significant increases were in ear dry weight (229 g m^{-2} compared with 186 g m^{-2}, SED = 9·5), stem dry weight (990 g m^{-2} compared with 876 g m^{-2}, SED = 40) and total dry weight (1571 g m^{-2} compared with 1401 g m^{-2}, SED = 60). However, by final harvest the differences had disappeared. Final grain yields for both treatments and controls were the same and similar to those from the 1976 experiment, equivalent to 7 t ha^{-1} (on 85% dry matter basis). This is high compared with field yields of Kleiber spring wheat. The mean yield for the 3 years 1972 to 1974 at Rothamsted was 5·6 t ha^{-1} (Pearman, Thomas and Thorne, *Annals of Botany* (1977), **41**, 93–108). Compared with this data, our straw dry weight was much larger (1157 g m^{-2} 682 g m^{-2}) as was total dry weight (1758 g m^{-2}: 1180 g m^{-2}).

The results indicate that photosynthesis is unlikely to be the factor limiting grain yield in Kleiber spring wheat under the experimental conditions. The high straw yields suggest that there was excess carbohydrate available even without CO_2-enrichment. The rates of photosynthesis were higher in flag leaves from the enriched crops (e.g. on 5 July when mean photosynthetically-active radiation above the crop was 1692 $\mu E\ m^{-2}\ s^{-1}$, SED = 27, net photosynthesis was 29·2 and 58·3 mg $CO_2\ dm^{-2}\ h^{-1}$, SED = 1·8, in air-enriched with 320 vpm and 1000 vpm CO_2 respectively). The fate of this extra photosynthate is not yet clear. (Kendall, Soffe and Thomas)

Effect of aerial pollutants on cereal growth and yield. During the last 4 years the growth and yield of barley grown in carbon-filtered and ambient field air has been compared at sites near the brickworks in the Marston valley. The experiment conducted at Woburn in 1976 using spring barley, var. Abacus (*Rothampsted Report for 1976*, Part 1, 40) was repeated in 1976/77 using winter barley, var. Maris Otter.

Despite nearly equal temperatures and relative humidities inside and outside the chambers, the development of plants in the chambers was 2 weeks ahead of that out-

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side. There were no signs of visible injury except for slight awn scorching on plants in unfiltered chambers and in outside plots towards the end of the season. There was an increase in total dry weight of 20% for the filtered against the unfiltered chambers but at the final harvest there was a smaller difference in grain weight. Grain yields were appreciably higher in 1977 than in 1976.

Tests in a wind tunnel have investigated how the open-top chambers can be made more efficient in preventing the incursion of ambient air whilst maintaining temperatures similar to those outside the chamber. The modified chambers are hexagonal (for ease of construction), with a sloping collar at the top and an internal baffle which improves filtration efficiency at higher ambient wind speeds.

It is planned to use the new chambers next year on a site at Thrupp End Farm (Lidlington) which has a different soil type and slightly higher levels of pollution than Woburn. Spring barley, var. Abacus, will be grown and both fluoride and sulphur dioxide levels monitored throughout the growing season. The chambers will also be used for studies on the growth of ryegrass at Great House Experimental Husbandry Farm, near Manchester, in association with ADAS and the Department of the Environment. (Buckenham and Parry)

Root growth of barley: effects of irrigation, P and K. The effect of water supply on barley root growth was investigated on sandy loam at Woburn (Butt Close field). Plant nutrients which are relatively non-mobile in the soil (P and K) are likely to be more available with abundant soil water. Irrigation versus nil was applied to the whole plots of the experiment, each subdivided into four for factorial application of P at 0 or 100 kg P_2O_5 ha^{-1} and K at 0 or 120 kg K_2O ha^{-1}.

Half of the experiment was sown on 15 March and half on 26 May (after failure of a sowing on 26 April), to permit study of the effect of dry periods in June and July on the actively-growing roots of a young crop, as well as to compare their growth with-root growth of a crop sown at the normal time. Evidence of a large difference in rate of development of the two sowings is given by the final yields, the mean yield of the first sowing being 4·5 t ha^{-1} gain at 85% dry matter without irrigation and 5·9 t ha^{-1} irrigated. The second sowing mean was 1·6 t ha^{-1} without response to irrigation. The first sowing, but not the second, appeared to respond to P and K fertiliser, especially when unirrigated. Detailed growth analysis was undertaken and the results still await statistical analysis. (Welbank and Taylor)

Cytokinins and endosperm cell division in wheat. Rapid changes in amounts of free base and nucleoside cytokinins occurred during the coenocytic phase of endosperm division and degeneration of antipodal cells in the embryo sac of young wheat grain (*Rothamsted Report for 1976*, Part 1, 42). The cytokinins from large-scale extracts of whole wheat ears harvested at various times up to 5 days after anthesis have been isolated and partly identified. Purification of the butanol soluble fractions from methanolic extracts on columns of 'Polyclar AT' using 0·02 M-buffer pH 3·5 and of 'Sephadex LH 20' using 80% ethanol removed over 90% of the impurities and separated the cytokinins as a group. Reverse phase separation of the cytokinins was achieved on columns of 'Sephadex LH20' using 35% ethanol the more polar compounds being rechromatographed on 'Sephadex LH20' using water. Soyabean callus assays of column eluates provided evidence for compounds with retention volumes similar to zeatin, zeatin riboside and their corresponding side chain O-glucosides. Zeatin was the predominant cytokinin during the first 3 days after anthesis and zeatin riboside on days 4 and 5. Unresolved problems with variable derivatisation of authentic zeatin with a number of silylating reagents have delayed further analysis of the zeatin-like factor by gas chromatography and initial

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attempts to further purify the presumed zeatin riboside and side chain O-glucosides on silica gel prior to derivitisation and gas chromatography gave poor recoveries. These problems could be circumvented by using high pressure liquid chromatography (HPLC) equipment. (Lenton)

Germination in developing wheat grains. Developing wheat grains are incapable of germinating until they are almost ripe, whereas embryos removed from these grains can germinate from about 3 weeks after anthesis. The possible role of growth substances in this inhibition of germination has been studied. The outer pericarp inhibits germination until it becomes fused to adjacent layers, but there is no evidence that this is due to growth substances; it may simply be a physical barrier to gas exchange. Part of the inhibition due to the tissues surrounding the embryo can be replaced by a low concentration of abscisic acid (0·1 μg ml^{-1}). This delays germination rather than preventing it completely. Germination can be accelerated by the addition of 10 μg ml^{-1} gibberellic acid (GA) and to a lesser extent by 2·5 μg ml^{-1} benzyl adenine.

Some cultivars pass through a period of low germination of the isolated embryos (King, *Planta* (1976), **132**, 43). This was confirmed for Maris Huntsman, but not Kleiber or Cappelle–Desprez. This again could be overcome by GA and partly overcome by benzyl adenine application. There was no correlation of changes in ability to germinate with free endogenous growth substances but the inhibitory period of isolated embryos coincided with low levels of 'bound' gibberellin and increasing amounts of 'bound' abscisic acid. At one harvest intact grains germinated better than isolated embryos and this coincided with a high level of 'bound' gibberellin in the tissues surrounding the embryos. (Radley)

Grain enlargement in wheat. When most grains are removed from a wheat ear soon after anthesis the remaining grains have a final dry weight greater than grains from intact ears. It has been shown recently that these large grains contain a large number of endosperm cells (Brocklehurst, *Nature* (1977), **266**, 348). The development of these grains and correlations of growth and growth-substance content have been studied in wheat, var. Kleiber. When most of the grains were removed from wheat ears the remaining grains developed increased numbers of aleurone and endosperm cells, and the increased grain volume was accompanied by an enlarged endosperm cavity. The giant grains usually synthesised starch more rapidly than normal grains. Flag leaf photosynthesis was unaffected and additional sugar was retained in the culm and glumes. Total nitrogen and free amino acid content increased. Gibberellin and auxin concentrations were greater in the glumes of the partly degrained ears, and auxin in the grains was also greater than in equivalent grains from intact ears. (Radley)

Sugar beet

Temperature and leaf development. Low temperatures in spring are probably the major factor restricting the early development of the leaf canopy (*Rothamsted Report for 1971*, Part 1, 101); breeding and selection might lead to varieties capable of sustaining leaf production and expansion at low temperatures. Studies of the early leaf growth of a range of genotypes at temperatures from 7 to 20°C are being made in controlled environments to examine the extent of genetic variability in the responses to temperature. Initial observations on varieties grown commercially in Britain showed that Anglo Maribo Polybeet, Sharpe's Megapoly, Hilleshog's Monotri and Amono consistently produced more leaf area than Sharpe's Klein Monobeet and Hilleshog's Nomo and Vytomo. The differences in leaf area were due more to differences in areas of individual leaves than in

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leaf number per plant. Leaf relative growth rate was similar both for plants within a variety and for all varieties. Therefore, differences in leaf area finally established were largely predetermined by the amount of leaf area established soon after seedling emergence.

There were few interactions between variety and temperature but some varieties, notably Anglo Maribo Polybeet, Hilleshog Amono and Sharpe's Klein Monobeet, had a lower temperature optimum for leaf area development than the others and Bush Mono G performed less well at cool temperatures than at warm ones relative to the other varieties. Cool temperatures decreased the rate of leaf production, mean area per leaf, leaf relative growth rate, the maximum potential size of individual leaves and hence total leaf area per plant. (Milford)

Effect of light intensity and duration on growth

Diurnal growth patterns. Sugar beet showed photomorphogenic responses to light of different quality given at the end of the day. Extending the daylength from 12 to 16 h with 4 h of low-intensity light from tungsten lamps increased both lamina expansion and petiole growth; whereas subjecting the plants to a short exposure of far-red light at the end of a 12 h day increased only petiole growth (*Rothamsted Report for 1976*, Part 1, 42). The nature of these responses has been examined in greater detail using transducers (Linear Variable Differential Transformers) to relate growth patterns to the timings of the treatments.

When grown at a constant temperature of 15°C lamina expansion (measured as extension) of both control plants (12 h photoperiod) and treated plants (12 h photoperiod extended with 4 h tungsten light) was 0·2 mm h^{-1} during the day. In the dark, the rate of expansion in control plants increased immediately to a constant 0·5 mm h^{-1} and reverted rapidly to the daytime rate at the onset of the next photoperiod. During the 4 h with tungsten lights, the rate of lamina expansion of treated plants rapidly increased to 0·8 mm h^{-1} and declined during subsequent darkness to the same rate as the controls.

Petioles of control plants grew at a rate of 0·08 mm h^{-1} in both light and darkness. Their response to the tungsten extension treatment was neither as immediate nor as rapid as that of the laminae. In tungsten light there was a 1 to 2 h lag after which petiole extension gradually increased during the next 2–3 h to a rate of 0·5 mm h^{-1}; this was maintained throughout the night and then decreased over the first 6 h of the following photoperiod to a rate of 0·15 mm h^{-1} (cf. 0·08 mm h^{-1} in the control plants). A short exposure to far-red light at the end of the day produced a different response: petiole growth rate was increased immediately to 0·4 mm h^{-1} and declined more rapidly during the next photoperiod. These different patterns of petiolar growth suggest that the stimulus of the tungsten daylength-extension treatment is perceived in the laminae and is transmitted to the petioles to induce the growth response where the stimulus of far-red light is perceived directly by the petioles. (Milford, Pocock and Lenton)

Developmental anatomy and gibberellins. It was evident that the differences in leaf area due to extending daylength with 4 h tungsten light were established at an early stage of development (*Rothamsted Report for 1976*, Part 1, 42). Sequential harvests of the fifth leaf were taken from plants grown at 15°C in a 12 h (control) and a 12 h + 4 h tungsten photoperiod (treated) to relate changes in leaf area, cell number and gibberellin content.

To overcome variation between individual plants, results are expressed on a developmental index based on the position of leaf five in relation to an index leaf of a given size and age, in this case 55 mm in length and 10 cm^2 in area (stage 0). Leaves older than this stage are numbered +1, +2 etc. and a fully expanded leaf occurs at stage +10. Leaves

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younger than stage 0 are numbered −1, −2 etc. with stage −4 being 5 mm in length and 10 mm^2.

The area of leaf five in both control and treated plants reached 20 cm^2 by stage +1 at which point the leaf entered the linear phase of expansion. This phase ceased in control plants by stage +5 giving a final area of 190 cm^2; in treated plants expansion continued until stage +8 to give a final area of 260 cm^2.

Cell number per leaf increased steadily in control plants from 2×10^6 at stage −3 to 75×10^6 at stage +6 when cell division ceased. The initial increase in cell number in treated plants is more rapid and continued until stage +8 giving a final cell number of 100×10^6. It was the difference in the rate of cell division between −3 and +1 which established the difference in final cell number and leaf area.

Gibberellin content per leaf and per cell was greater in treated than control leaves at all stages of development. Maximum gibberellin content per leaf occurred at stage +2 (40 cm^2) at the start of the linear phase of expansion whereas the concentration per cell declined steadily during development from stage −2.

The main effect of daylength extension on leaf development was an increase in the rate of cell division when the leaf area was only 5 to 10 cm^2 which was reflected in greater final cell number. This increased rate of division coincided with the maximum difference in gibberellin content per cell but further experiments are required to establish gibberellin as the cause. (Pocock and Lenton)

Endogenous gibberellins. Both the changes observed in naturally-occurring gibberellins and the effects of applied GA suggest an involvement of gibberellins in photoperiodically-induced leaf expansion in sugar beet (*Rothamsted Report for 1976*, Part 1, 42). Identification of the main biologically-active gibberellin of sugar beet has been attempted following the acquisition of new combined gas chromatography-mass spectrometry (GC–MS) facilities in the Insecticides and Fungicides Department. For this purpose apices and young leaves (<20 mm in length) were dissected from 4000 sugar-beet seedlings and extracted with cold aqueous methanol. The ethyl acetate soluble acids were purified in a column of 'Polyclar AT' using 0·1 M-phosphate buffer pH 5·0 and on silica gel thin layers developed in EtOAc : $CHCl_3$: CH_3COOH 15 : 5 : 1 by vol. The main biologically-active gibberellin, Rf 0·3 to 0·4 (2·1 μg GA_3 equivalents), was methylated with diazomethane (CH_2N_2), trimethylsilylated with N,O-bis-(trimethylsilyl)-acetamide(BSA) and analysed by gas chromatography isomethermally at 210°C on a column of 2% OV-101. A peak with retention time corresponding to MeTMSi GA_3 and area equivalent to that calculated from bioassay was subjected to combined GC-MS by continuous monitoring of ions within the mass-range m/e 400 to 550. Examination of the mass spectrum showed two compounds with parent ions at M^+ 474 and M^+ 504. The compound with a parent ion at M^+ 474 is unidentified but that of M^+ 504 is consistent with the structure of MeTMSi GA_3. Until relative retention data and line diagrams of MeTMSi GA_{30} (M^+ 504) and MeTMSi GA_{22} (M^+ 504) are available these and other possibilities cannot be excluded. (Lenton, with Pickett, Insecticides and Fungicides Department)

Growth regulator short-term trials. In addition to full-season screening procedures, short-term trials have been started using three to four-leaf plants grown on for a further month after treatment. These tests will be used to determine the best method of applying small volumes of regulators (spray, micro-drop to the apex or leaf, soil drench, soil injection) and to characterise the primary effects of the main groups of plant growth regulators. Furthermore, they will act as an initial screen for new chemicals, the effects of which are completely unknown on sugar beet, and which could not be justifiably incorporated into larger scale trials without further information.

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Mefluidide (supplied by Fisons Ltd.) was one such chemical. It suppresses growth of many plants and is thought to affect cell expansion. The compound was dribbled into the apex of plants at the eight-leaf stage in 200 μl water containing 0, 0·36, 0·72 and 1·44 mg a.i. (equivalent to 0, 0·25, 0·5 and 1·0 kg ha^{-1}). The regulator suppressed growth of the whole plant and at the highest concentration acted as a mild herbicide showing phytotoxic effects on the leaves and petioles. Sugar analyses have not yet been completed but root weights were so low that it is unlikely that sugar yield per root will be improved. (Pocock)

Potatoes

Leaf canopy structure and crop growth. With the current interest in maximisation of yield, high rates of fertiliser, high plant densities and frequent irrigation are often applied to potato crops but yields are still largely dependent on radiation interception and the efficient use of light by the crop. Irrigation and increased fertiliser application or plant densities affect leaf canopy structure, particularly branching of the above-ground stems, and increase the tendency to lodge. A preliminary experiment examined the effects of modifying haulm structure by mechanical or chemical means on crop growth, radiation interception, photosynthesis and yield. Treatments tested were:

(i) excision of stem apex at tuber initiation;
(ii) excision of axillary branches from tuber initiation onwards;
and (iii) application of 15 ml^{-1} plant of 1 or 10 ppm morphactin (chlorflurecol-methyl) at tuber initiation.

Chlorflurecol suppresses apical dominance temporarily and stimulates axillary branch growth.

The summer was cool and haulm growth slow, with peak leaf area indices of 3·5 being achieved only in early September. All treatments depressed crop growth for 2 weeks after tuber initiation, but there was considerable compensatory growth thereafter. Although leaf areas were similar throughout the season, the excision treatments greatly affected haulm structure. Removal of the apex resulted in increased branching, giving a more compact bushy plant with numerous small leaves. Axillary branch removal gave straggly plants with fewer but larger leaves; the stems lodged earlier and during August and early September this crop intercepted 10% less radiation, mainly due to decreased leaf cover over the ridge. Morphactin at 1 ppm had little effect on crop growth, but at 10 ppm caused leaf distortion, failure of leaves to expand fully, fusion of leaflets, increased leaf thickness and smaller leaf areas. Although later-formed leaves were less affected, leaf areas were low throughout the season (maximum LAI 2·1) and during August and early September the crop treated with chlorflurecol at 10 ppm intercepted 25% less radiation compared with the apex removed treatment. Despite marked differences in haulm structure, leaf areas and radiation interception, crop growth and tuber bulking were unaffected by treatment until early September. This was surprising, for the chlorflurecol 10 ppm treated crop clearly was less efficient at intercepting radiation. However, between 2 and 12 weeks after treatment net assimilation rate was higher with chlorflurecol at 10 ppm. Photosynthetic rates were measured but data are not yet available and the causes of this increase are not known. Senescence started earlier with the chlorfluorecol 10 ppm treatment and final yields were decreased mainly because of the lower average tuber weights rather than fewer tubers. More detailed measurements of light interception, photosynthesis and respiration on crops with varying canopy structures will be made in 1978.

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TABLE 1

The effects of apex excision, lateral excision and chlorflurecol treatment on tuber yields and tuber number in potatoes

	Apex excised	Laterals excised	Chlorflurecol 1 ppm	Chlorflurecol 10 ppm	Untreated
Total tuber yield (t ha^{-1})	46·6	48·7	46·1	38·7	47·5
Total tuber number ($\times 10^{-3}$ ha^{-1})	414	471	404	411	442

Plants were also examined prior to tuber initiation to study the relationship between stolon growth and tuber formation; this work will be expanded in 1978. (Wood, Antoniw and Taylor)

Weed biology

Park grass. The usual spring and autumn surveys of all plots were made. The most noticeable feature of the spring survey was the abundant flowering of meadow foxtail (*Alopecurus pratensis*) on plots where it has been present in smaller amounts in recent years. A similar increase in meadow foxtail was noted after the drought of 1921. The seven plots particularly affected in 1977 were 7d, 11^{2}b, 13d, 14d, 15a (the half nearest to plot 14), 16d and 20^3. Meadow foxtail had completed its spring growth before the drought became intense in 1976 and was probably less severely checked than later-flowering species, e.g. cocksfoot (*Dactylis golmerata*) and false oat grass (*Arrhenatherum avenaceum*); it was therefore able to dominate them in the spring of 1977 more effectively than after a more normal summer. A hay sample was taken from plot 14d, where meadow foxtail provided 37% and 38% by weight of hay in 1975 and 1976, for comparison with previous years, but this sample has not yet been sorted.

Bulbous buttercup (*Ranunculus bulbosus*), which has not been seen on Park Grass for some years, flowered on plot 2a. It also flowered more freely on Harpenden Common than in recent years, so this too may have been favoured by the hot dry weather of 1976.

Most of the narrow central strips cut short in certain plots in 1973 and 1974 to allow access to Entomology pitfall traps (*Rothamsted Report for 1975*, Part 2, 63–89) are now indistinguishable from the surrounding vegetation, but on all sections of plot 16 the central strip was still clearly visible in the spring, and in the autumn meadow vetchling (*Lathyrus pratensis*) was flowering more freely near this strip than elsewhere on plot 16a.

Salad burnet (*Poterium sanguisorba*) was far more abundant on unmanured plots 3a and 3b than on the adjacent plots 2a and 2b, unmanured following dung from 1856 to 1863. On plot 3c it was confined to a narrow band adjacent to 3b, suggesting vegetative invasion of 3c when the soil pH is still only 5; plot 3b is now pH 6·5. On the heavier-yielding unmanured plot (12), salad burnet is less abundant than on plot 3. Its abundance therefore seems to be inversely related to soil fertility and directly to soil pH.

The restharrow (*Ononis repens*) seedlings which appeared in one corner of plot 4^{1}c in 1976 are now well-established miniature shrubs.

Parts of a large fairy-ring visible as segments of a circle of lush growth on plots 2a and 3a in spring were marked in autumn by grasses flowering there but not elsewhere on those plots, meadow foxtail (out of season) and false oat grass (*Arrhenatherum avenaceum*) on plots 2a and cocksfoot (*Dactylis glomerata*) on plot 3a.

Broadbalk. The wet autumn and winter and windy spring profoundly affected weed control in the 1977 crop of winter wheat. The crop was drilled into very wet soil on 23 to

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24 November 1976 and further rain prevented the post-drilling application of terbutryne to control blackgrass (*Alopecurus myosuroides*) and some autumn-germinating broad-leaved weeds. Numerous blackgrass seedlings had been destroyed at ploughing and more during pre-sowing cultivations and it was hoped that this, combined with drilling after the main germination-period of the species, would leave few seedlings to infest the crop. However, sufficient seeds remained dormant in the wet soil to give a spring flush of germination and by late July every plot was infested, section 4 (after potatoes and beans) very lightly, section 5 (wheat after fallow) slightly more, and the other sections severely, although unsprayed section 8 had less dense blackgrass than the three sections with continuous wheat plus herbicides.

The first dry period after sowing was in mid-March. This permitted rolling, and subsequent inspection of the plots. Sections 0 and 1 at the top of the slope crumbled to a good tilth except for a large area at the lower ends of plots 7 and 8 on section 1, which had been severely waterlogged. Rolling was ineffective lower down the field, and where there had been severe waterlogging, especially at the bottom of section 9, the soil surface had sunk and dried to a hard crust. These areas became covered with dense carpets of annual meadow-grass (*Poa annua*) and bore very little crop.

The wheat on sections 0 and 1 also missed its routine spray in May against broad-leaved weeds, because of the risk of drift down-wind on to the beans on sections 2. This, combined with lack of terbutryne in autumn, allowed establishment of autumn and winter-germinating weeds. The very herbicide-sensitive corn buttercup (*Ranunculus arvensis*) was more abundant on section 1 (continuous wheat, with herbicides annually since 1967) than for many years, but its incidence on section 0 (continuous wheat, with herbicides annually since 1957) was almost unaffected. It occurred on 13 plots out of 20 on Section 1 compared with only one plot in 1974, but only two plots of section 0 compared with none in 1974. This was not just an effect of weather, as on the unsprayed section 8, corn buttercup was recorded on 16 plots in 1977 and 13 in 1974. Corn buttercup seeds have a long dormancy, evidently sufficient to re-infest plots after 10 years but not after 20 years. Transference of fresh seeds from the unsprayed section 8 is unlikely as farm machinery does not cross the intervening potato, bean and fallow sections while harvesting wheat.

The beans on section 2, where weeds are controlled only by inter-row cultivation, showed the usual infestations of knotgrass (*Polygonum aviculare*) and black bindweed (*P. convolvulus*) but orache (*Atriplex patula*) was less plentiful in 1977.

The potatoes on section 7 were relatively clean except for the expected patches of horse-tail (*Equisetum arvense*) on low nitrogen and no nitrogen plots and a new phenomenon for Broadbalk, patches of field bindweed (*Convolvulus arvensis*) climbing over the potato haulms, and even over the horsetail, especially on plots 2.1 and 2.2 (dung), 3 (unmanured) and 5 (P K Mg). This suggests distribution by area rather than in association with fertiliser treatment. The field bindweed on Broadbalk did not flower in the poor summer of 1977 (*Rothamsted Report for 1976*, Part 1, 46).

Germination continued in all three sets of pans of Broadbalk soil (*Rothamsted Reports for 1974*, Part 1, 39; *for 1975*, Part 1, 47–48; and *for 1976*, Part 1, 46–47). The 1974 set have now completed the 3-year period for which such pans are normally kept. A further 2000 seedlings were removed from these pans between September 1976 and September 1977, 1500 of them poppies (*Papaver rhoeas* and *P. argemone*). The percentage of the total germination occurring in the third year varied from 15% for poppies to 0·3% for black-grass, but the additional seedlings did not affect the relative abundance of species (*Rothamsted Report for 1976*, Part 1, 46–47) nor the order of weediness of plots (fertiliser treatments) or sections (cropping). Germination of a few species continued to the end of the 3-year period so 18 pans containing them were retained when the other 80 were thrown away. Poppies are the most numerous species in the retained pans to mid-Novem-

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ber 1977, with ten and 12 seedlings in the two pans from the unsprayed section of the dung plot. Although this is only 0·5% of the total germination of poppies in these pans, it represents over 4×10^6 ha^{-1} viable seeds surviving into the fourth year even under ideal conditions for germination.

The number of seedlings emerging in the first years of all three sets of pans can now be compared. Blackgrass is the most abundant species in all 3 years but the total seedlings (approx. 9500, 30 000 and 8000) clearly reflect the increase which followed the failure to apply terbutryne to control it on the sprayed plots of winter wheat in the middle year. Numbers changed little in the same 3 years on the unsprayed section (6500, 6500 and 5400). Blackgrass as a percentage of all seedlings recovered in the first year, rose from 57% in 1974 to 80% in 1975 and fell to 40% in 1976 when terbutryne was again applied. Scentless mayweed (*Tripleurospermum maritimum* ssp. *inodorum*) and wall speedwell (*Veronica arvensis*), both predominantly autumn-germinating, showed similar patterns of abundance to blackgrass and, surprisingly, so did spring-germinating orache, while poppies knotgrass and Venus' looking-glass (*Legousia hybrida*) showed the opposite, with the unsprayed year the lowest. Probably competition with uncontrolled blackgrass accounted for this. Orache is almost confined to the three course rotation sections, where blackgrass is at its lowest density, so it was not depressed by stronger competition in 1975, but the reason for its abundance in that year is not yet known. Corn buttercup, quoted from the field records as an example of a broad-leaved weed benefiting from failure to apply herbicides, is not abundant in pans because it is very susceptible to any of the herbicides used in spring to control dicotyledons; there were applied in all 3 years in which pans were taken.

According to the results of the first years of these three sets of pans, cropping-sequence has a greater effect than fertilisers on the numbers of viable weed-seeds in soil. The mean of all plots ranged from $2 \cdot 2 \times 10^6$ ha^{-1} in wheat with herbicides in the wheat/wheat/fallow rotation to 44×10^6 ha^{-1} in continuous wheat without herbicides, compared with the mean of all sections from $5 \cdot 3 \times 10^6$ ha^{-1} on plot 5 (P K Mg) to 30×10^6 ha^{-1} on the dung plot (2.2), nearly 12×10^6 of the latter being poppies from the unsprayed section. (Thurston and Williams)

Staff and visiting workers

E. D. Williams was transferred to the ARC Weed Research Organisation on 1 September 1977 to continue his studies on the biology of agriculturally important weeds. Work on the occurrence and distribution of weeds on the classical experiments at Rothamsted will be continued here by Miss Thurston.

D. W. Wood was appointed in January and Linda D. Antoniw in March to undertake studies on the physiology of the potato. Anne H. Buckenham was appointed in August to assist in the work relating to the effect of aerial pollutants on crop plants. T. O. Pocock was awarded the Ph.D. Degree of London University.

Dr. Daria Generowicz spent a period of 9 months in the department, sponsored by the British Council, on leave from the Institute of Plant Biology, Warsaw. Dr. G. R. Roberts of the Tea Research Institute in Sri Lanka has commenced a 1 year visit sponsored by the Nuffield Foundation to undertake studies on photorespiration in relation to the tea plant. Dr. R. Martinez-Carrasco, after completing his earlier studies returned to Spain but then rejoined the department for a further short period to continue his work on the cereal crop sponsored by the Spanish Higher Council for Scientific Research. Mrs. Manuela Chaves of the Higher Institute of Agronomy, Lisbon, spent a short period visiting the department to learn techniques relating to the field measurement of photosynthesis. Mrs. Celeste Arrabaca of the University of Lisbon has commenced studies for a higher degree sponsored by the Portugese National Institute for Scientific Investigations.

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Sandwich course students who worked in the department were Anne Couth, Frances Barnby, S. R. McMillan, D. J. Blackwell and M. C. Thompson.

C. P. Whittingham attended a meeting and was elected Chairman of the Interim Council of the newly formed Federation of European Societies of Plant Physiology (FESPP) in Vienna. He also lectured to the Inaugural Meeting of the Portuguese Society of Plant Physiologists and was the UK representative at the UN/ECE Preparatory Meeting in Geneva for the Symposium on the Effects of Pollution on Vegetation.

Susan M. Thomas attended the Bat-Sheva Seminar on Physiological Aspects of Wheat Breeding at the Weizmann Institute of Science, Rehovot, Israel from 24 April to 4 May. Gillian N. Thorne gave a paper at the International Symposium on Production of Biomass and Yield Formation of Field Crops in Prague, organised by the Czechoslovak Scientific and Technical Society. D. W. Lawlor was invited to the Boyce Thompson Institute, Yonkers, New York to give a paper at the International Conference on Stress Physiology in Crop Plants from 28 to 30 June; he also visited Cornell University and DuPont Nemours Research Laboratories, Delaware. In July D. W. Lawlor visited the Deutsche Forschungsgemeinschaft meeting in Darmstadt, Germany in July and gave a paper on carbon metabolism in water-stressed plants. Joan M. Thurston went to Uppsala, Sweden to attend the Council Meeting of the European Weed Research Society and organised a session on weed control of special seeds.

Publications

General Papers

1 Thorne, G. N., Thomas, S. M. & Pearman, I. (1978) Effect of nitrogen on photosynthesis and respiration in crops of winter wheat. *Proceedings of Symposium on 'The production of biomass and yield formation of the field crops.'* Czechoslovakia 1977,

Paper in Rothamsted Report, Part 2

2 Williams, E. D. (1978) Botanical composition of the Park Grass plots. *Rothamsted Experimental Station. Report for 1977*, Part 2, 31–36.

Research Papers

3 Bird, I. F., Cornelius, M. J. & Keys, A. J. (1977) Effects of temperature on photosynthesis by maize and wheat. *Journal of Experimental Botany* **28,** 519–524.

4 Bird, I. F., Cornelius, M. J., Keys, A. J. & Whittingham, C. P. (1978) Intracellular labelling of sucrose made by leaves from $^{14}CO_2$ of (3-^{14}C) serine. *Biochemical Journal* **172**, 23–27.

5 Brough, A., Parry, M. A. & Whittingham, C. P. (1978) The influence of aerial pollution on crop growth. *Chemistry and Industry* No. 2, 51–53.

6 French, S. A. W. & Humphries, E. C. (1977) The effect of partial defoliation on yield of sugar beet. *Annals of Applied Biology* **87,** 201–212.

7 Keys, A. J., Sampaio, E. V. S. B., Cornelius, M. J. & Bird, I. F. (1977) Effect of temperature on photosynthesis and photorespiration of wheat leaves. *Journal of Experimental Botany* **28,** 525–533.

8 Kumarasinghe, K. S., Keys, A. J. & Whittingham, C. P. (1977) Effects of certain inhibitors on photorespiration by wheat leaf segments. *Journal of Experimental Botany* **28,** 1163–1168.

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9 Kumarasinghe, K. S., Keys, A. J. & Whittingham, C. P. (1977) The flux of carbon through the glycollate pathway during photosynthesis by wheat leaves. *Journal of Experimental Botany* **28,** 1247–1257.

10 Lenton, J. R. & Milford, G. F. J. (1977) Plant gowth regulators and the physiological limitations to yield in sugar beet. *Pesticide Science* **8,** 224–229.

11 Makunga, O. H. D., Pearman, I., Thomas, S. M. & Thorne, G. N. (1978) Distribution of photosynthate produced before and after anthesis in tall and semi-dwarf winter wheat, as affected by nitrogen fertiliser. *Annals of Applied Biology* **88,** 428–437.

12 Milford, G. F. J., Cormack, W. F. & Durrant, M. J. (1977) Effects of sodium chloride on water status and growth of sugar beet. *Journal of Experimental Botany* **28,** 1380–1388

13 Pearman, I., Thomas, S. M. & Thorne, G. N. (1978) Effects of nitrogen fertiliser on the distribution of photosynthate during grain growth of spring wheat. *Annals of Botany* **42,** 91–99.

14 Radley, M. (1977) A technique for the examination of endosperm cells in cereal caryopses. *Annals of Applied Biology* **86,** 133.

15 Soffe, R. W., Lenton, J. R. & Milford, G. F. J. (1977) Effects of photoperiod on some vegetable species. *Annals of Applied Biology* **85,** 411–415.

16 Thorne, G. N. (with Bayles, R. A. & Evers, A. D.) (1978) The relationship of grain shrivelling to the milling and baking quality of three winter wheat cultivars grown at different levels of nitrogen fertiliser. *Journal of Agricultural Science* **90,** 445–446.

17 Wheeler, A. W. (1977) Auxin-like growth activity of phenylacetonitrile. *Annals of Botany* **41,** 867–872.

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