ROTHAMSTED RESEARCH

Report for 1975 - Part 1

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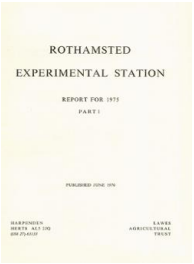

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Introduction

Considerable effort in the Botany Department has been devoted to studying the physiology of cereal crops and in particular of wheat. Contrary to opinions originating from American workers, our measurements indicate that if the process of photorespiration could be suppressed, without any harmful consequences, in cereal crops grown in the United Kingdom, the expected increase in growth rate would be of the order of 25%. This increase, which is lower than that which has been estimated previously, takes into account the actual growing conditions for field crops in this country. So far we have been unsuccessful in finding a chemical which can be used under field conditions to effectively inhibit the process of photorespiration. Experiments with Maris Huntsman have indicated that after higher applications of nitrogen fertiliser, photorespiration is increased.

Studies of the influence of pollutants in the atmosphere, and in particular of sulphur dioxide, suggest that losses in yield of economic importance may be experienced in several areas of the United Kingdom.

The second arable crop studied in detail has been sugar beet. The work has been directed towards analysing those factors which control the potential of the root for the storage of sucrose. In addition the factors which limit the establishment of the crop at lower temperatures have been investigated because of the proven importance of achieving growth early in the season.

At the present time relatively little work is being undertaken on the potato crop, in

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spite of the urgent need for further studies on the physiology of this crop. At the present time we are unable to transfer or appoint new staff to undertake this work.

Due to the moratorium on the appointment of new staff, which existed for part of last year, the Botany Department is functioning with three out of 12 Assistant Scientific Officer posts vacant. This has resulted in some reduction in the work on weed biology and at present work on blackgrass has been discontinued. In other subjects the programme of work has been maintained and indeed the number and extent of pot experiments in the glasshouse has been greater than usual; this has only been achieved through the special efforts of those in post, particularly those in support posts.

There has been little opportunity to instal new facilities. Plans and estimates have been prepared for the replacement of the older, wooden glasshouses, which are now in a poor state of repair, but it has not been possible to make financial provision for the work.

Cereals

Photosynthesis and photorespiration

Photosynthesis of maize and wheat at different temperatures. Experiments were undertaken to elucidate the difference in growth response to low temperatures of wheat and maize. Kleiber spring wheat and Anjou maize were grown in constant environment rooms at day/night temperatures of 23/18°C, humidities of 85/90% and a 16 h day at 580 μE m^{-2} sec^{-1} of photosynthetically active radiation. After three weeks, the plants were divided between four rooms with daylength and light intensities as above but each at different temperature regimes; 13/10, 18/14, 23/18 or 28/22°C, with corresponding humidities of 75/90, 80/90, 85/90 and 85/90%. Measurements were made on wheat plants when they had reached anthesis, i.e. at 54, 49, 40 or 35 days in day temperatures of 13, 18, 23 and 28°C respectively and on maize plants when the ninth leaf was fully expanded, i.e. at 50, 27, 15 and 13 days. Plants were taken from the room in which they were grown to each of the other rooms and after 40 min in the new environment photosynthetic rates were measured.

The flag leaf of wheat and leaf nine of maize photosynthesised as fast or faster than other leaves on the plants at the stages when the measurements were made. For measurements made at 23 and 28°C, net photosynthesis by maize leaves from plants grown at 18, 23 or 28°C was significantly faster than for wheat leaves grown at any of the four temperatures; leaves from maize grown at 13°C, which were yellow and not fully developed, photosynthesised at insignificant rates (less than 1·5 mg CO_2 dm^{-2} h^{-1}). At all four temperatures, net photosynthesis by leaves from wheat grown at 18°C was significantly faster than by leaves from wheat grown at 23 or 28°C and except when measured at 13°C the mean rates for leaves grown at 18°C were faster than for leaves grown and measured at 13°C. At all four temperatures at which measurements were made, leaves from maize grown at 23°C photosynthesised faster than leaves from maize grown at 18 or 13°C and except when measured at 28°C, faster than leaves from maize grown and measured at 28°C. So the day temperatures for growth that produced leaves with fastest rates of net photosynthesis were 18°C for wheat and 23°C for maize; the rates for maize were significantly faster than for wheat when measured at the two hotter, but not at the two cooler, temperatures.

The optimum temperature for photosynthesis by wheat leaves was near 18°C; for maize grown at 18 or 23°C the optimum was near 23°C but for maize grown at 28°C it was 28°C or above. Maize varieties grown in hot climates have maximum rates of photosynthesis near 35°C. Breeding and selection have produced varieties better adapted to growth in temperate climates; in further improvements the aim should be to obtain maize with a temperature optimum for photosynthesis nearer 18°C and which develops leaves with the fastest rates of photosynthesis when the growth temperature is 18°C or

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less. In the present experiment, maize grown at 18°C had leaves less effective for photosynthesis at 13 and 18°C than wheat grown at these lower temperatures. Grown at 13°C maize did not produce effective leaves.

The above observations are consistent with field observations (*Rothamsted Report for 1974*, Part 1, 29) when photosynthesis per unit area of leaf was slower in maize than wheat except at the highest light intensities. Maize in the field would have experienced temperatures mostly below 18°C which are sub-optimal for development of the active photosynthetic tissue. (Bird, Cornelius and Keys)

Rapid measurement of gross and net photosynthesis. An area of leaf 1 × 10 cm was enclosed between the two halves of a cup-type leaf chamber mounted on tongs. The act of closing the chamber admitted air containing $^{14}CO_2$ from a light alloy cylinder so that the air passed over both sides of the leaf; the total flow rate was controlled by a pressure-reducing valve and a flow regulator (Platon 'Flostat'), at 500 cm^3 min^{-1}. For 5 sec the gas from the chamber was directed to waste through a soda-lime tower; for the next 40 sec it was directed into a plastic-covered aluminium foil bag. The concentration of carbon dioxide in this sample of gas was subsequently measured with an infra-red gas analyser (IRGA). The piece of leaf was frozen in liquid nitrogen immediately the gas sample had been collected and the radioactivity present determined after combusting it in a Packard sample oxidiser. The results were used to calculate net and gross photosynthesis.

Where gross and net photosynthesis were measured consecutively on the same piece of leaf using different gas mixtures, as in the experiment in which maize and wheat were compared in the constant environment room, there were two main sources of error. A transient and variable decrease in photosynthetic rate occurred soon after the leaf was clamped in the chamber and this led to an underestimate of the rate of gross photosynthesis. Secondly, it was found that the amount of ^{14}C in the 0·5 cm^2 disks, punched from the leaf, varied in a random way depending on the position in the 1 × 10 cm area of leaf from which they were taken. The mean value for three leaf disks for each measurement was used.

The method described above gave the same values for gross and net photosynthesis for maize leaves as expected, but the rate of gross photosynthesis by wheat was greater than that of net photosynthesis. The calculated rate of photorespiration for wheat was about one-fifth to one-quarter that of gross photosynthesis. This suggests that for wheat grown in a climate like that of the United Kingdom, the increase in growth rate which might be obtained if photorespiration could be suppressed without any harmful consequences, would be of the order of 25%. This would not necessarily result in the same percentage increase in grain yield. (Bird, Cornelius and Keys)

Inhibitors of photorespiration. Ethyl glycidate (Ethyl-2,3-epoxypropionate) (Zelitch, *Archives of Biochemistry and Biophysics* (1974), **163**, 367), which has been claimed as an effective inhibitor of photorespiration, was sprayed on to field plots of Kleiber spring wheat and Cargill Primeur maize at one of two rates (0·27 and 0·77 kg ha^{-1}) at one of three dates (24 June, 11 July or 29 July 1975 on wheat; 11 July, 29 July or 7 August 1975 on maize). Treatments were replicated in three blocks for wheat but there was no replication for maize. The mean grain yield of wheat was 2·91 ± 0·13 t ha^{-1} at 85% dry matter; for maize, the overall mean for three harvests in late August was 41·37 ± 2·35 t ha^{-1} fresh shoot (19·7% dry matter). Analysis of variance showed no significant treatment effect on yield for either species.

In a pot experiment solutions of ethyl glycidate (2·32 g l^{-1}) and two compounds from the American Cynamid Company, 'AC 99850' (6·63 g l^{-1}) and 'AC 23380' (3·62 g l^{-1})

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were applied every week from 10 June to 30 July to plants of Kleiber spring wheat. The eight plants in each pot were sprayed with a total of 4 ml of water containing spreader only (control) or an inhibitor solution. Treatments were replicated in three blocks. The procedure described above was used to measure gross and net photosynthesis. Two measurements were made on each replicate on each of five occasions using air containing 325·5 vpm $^{14}CO_2$ sp. act. 0·678 μCi μmol^{-1}. The overall means for the experiment were: net photosynthesis 26·4 mg CO_2 dm^{-2} h^{-1}; gross photosynthesis 34·3 mg dm^{-2} h^{-1} and, by difference, photorespiratory CO_2 release 7·90 mg dm^{-2} h^{-1}, i.e. about one-quarter that of gross photosynthesis. The mean light intensity was 1300 μE m^{-2} sec^{-1}. Analysis of variance showed no significant effect of spray treatment on either CO_2 exchange rate.

Two pots from each replicate treatment were used (11 August 1975) to measure total fresh weight, number of ears and dry weights of straw, ears and grain. The mean total dry weights per pot were 94·9, 94·4, 93·8 and 95·5 $\pm$ 2·21 g for control, ethyl glycidate, 'AC 99850' and 'AC 23380' treatments respectively; there were no significant effects of treatment on any of the parameters of yield.

A day before and a day after a spray treatment one flag leaf from each replicate was supplied with air containing 270 vpm $^{14}CO_2$ (13 μCi μmol^{-1}) in the light for 10 sec using a technique similar to that of Shimshi (*Journal of Experimental Botany* (1969), **20**, 381). After detaching the leaf chamber, leaves were left for 20 sec to assimilate $^{12}CO_2$ from the ambient atmosphere, then a disk from the piece of leaf exposed to $^{14}CO_2$ was cut and quickly frozen in liquid nitrogen. The products of photosynthesis were subsequently extracted and separated by two-dimensional thin layer chromatography on cellulose powder. No significant effect of the spray treatments was found on the relative amounts of ^{14}C in photosynthetic products.

Evidently, if the various chemicals were taken up by the plant in sufficient amounts they were not effective in reducing photorespiration. (Bird, Cornelius and Keys)

Response of three varieties of winter wheat to large amounts of nitrogen

Growth. In previous experiments with Kleiber spring wheat, increased amounts of nitrogen increased leaf area and photosynthesis per unit area of ground relatively more than grain yield (*Rothamsted Report for 1974*, Part 1, 25). This inefficiency of crops given nitrogen was not caused by diversion of dry matter from the grain to stem and leaf growth; probably it was caused partly by the larger respiratory loss of CO_2 from the larger stems containing much protein. This investigation was continued in 1975. The response of three varieties of winter wheat to eight amounts of nitrogen (0–210 kg ha^{-1}) was investigated in a field experiment. The varieties used were the old low-yielding Cappelle–Desprez(C), and the newer Maris Huntsman(H) and semi-dwarf Maris Fundin(F).

With all three varieties, nitrogen increased leaf area relatively more than grain yield. The responses to nitrogen were much larger than in previous spring crops perhaps because the wet winter and preceding oat crop had depleted soil nitrogen. Leaf area was increased by nitrogen throughout the range tested, but grain yield and most other growth attributes increased only with amounts up to 150 kg N ha^{-1}. Varieties differed little from each other in dry weight or leaf area with 0 or 30 kg N ha^{-1} but with more nitrogen grain yield of F and H was greater than that of C, and straw yield and shoot dry weight at all times after anthesis was greater for C and H than for F. Total leaf area was greatest for H and least for F but leaf area above the flag leaf node, which produces most of the carbohydrate in the grain, was similar for all three varieties. Mean grain yields with 0 or 210 kg N ha^{-1} were C 3·6/6·5, H 3·4/7·0, F 3·1/6·9, $\pm$ 0·24 t ha^{-1} (85% dry matter). Equivalent straw yields were C 3·7/8·2, H 2·7/8·2, F 2·4/7·6, $\pm$ 0·30 t ha^{-1} dry matter,

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and equivalent values of leaf area index at anthesis were C 3·0/10·2, H 2·8/11·6, F 2·7/8·3 ± 0·47. Effects of nitrogen and variety on growth and yield were not consequences of effects on development, which was altered little by treatment. Anthesis and complete senescence of the leaves were delayed three days by the larger amounts of nitrogen and anthesis of F was three days earlier than of C and H. Consequently the period of grain growth ranged from 40 days (C and H) to 43 days (F)—unusually short because the hot weather hastened leaf senescence. Nitrogen increased grain yield by increasing the number of ears and number of fertile spikelets per ear, and hence the number of grains per ear. Dry weight per grain of C and F was decreased by nitrogen throughout the range tested; that of H increased with nitrogen up to 90 kg ha^{-1} and then decreased slightly. F had most and C least grains per spikelet and hence grains per ear. F had smaller grains than the other varieties.

Measurements of stems and leaves at intervals after anthesis showed that dry weight of the shoot (excluding the ear) increased for about two weeks after anthesis and then decreased to values less than at anthesis. The decrease was greater with more nitrogen, especially for F. So, as with spring wheat, nitrogen did not increase the retention of assimilate in the stems, and may even have decreased it. (Pearman, Thomas and Thorne)

Water use. Neutron probe access tubes placed in the six plots receiving no nitrogen and the six plots receiving 210 kg N ha^{-1} enabled evaporation to be measured between 30 April and maturity (8 August). Evaporation between 30 April and 26 June, close to anthesis, was 35% (52 mm) greater with 210 kg N ha^{-1} than with no nitrogen. Between anthesis and maturity evaporation was decreased by 13% (8 mm) by nitrogen, evident as less loss of water from the soil down to a depth of 90 cm which more than compensated for a slightly increased depletion between 90 and 120 cm. Thus evaporation was influenced by the crop growth before plant cover was complete and thereafter was slightly decreased by the drier soil of the high nitrogen plots. (Thorne)

Photosynthesis and photorespiration. Gross photosynthesis per unit area both of the flag leaf and of the leaf below the flag leaf (second leaf) decreased significantly throughout the range of nitrogen tested. Nitrogen at 150 kg N ha^{-1} and above decreased photosynthesis of flag leaves of H measured eight days after anthesis slightly more than of C and F, but there were no varietal differences in second leaf photosynthesis, nor in photosynthesis of flag and second leaves measured 22 days after anthesis. The mean rate for flag leaves with 210 kg N ha^{-1} was 70% of that with no nitrogen, and the corresponding value for second leaves was 35%. These effects of nitrogen were more marked than in the spring wheat crops in 1973 and 1974 (*Rothamsted Report for 1973*, Part 1, 90 and *for 1974*, Part 1, 26). The reduction can be explained partly in terms of a reduction in light penetration into the denser crops, but at eight days after anthesis the reduction in photosynthesis of flag and second leaves above 120 kg N ha^{-1} was greater than that expected from the reduction in light penetration alone. Leaves developing in shady conditions may have reduced photosynthetic capacity. The intensities of photosynthetically active radiation (measured with a quantum sensor) in crops given 0 or 210 kg N ha^{-1}, expressed as a percentage of the intensity above the crop, were 85/53 at the level of the flag leaf, 62/26 at the leaf below the flag leaf and 35/4 at the ground. The interception of light by the canopies of crops of the three varieties given different amounts of nitrogen was as expected from their leaf areas; i.e. there were no indications of any differences in leaf arrangements between treatments that affected light interception.

In spite of the reduction in photosynthesis per unit leaf area, the large increase in leaf area with nitrogen resulted in an increase in total photosynthetic production per unit area

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of land. The gross photosynthetic production of the combined flag and second leaf laminae with 210 kg N ha^{-1} was about 2·5 times that with no nitrogen. Photorespiration was determined in the field from simultaneous measurements of $^{14}CO_2$ and $^{12}CO_2$ uptake. Measurements of rates in flag leaves of H were made on four occasions at the different levels of nitrogen. Up to 150 kg N ha^{-1}, the CO_2 loss was about 23% of the rate of $^{14}CO_2$ fixation (with 30 kg N ha^{-1}, 3·6 mg CO_2 dm^{-2} h^{-1} lost). With 180 kg N ha^{-1} this loss was significantly increased to 33% of the $^{14}CO_2$ fixation, and to 46% with 210 kg N ha^{-1}. Thus the net photosynthetic production of flag leaves did not increase continually through the range of nitrogen tested, but reached a maximum value with 180 kg N ha^{-1} of 3·8 times the rate with 30 kg N ha^{-1} and declined to 3·2 times with 210 kg N ha^{-1}. The efficiency in grain production of leaves from plants given large dressings of nitrogen may be partly related to an increased loss of CO_2 in photorespiration. (Pearman and Thomas)

Dark respiration. Respiration rates of ears and shoots (leaves plus stems) were measured between nine and 28 days after anthesis by taking plants growing in paper pots sunk in the field plots into a dark growth room at 14°C. No effects of radiation or temperature during the day immediately before respiration was measured were observed.

The mean respiration rate of ears was 0·62 mg CO_2 g^{-1} dry weight h^{-1}; it decreased with later sampling (age), increased with nitrogen, and was less for F than C and H. The varietal difference and about a third of the nitrogen effect could be due to differences in physiological age because F and the low nitrogen plants reached anthesis earlier. The mean respiration rate of shoots was 0·22 mg CO_2 g^{-1} dry weight h^{-1} and unaffected by sampling time, nitrogen or variety. The approximate loss in dry weight per unit ground area caused by respiration of the shoot between anthesis and maturity, was slightly greater for C and H than for F and increased about 2·5 times by the addition of 210 kg N ha^{-1}. This loss in dry weight due to respiration was considerably less than the observed decrease in shoot dry weight, suggesting that carbohydrate formed before anthesis may have contributed to grain growth. This phenomenon, which was not observed in previous experiments with spring wheat, needs confirmation. (Pearman and Thomas)

Effect of late nitrogen sprays. Urea sprays that do not scorch leaves, applied after anthesis, increased grain yield, sometimes more than similar amounts of nitrogen applied to the soil in the spring (*Rothamsted Report for 1974*, Part 1, 27, 80). A late nitrogen application was tested again in 1975 by spraying 1·5 m^2 of each plot four days after anthesis with a 3% solution of urea supplying 30 kg N ha^{-1}. The spray did not delay the unusually fast leaf senescence caused by the hot weather, as judged by eye. At maturity, shoot dry weight and ear number were unaffected by the spray and grain yield was increased by about 0·3 t ha^{-1}, irrespective of variety or amount of nitrogen supplied from the spring application. The spray increased grain yield by increasing the number of grains per spikelet, whatever the previous nitrogen treatment, and also grain size except with more than 150 kg N ha^{-1} when grains were already small and somewhat shrivelled. (Thorne)

Conclusions. In grain yield the two modern varieties (H and F) responded slightly better to nitrogen than did C, but differed little from each other. None of the three varieties differed much from each other in rates of photosynthesis or respiration or in leaf-area index of the top two leaves and stem above the flag-leaf node, although F had less stem dry weight than C and H. H and F had more grain than C with ample nitrogen because their ears had more grains, due to more grains per spikelet, and possibly attracted

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more assimilate from the stem as a consequence. Whether or not this occurred should be shown by data still awaiting analysis on the distribution of ^{14}C within plants. (Pearman, Thomas and Thorne)

Carbon metabolism of wheat leaf segments. Potassium glycidate (20 mM) decreased the rate of photosynthesis by wheat leaf segments at both 20 and 28°C and relatively less glycine was made suggesting decreased metabolism by the glycollate pathway. Less concentrated solutions of inhibitor had no effect on rate of photosynthesis but a 2 mM solution did decrease glycine synthesis. Whereas Zelitch (*Archives of Biochemistry and Biophysics* (1974), **163,** 367), who kindly sent the sample of glycidate, had found that a 20 mM solution decreased photorespiration and stimulated photosynthesis 50% in sunflower leaf disks, we were unable to repeat his work with wheat leaf segments.

Both potassium glycidate (20 mM) and isonicotinyl hydrazide (INH) (150 mM) inhibited metabolism of [U-^{14}C] D-glyceric acid supplied to wheat leaf segments; INH caused relatively more ^{14}C to accumulate in glycine and serine and less in sucrose, while potassium glycidate decreased ^{14}C incorporation into glycine and increased ^{14}C in phosphate esters and serine. Another inhibitor, sodium L-2-hydroxy-3-butynoate, did not decrease metabolism of [^{14}C] glycerate; it caused accumulation of ^{14}C in glycollate but did not affect sucrose synthesis.

After steady photosynthesis, in the absence of inhibitors in 150 vpm $^{14}CO_2$ in air a change to 1000 vpm $^{12}CO_2$ caused a rapid decrease of ^{14}C in glycine, synthesis of ^{14}C sucrose and serine, and evolution of $^{14}CO_2$. Initially the amount of $^{14}CO_2$ evolved equalled one-quarter that of the ^{14}C lost from glycine but after 2 min in 1000 vpm $^{12}CO_2$ more $^{14}CO_2$ was evolved than could be accounted for simply by conversion of glycine to serine. However, ^{14}C in serine began to decline after 2 min and the ^{14}C lost from glycine and serine accounted for ^{14}C appearing almost equally in sucrose and CO_2. When [^{14}C] serine was supplied to leaf segments in 1000 vpm $^{12}CO_2$ glycollate and glycine became labelled, suggesting recycling of some serine carbon through the glycollate pathway. However, unlike [^{14}C] serine made in leaf segments by photosynthesis, 70% of the ^{14}C was incorporated into sucrose and only 5% into CO_2. Perhaps [^{14}C] serine supplied to leaf segments through the cut base is metabolised at a site where sucrose synthesis predominates, whereas photorespiration takes place at sites near where serine is made during photosynthesis.

The total amounts of glycine and serine in leaf segments were measured colorimetrically. During steady photosynthesis in 150 vpm $^{14}CO_2$ in air, the glycine remained constant at 5·2 and serine at 1·0 μmol g^{-1} fresh weight. No significant changes were observed upon change to 150 vpm $^{12}CO_2$ in air. A change to 1000 vpm $^{12}CO_2$ in air caused glycine to decrease quickly for 2 min and then slowly to 2·7 μmol g^{-1} fresh weight; serine increased to 2·25 μmol g^{-1} fresh weight in 2 min then remained constant. A change to CO_2-free air and darkness caused a rapid decrease in glycine to 2·1 μmol g^{-1} fresh weight in 2 min and a slower fall to 1·5 μmol. Over the same period serine increased to 2·3 μmol g^{-1} fresh weight. Comparing these various values with changes in ^{14}C labelling it was concluded that not all the glycine and serine in leaves was in metabolically active pools and that the active pools did not become fully saturated with ^{14}C during 15 min photosynthesis in $^{14}CO_2$. From initial rates of decrease in glycine, following changes from steady-state conditions, values for rates of carbon flow through the glycollate pathway were calculated (*Rothamsted Report for 1974*, Part 1, 30). The rates were faster than those calculated from changes in ^{14}C labelling of glycine and this is consistent with active metabolic pools not being fully saturated with ^{14}C. The rates of metabolism of glycine *in vivo* observed in this manner, relative to the rate of photosynthesis, are consistent with rates of photorespiration reported above for wheat. (Kumarasinghe)

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Ribulose bisphosphate carboxylase/oxygenase. The enzyme ribulose 1,5-bis-phosphate (RUBP) carboxylase not only has a role in CO_2 fixation, but also has oxygenase activity resulting, in the presence of oxygen, in the production of phosphoglycollate from RUBP and ultimately loss of CO_2. The relative activities of the carboxylase and oxygenase may determine photosynthetic efficiency and the enzyme may be one site at which the flow of carbon into photorespiration could be regulated. Since wheat is photosynthetically more efficient in cool temperatures (13–18°C) than in warm temperatures (25–35°C), the relative activities of the carboxylase and oxygenase were determined in extracts of wheat leaves grown at 28, 23, 18 or 13°C. Carboxylase activity extracted from flag leaves was increased when the temperature of growth was lowered; for example, it was $8{\cdot}1 \pm 0{\cdot}2$ μmol CO_2 leaf^{-1} min^{-1} at 23°C and $11{\cdot}5 \pm 0{\cdot}3$ μmol CO_2 leaf^{-1} min^{-1} at 13°C. Oxygenase activity did not increase as rapidly as the carboxylase, as the temperature of growth was lowered; $1{\cdot}40 \pm 0{\cdot}07$ μmol O_2 leaf^{-1} min^{-1} at 23°C, $1{\cdot}71 \pm 0{\cdot}03$ μmol O_2 leaf^{-1} min^{-1} at 13°C. In this investigation (as in others in the literature), the activity of RUBP carboxylase extracted from leaves was more than adequate to support the rates of photosynthesis of the tissue (see also *Rothamsted Report for 1974*, Part 1, 28); however, the activity of RUBP oxygenase extracted could not account for measured rates of glycollate synthesis, and its role as the sole producer of glycollate is being questioned. (Thomas and Zima)

To determine whether there were changes in the relative activities of RUBP carboxylase and RUBP oxygenase during leaf development, extracts of leaves from young wheat plants, and of flag leaves of wheat grown in the field and in the glasshouses were assayed throughout development. The activities of the two enzymes increased to a maximum and then declined in parallel during development; there were no significant changes in the ratio of the two activities. (Hall and Thomas)

Effects of water stress on photosynthesis and photorespiration of sunflower and maize. The exchange of carbon dioxide and water vapour of leaves attached to plants grown under constant conditions with 400 μE m^{-2} sec^{-1} irradiance at 400–700 nm wavelength for sunflower and 600 μE m^{-2} sec^{-1} for maize was measured after 4 to 10 h water stress produced by exchanging a nutrient by polyethylene glycol solutions. An area of leaf (26·5 cm^2 sunflower, 18 cm^2 maize) was enclosed in a leaf chamber at 25°C, and the rates of apparent (net) photosynthesis (APS) and true (gross) photosynthesis (TPS), estimated from the uptake of $^{12}CO_2$, measured with an IRGA and of $^{14}CO_2$ measured with an ionisation chamber; photorespiration was calculated by difference.

In sunflower, not suffering from water stress, the rate of photorespiration was 20% of the rate of APS and the specific activity of the CO_2 evolved was high. As leaf water potential decreased photorespiration also decreased but increased as a proportion of the rate of photosynthesis. Water-stressed plants evolved CO_2 in photorespiration of low specific activity suggesting increased use of storage substances (principally carbohydrates) as substrate for photorespiration. Under all conditions of water stress, maize produced negligible amounts of CO_2, even when photosynthesis was reduced to zero, which occurred at much greater water potentials than in sunflower. The rate of CO_2 evolution from dark respiration was less in maize than in sunflower.

Analysis was made of the products of photosynthesis of leaves fed radioactive CO_2. In sunflower, as water stress increased, more radioactivity was incorporated into amino acids and less into phosphoglyceric acid and sucrose. This suggests that stress, by decreasing stomatal conductance, limits the supply of CO_2 to the chloroplasts; consequently, more carbon flows into the intermediates of the glycollate pathway, glycine and serine. However, whereas the specific activity of phosphoglyceric acid approached that of the supply gas after only 15 min feeding the specific activity of glycine was only 60% that of

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the fed gas whilst that of serine was even less. This is consistent with the formation of some amino acids from unlabelled reserves. At most severe stress, little CO_2 was evolved from the photorespiratory system and metabolism was wholly associated with tricarboxylic acid cycle respiration in mitochondria. The pattern of incorporation of radioactive carbon into maize was similar to that in sunflower. Water stress increased the amount of radioactivity in amino acids and decreased that in sucrose. However, compared to sunflower the specific activity of aspartate and alanine was greater than that of glycine and serine in maize and their activity decreased with increasing water stress. Both in maize and in sunflower amino acids, and particularly proline, accumulated with the most severe stress. (Lawlor, with Professor H. Fock, University of Kaiserslautern, West Germany)

Environmental factors controlling the water potential of leaves of barley, maize and sunflower. Previous work (*Rothamsted Report for 1972*, Part 1, 40, and *for 1973*, Part 1, 99) showed that the Ohm's law analogue of water movement from soil through the plant does not apply in several crops because the leaf-water potential was independent of the water flux over a wide range. This conclusion, which may be of importance in irrigation practice and for selecting conditions for optimal crop growth, was tested further in collaboration with M. J. Aston (Physics), using plants grown in nutrient solution. The roots were placed in aerated nutrient solution in a sealed container and the foliage in a large chamber, thus enabling both the rates of water uptake and water loss to be measured continuously. Water potential of leaves was estimated using the β-gauge technique and with the pressure bomb. The leaf-water balance was calculated from the rates of water uptake and loss.

The humidity of the air around the leaves and the illumination were varied to cause large changes in transpiration. The leaf-water potential decreased by about 2 bar when plants were illuminated after a period in the dark, but subsequently lowering the humidity to increase transpiration did not cause any further significant fall in leaf-water potential. Cooling of roots or adding polyethylene glycol to the solution around the roots reduced the rate of water absorption, resulting in a fall in leaf-water content and potential and closure of stomata. These changes were reversible. Full analysis of the data has still to be completed. (Lawlor)

Root growth. In an attempt to produce root systems of different size at a given stage of crop growth, for studying relationships between size and activity of root systems, areas within plots of barley were shaded for a few weeks shortly after seedling emergence and other plots sown at a later date. In an earlier experiment shading for periods of one or two weeks decreased the dry weights of both roots and shoots to a similar extent, but more prolonged shading decreased root more than shoot weight (*Rothamsted Report for 1973*, Part 2, 38–42).

Barley, cv. Julia, was sown on 30 April and 16 May in plots 12 rows wide and divided into 1·8 m long sub-plots for shading treatments. Shades covering an area 1·8 m (ten rows) $\times$ 1·8 m reducing daylight to about 48 % (*Rothamsted Report for 1973*, Part 2, 38) were erected randomly on half the sub-plots of the early-sown crop from 22 May to 9 June. The late-sown crop was not shaded because of poor establishment and non-uniformity. Fertiliser supplying 100 kg N ha^{-1} was applied to all the plots of both sowings on 9 June when the shades were removed.

The early-sown crop, which had a mean density of 286 plants m^{-2}, was sampled on 22 May, before shading, and all treatments were sampled on 9 June and at weekly intervals thereafter until 23 July.

At the end of the shading period the total root dry weight on shaded plots was 19 g m^{-2}

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compared with 24 g m^{-2} on unshaded controls; the difference was less than half that found in the earlier experiment. The difference, which persisted until at least 9 July, was due to a greater weight of roots in the top 30 cm of soil on unshaded plots. The amount of roots in layers below 30 cm on unshaded plots was unexpectedly less than on shaded plots. Shading caused greater leaf expansion than occurred in full daylight, although the number of leaves per plant remained the same: leaf area index (LAI) increased from 0·25 on 22 May to 0·9 on 9 June under shade or to 0·6 on unshaded plots. This advantage in LAI was reflected in more rapid shoot growth of the shaded crop on return to full daylight: shoot dry weights on 9 June for shaded and unshaded sub-plots were 39 and 37 g m^{-2} respectively and these increased to 89 and 62 g m^{-2} by 18 June. Differences between shading treatments in LAI and shoot dry weight generally decreased at later samplings.

The rate of root growth of the late-sown crop was roughly similar to that of the early-sown crop so that at 2 July there was only half the amount of root. Shoot growth-rate of the late-sown crop was slightly less than that of the early-sown crop until 16 July, but was equal to it by 23 July.

Final grain yields were 3·7 t ha^{-1} for the shaded, 3·3 t ha^{-1} for the unshaded and 1·2 t ha^{-1} for the late-sown crop.

The small effect of shading on shoot dry-weight growth was probably the result of the appreciably increased leaf expansion that accompanied it, offsetting to a large extent the decreased light intensity. This presumably is related to the unexpectedly small response in total roots to shading. (Taylor and Welbank)

Growth substances in developing wheat grains. It was shown previously (*Rothamsted Report for 1970*, Part 1, 102 and *for 1971*, Part 1, 110) that cytokinins, gibberellins and auxins reach their maximum concentration at different stages of development of wheat grains. Additional data concerning gibberellins and abscisic acid have now been obtained. Field-grown wheat, cv. Kleiber, was harvested at weekly intervals and examined for growth substance content. Total gibberellins reached maximum content (77 ng GA_3 equivalent per 1000 grains), four weeks after anthesis, with a second peak at seven weeks (maximum dry weight). Abscisic acid content was maximum (5 μg per 1000 grains) at six weeks, when the water content of the grain began to decrease sharply. Auxin content was high (200 to 270 μg indole-3-acetic acid (IAA) equivalent per 1000 grains) from four to six weeks after anthesis.

Abscisic acid may accelerate ripening in wheat; it may also prevent premature germination of the embryos during the later stages of grain development. Intact grains did not germinate until nearly ripe, whereas embryos isolated from immature grains germinated readily; they could be prevented from doing so by the addition of abscisic acid.

When applied to wheat florets abscisic acid caused a marked increase in the proportion of sugar found as reducing sugars. In the rachis this was mainly due to an increase in reducing sugar concentration, while in the glumes there was a marked decrease in sucrose. The effect on the sugar content of the grain was small, but reducing sugars were increased in some cases.

At least five gibberellins were found to be present in the grains and the distribution of these differed in the various tissues. (Radley)

Wheat seeds (var. Kolibri and Kleiber) were surface-sterilised, germinated for two days in moist boxes and then planted on to rafts of polythene granules floating on Hoagland's solution and grown at 20°C in darkness. Gibberellin contents increased with time to give a broad peak of activity (*c.* 400 pg per endosperm) between days 7 to 11 then declined. The acidic gibberellin-like compounds were isolated from 5000 endosperms, harvested after eight to nine days growth (shoot length 150 mm) and purified on columns of Polyclar AT,

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silica gel thin-layers and silica-impregnated glass-fibre sheets. Biological activity was associated with markers of GA_1 and GA_3 and the remainder of the extract will be used to attempt identification by combined gas chromatography–mass spectrometry. (Lenton)

Dwarfing of barley by chlormequat chloride (CCC). Humphries (*Rothamsted Report for 1969*, Part 2, 135–147) reported that chlormequat shortens stems of wheat but not of barley plants. Lord (*Rothamsted Report for 1972*, Part 1, 193–194) found that chlormequat was taken up more slowly into barley than into wheat leaves and this may explain the differences in response. In glasshouse tests chlormequat was applied to barley (var. Proctor) in different ways at several stages of growth, attempting to shorten barley stems. The effects were compared with those on wheat (var. Kolibri).

Single or multiple doses of chlormequat were applied to the soil of potted barley plants. The main-stem growth of barley was diminished most when chlormequat was applied as the fifth main-stem leaf was emerging. The two lowest internodes and the top internode (peduncle) of the main stem were shortened, but the height of the tall tillers was the same as the main stems and the tall tillers of untreated plants; thus giving the superficial appearance that chlormequat had no effect. The overall height of wheat plants was diminished. After these tests, the effects of chlormequat remaining were assessed by growing wheat in the soil after sieving out the roots of the previous crop. The height of the main stems of wheat plants grown in soils previously treated with chlormequat was shorter than those in untreated soil. However, the degree of shortening of test plants was not affected by the timing, the amount of chlormequat applied or the previous crop.

Preliminary tests of localised surface application of measured doses of chlormequat to barley plants showed that plants were shortened more when the aqueous solutions of chlormequat contained a wetter (e.g. acetone or Tween-20). In tests from emergence of the third to the seventh leaf of the main stem, the effects of chlormequat applied to the cavity (lumen) within the youngest rolled-up leaf, decreased progressively with plant age; with the youngest plants tested, 0·5 mg chlormequat had no effect, 5 mg shortened the main stems and 50 mg killed the plants. (Wheeler, with Lord, Chemical Liaison Unit)

Effects of aerial pollutants on cereal growth. The Bedfordshire brickworks have not been fully operational during the past year. Consequently pollution levels have been low with only eight daily values over 150 $\mu g\ m^{-3}$ sulphur dioxide recorded at either Woburn or Elstow.

Winter barley, var. Maris Otter, was grown at Woburn Experimental Farm in three closed plastic chambers with either filtered, ambient or sulphur dioxide-polluted air. The mean sulphur dioxide levels were 7·2 $\mu g\ m^{-3}$, 37 $\mu g\ m^{-3}$ for the filtered and ambient chambers respectively. In the field the mean value was 51·5 $\mu g\ m^{-3}$. Temperature and relative humidity in these closed houses differed from that outside. No visible damage occurred on any of the plants grown in the filtered or ambient air. In the fumigated chamber a high dose of sulphur dioxide was given for one week (19–25 April 1975), producing a mean concentration of 951 $\mu g\ m^{-3}$, at the four-leaf stage. It caused severe necrosis of the leaves. The plants subsequently recovered and no further fumigations were given. At final harvest these plants were not significantly lower in total dry weight and grain weight from the ambient plants. The dry matter yield of the plants grown in filtered air was higher than that of plants in ambient air.

	+ filter	— filter	fumigated
Total dry weight kg m^{-2}	1·4	1·1	0·95

This was not reflected in the grain yield where no significant difference was recorded. Analysis of the plant material for sulphur showed a lower level in the plants grown in

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filtered air compared with plants grown in unfiltered air, or in outside air, or in the fumigated chamber. Fluoride analysis is not yet completed.

	+ filter	— filter	fumigated	field material
Mean S content (%)	0·37	0·47	0·51	0·48

An alternative type of chamber with an open top was tested at a site near Elstow. Spring barley, var. Julia, was grown in four chambers and on two outside plots. Two of the open-top chambers were ventilated with ambient field air and two with clear air. The temperature, relative humidity and soil moisture inside the chambers closely followed the conditions outside. The sulphur dioxide levels were reduced by the filtration system to a mean daily level of 36 $\mu g\ m^{-3}$, with a maximum daily level of 80 $\mu g\ m^{-3}$ compared with a mean daily level of 71 $\mu g\ m^{-3}$ with a maximum daily level of 224 $\mu g\ m^{-3}$ outside. There were no signs of visible injury on any of the plants and no significant difference in dry weight or grain yield. There was some variation within a single treatment, but the mean dry weight of plants from the filtered chambers was always slightly higher than that from the unfiltered chamber.

A winter barley experiment, var. Maris Otter, using both closed and open-top chambers on the same site at Woburn is now in progress. (Brough and Parry)

Measurements of the rate of photosynthesis per unit leaf area of barley flag leaves were made using $^{14}CO_2$ at Woburn on 17 June and 1 July and at Elstow on 11 July 1975.

At Woburn on 17 June mean rates of photosynthesis in the filtered house were higher by 13%; in the fumigated house, in which the plants were recovering, the rate was higher by 11% than those in the ambient house with unfiltered air. By 1 July mean rates of plant photosynthesis had decreased appreciably. For the remaining green leaves in the filtered house, rates were again higher by 13% and in the fumigated house by 41% compared with the ambient house.

In the open-top chambers at Elstow mean photosynthetic rates for the filtered house were higher by 13% and those for the outside plot higher by 3% than those for the ambient house. Mean photosynthetic rate for the ambient house was 11·9 mg CO_2 $dm^{-2}\ h^{-1}$. (Kendall)

In laboratory experiments using 16 varieties of spring barley the sensitivity to sulphur dioxide on the basis of the change in photosynthesis rates varied from 60% inhibition to 12% stimulation consequent upon fumigation with a concentration of 160 $\mu g\ m^{-3}$ sulphur dioxide for 3 h.

Time concentration effects were also investigated with a sensitive variety (Julia). Five minutes exposure to 2500 $\mu g\ m^{-3}$ produced an inhibition of 25–30% in the rate of photosynthesis whereas 500 $\mu g\ m^{-3}$ resulted in 25–30% inhibition after 30 min fumigation. Measurements made over a range of concentrations and exposure times indicated the interaction between concentration and fumigation time. (Kendall)

Sugar Beet

Growth physiology

Effect of photoperiod on plant growth. A major limitation to yield under British conditions is the slow establishment of leaf cover early in the season. At this stage temperature, light intensity and daylength are likely to be the major environmental limiting factors. Previous studies have established that temperature, but not light intensity, greatly affect early leaf growth (*Rothamsted Report for 1970*, Part 1, 97 and *for 1971*, Part 1, 102). The effect of extending daylength from 12 to 16 h has now been examined in growth rooms comparing:

(a) A 12 h photoperiod with growth-room lighting from fluorescent tubes supplemented

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with tungsten lamps (14% of total wattage) giving a light intensity of 123 W m^{-2} of visible radiation, i.e. 530 J cm^{-2} during the photoperiod.

(b) Treatment (a) extended with 4 h incandescent light of low photosynthetic activity (0·6 W m^{-2}) at the red end of the spectrum from tungsten lamps only.

(c) 16 h of fluorescent and tungsten lighting but of reduced intensity so as to maintain the same total radiation as in (a).

These treatments were given for six weeks starting at the two-leaf stage of plants growing in temperatures of 15°C during the 16 h that included the photoperiod at 11°C for 8 h.

Treatment (c) accelerated early plant growth compared with treatment (a). Leaf area was increased from 13 to 15 dm^2 because the size, but not the number, of leaves was increased. Lamina dry weight increased from 14·2 g to 16·8 g, petiole dry weight from 3·5 g to 4·7 g and root dry weight from 7·3 g to 9·7 g. Leaf thickness, specific leaf area and average petiole length were unchanged. Treatment (b) increased leaf area even more (to 19 dm^2), also by increasing the size, but not the number, of leaves. Lamina dry weight increased to 17·4 g, petiole dry weight to 6·2 g, and root dry weight to 9·2 g. The plants grew more upright; the mean length of the petioles almost doubled—in proportion with change in their dry weight—but laminae were thinner and specific leaf area greater than in the other two treatments. Plants grew faster in treatment (c) than treatment (a) because their net assimilation rate was greater indicating a change in either photosynthesis, or respiration, or both; the partition of dry matter produced between leaf and the other growth was unchanged. By contrast, plants given red light at the end of the day grew faster because they had a greater leaf area ratio resulting from a direct photomorphogenic effect on leaf expansion.

A detailed examination of a single leaf (leaf 5) when fully expanded, showed that treatment (c) increased only the number of epidermal cells whereas treatment (b) increased both their number and size. The rate of $^{14}CO_2$ uptake per unit leaf area was slower in treatment (b) and (c) than in treatment (a). The rate was slower in treatment (c) because the light intensity was less and slower in treatment (b) because the thinner leaves contained less chlorophyll per unit area. The rate per mg chlorophyll was the same in treatments (a) and (b). (Lenton and Milford)

Effect of leaf senescence in sugar beet. Part of the sugar accumulated in the sugar-beet root late in the season may come from reserves mobilised from senescent leaves and not from current photosynthesis. The contribution of senescent leaves to root growth was estimated by covering or removing leaves and petioles at the onset of senescence. Plants of sugar beet were grown in Kettering loam and peat mixture, with added NPK fertiliser. Leaves were covered with aluminium foil. The onset of senescence was taken to be when two consecutive daily observations showed that leaves were flaccid in the morning before water was given to the pots, adequate water having been given the previous evening. The senescing leaves were rated for area before treatment and weighed either when removed or when dead in the case of covered leaves. Axillary leaves were removed as soon as they appeared and their weight added to total dry matter. Leaf area was estimated frequently during the growing season. Half the plants were harvested in mid-July (13 weeks after sowing) at the time of maximum leaf area and the remainder in September (21 weeks after sowing).

By the first harvest from four to nine, with a mean of six, leaves per plant showed signs of senescence. There was little effect of the treatments upon lamina and petiole yields, except that removal or covering of lamina encouraged petiole growth. The total dry matter produced by treated and control plants was similar, but the roots of plants

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whose leaves were covered yielded 11·8% less than those of the control plants, and removing leaves yielded 16·3% less, suggesting that 4·5% dry matter moved from covered leaves into the roots. The differences in root yield were related to the respective differences in leaf-area duration and not to differences in efficiency of the leaves. More leaves died or were removed on treated plants than those which died naturally on control plants, indicating that the treatments encouraged senescence of leaves.

After the first harvest sugar-beet yellows virus and mildew spread through the plants, so the second-harvest data is not considered here. Samples of roots were taken for sugar determinations, but analyses of these are not completed. However, the results so far suggest that in the earlier stages of growth senescing leaves contribute significantly to root yield. (French)

Water relations. Experiments in controlled environments showed that leaf water potentials (ψ_1) of sugar beet were determined more by changes in soil moisture than by changes in the transpiration rate (*Rothamsted Report for 1973*, Part 1, 98). In 1975 these observations were extended to the field in an experiment at Broom's Barn. During the dry growing season large soil moisture deficits (150 mm) developed under non-irrigated plants; irrigation was applied to maintain a deficit of 25 mm. On a sunny day transpiration from plants of both groups was varied by leaving some plants unshaded to receive solar radiation at an intensity of 677 Wm^{-2} for much of the time and shading others to halve irradiance. At sunrise ψ_1 averaged − 6 bar in unshaded irrigated plants and − 11 bar in unshaded unirrigated ones but progressively decreased during the day in all treatments. Early in the afternoon, ψ_1 was − 24 bar in the unshaded, unirrigated plants, − 16 bar in unshaded, irrigated plants and − 14 bar and − 22 bar in shaded plants with and without irrigation respectively. Thus, slowing transpiration by shading the plants improved ψ_1 by 2 bar irrespective of whether or not they were irrigated and irrigation increased ψ_1 by 8 bar irrespective of whether or not the plants were shaded. Thus the relative effects of varying soil moisture and water flux through the plant were similar to those observed with pot-grown plants in controlled environments.

Earlier work indicated that water applied as mist to the foliage of the crop on days of high insolation would absorb a proportion of the incident radiation, reducing the proportion to be dissipated as sensible heat. Its presence on the leaf surface would also increase the vapour pressure of the air immediately adjacent, and hence decrease transpiration (*Rothamsted Report for 1974*, Part 1, 34). This was examined in the same field experiment. Mist irrigation maintained ψ_1 at − 12 bar throughout much of the day, i.e. 2 bar better than the best we observed in the shading-irrigation treatments. A proportion of the water applied reached the soil but the results suggest that part of the action of mist irrigation on ψ_1 is by decreasing the rate of transpiration. (Milford, with Durrant and Messem, Broom's Barn)

Endogenous gibberellins and bolting of sugar beet. It was shown in the last report (*Rothamsted Report for 1974*, Part 1, 35) that when sugar-beet plants bolted in the spring after over-wintering out of doors the endogenous gibberellin concentration increased. The experiment was repeated this year. In September plants of Sharpe's Klein Monobeet were lifted from the field, trimmed of all leaves more than 8 cm long and packed in damp peat in a room at 4°C. After four months they were potted up in 20 cm pots and placed in a warm greenhouse with extra lighting giving 16 h days. Half the plants were sprayed with 200 $\mu g\ ml^{-1}$ chlormequat chloride (CCC) weekly. Apical buds were examined weekly by low-power microscope and the surrounding tissue (stem and leaves up to 8 cm long) was extracted for growth substance determinations.

After one week the apices had changed from the flat vegetative form to a raised conical

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shape. The chlormequat-treated plants were less advanced than the untreated plants. Flower initials were visible after two weeks, especially in the untreated plants, and stem elongation was detected in both groups after three weeks. After five weeks stem lengths of the untreated plants varied from 9 to 22 cm, and the treated plants had stems of 7 cm or less. The gibberellin concentration increased sharply during the first two weeks in both groups of plants, thus accompanying the earliest changes in the apex. When stem elongation was detectable the gibberellin decreased, but it increased again in the upper part of the rapidly growing stem at the last harvest. The first increase was not significantly different in the two groups. The delay in bud development caused by chlormequat was not accompanied by an effect on the gibberellin content of the surrounding leaves. The effect of chlormequat on the bud may be independent of its effect on gibberellin metabolism or it may affect gibberellin synthesis in the bud more than in the leaves, or it may affect the response to gibberellin rather than its synthesis.

The concentration of an abscisic acid-like inhibitor increased when the vernalised plants were transferred to warm conditions and long days but this was eliminated by chlormequat. It is improbable that this inhibitor was affecting flower initiation, a conclusion reached also by other workers studying spinach.

A comparative approach was used in other experiments with a bolting 'susceptible' line G obtained from the Plant Breeding Institute at Cambridge and a bolting 'resistant' line selected from Sharpe's Klein AA by Dr. R. K. Scott at the University of Nottingham. Line G is a colchicine-induced dihaploid of extreme uniformity which will flower eventually under long days, although the process is much hastened by a short period of chilling. Conversely, the resistant material AA requires a long period of chilling before flowering under long days.

Plants of line G were grown under controlled environment conditions to different stages of reproductive development, examined under the dissecting microscope and the gibberellin contents of apical tissue and expanding leaves (3–4 g fresh weight per shoot apex) determined by bioassay. Gibberellin contents were large (*c.* 5000 pg GA_3 equiv. g^{-1} fresh weight) in apices at transition from vegetative to reproductive state, but reduced to 750 pg GA_3 equiv. g^{-1} fresh weight, as elongation commenced and the flowering stem became visible.

Autumn-sown plants of susceptible and resistant material were over-wintered outside in a glass-roofed cage and apical tissue (*c.* 150 mg per plant) harvested at intervals in the spring. The gibberellin content of apices of the resistant material was 2–3 ng g^{-1} fresh weight during March, whereas the susceptible line reached a peak of *c.* 20 ng g^{-1} fresh weight early in the month which declined to 3 ng g^{-1} fresh weight towards the end of the month. This transient peak of gibberellin activity occurred in a relatively mild week following a period of ground frosts and preceded any morphological change at the apex. It is concluded that naturally-occurring gibberellins are involved in the expression of the vernalisation stimulus. (Lenton, Pocock and Radley)

In another experiment Sharpe's Klein Monobeet seedlings sown in September in 25 cm flower pots in a glass-roofed cage were treated with several growth retardants, applied six times during the following March and April. None of the retardants prevented bolting, whether or not they were inhibitors of gibberellin biosynthesis. Chlormequat chloride (CCC) (200 mg in 100 ml, applied as a soil drench) delayed bolting, but by 16 June there was no significant difference in stem length. Ethephon ('Ethrel'), (50 mg in 50 ml, applied as a soil drench) had a similar but less marked effect and daminozide (20 mg in 10 ml applied to leaves) had an even weaker effect. 2-isopropyl-4-dimethylamino-5 methyl phenyl-1 piperidine carboxylate methyl chloride ('Amo-1618'), chlorphonium chloride ('Phosfon D') and abscisic acid (all 20 μg in 0·02 ml) and Imperial Chemical Industries Limited regulator 'PP 528' (5 or 20 mg in 10 ml) had no effect. These concentrations are

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effective on some other plant species but sugar beet appears to be less sensitive. Nevertheless roots of ethephon-treated plants did have a significantly higher dry weight, in agreement with the results described in the last report (*Rothamsted Report for 1974*, Part 1, 35). (Radley)

Phenylacetonitrile, a new plant-growth regulator. Phenylacetic acid (PAA) has been known since 1935 as a synthetic auxin, but recently Wightman and Rauthan (*Proceedings of the 8th International Conference on Plant Growth Substances*, Tokyo (1974), p. 15) described PAA as a naturally-occurring auxin. As indolyl-3-acetonitrile(IAN) is as active as indolyl-3-acetic acid (IAA) in some auxin bio-assays, so phenylacetonitrile (PAN) could be as growth active as PAA.

Both PAA and PAN stimulated elongation of wheat-coleoptile sections at concentrations of 1–3 $\times$ 10^{-4}M. 1–10 $\times$ 10^{-4}M PAA increased elongation of pea-epicotyl sections after 18 h but similar concentrations of PAN were only effective after 42 or 72 h incubation. Sections cut from young petioles of light-grown sugar-beet seedlings, or from etiolated hypocotyls of germinating sugar beet, elongated when treated with 3 $\times$ 10^{-5} to 3 $\times$ 10^{-4}M PAA but similar concentrations of PAN were ineffective. Both PAA and PAN, 3 $\times$ 10^{-4}M, stimulated rooting of hypocotyls of sugar-beet seedlings of which the roots had previously been removed, but 10^{-3}M PAA was toxic. 0·35 to 3·5 mg per plant PAN applied in small amounts of ethanol to sugar-beet seedlings, stimulated growth of the axillary leaves and increased the total leaf area and leaf fresh and dry weights; PAA usually did not initiate growth of the axillary leaves and 1·4 mg per plant was toxic.

Steam distillates of sugar-beet tissues were extracted with ethyl acetate and chromatograms of the extracts were assayed with wheat-coleoptile sections. Auxin activity was detected at Rf 0·7–0·9 on chromatograms of the ethyl acetate fraction containing non-acidic substances; the PAN marker spot ran at Rf 0·7–0·9 and IAN at Rf 0·9–1·0. Ethanolic eluates of this growth active material from chromatograms were examined in a high-pressure liquid chromatogram by J. Tinkler (Chemical Liaison Unit). The retention times, on the column, of the UV absorbing substances in the eluates were all different from that either for PAN or IAN. Thus, although PAN is active in several auxin bio-assays, its presence in sugar beet has not been confirmed. (Wheeler)

Growth regulator trials. Much of the work this year has been concentrated on the development of screening procedures in pot trials to provide a cheaper and less time- and labour-consuming method than field trials for evaluating the potential of chemical plant regulators. The importance of unrestricted growing conditions has previously been shown (*Rothamsted Report for 1974*, Part 1, 36) but to make better use of space and materials without confounding the results we must know when these limitations arise under different conditions.

Plants were grown outside in a glass-roofed cage and three container sizes were used: 13 cm and 20 cm pots and 25 cm diameter flower pails (with capacities of approximately 1, 4 and 13 litres respectively), filled with a loam/peat mixture to which was added fertiliser. The fertiliser level in one batch of pots of the first experiment was maintained up to the initial level as indicated by a conductivity-factor meter and plants were taken every two to three weeks throughout the season. The other batch had no additional fertiliser. Optimum growth throughout the season was only obtained with plants in 25 cm pails; growth rates in the smaller pots were reduced by the 12-leaf stage.

One plant growth regulator trial was conducted this year using plants of Sharpe's Klein Monobeet grown from seed sown in early April in a glass-roofed cage in large buckets (25 cm in diameter). In mid-July a supplementary nutrient feed was given. Five regulators were tested: gibberellic acid (GA_3) as 150 ppm aqueous solution at 100 ml m^{-2};

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American Cyanamid regulators 'AC 99524' and 'AC 92803' as 0·4% a.i. solution at 55 ml m^{-2} (equivalent to 2·2 kg a.i. ha^{-1} as used by Broom's Barn in 1974 (*Rothamsted Report for 1974*, Part 1, 66); 'AC 23380' as 0·25% a.i. solution at 100 ml m^{-2}; and SM3, a compound under field test by the British Sugar Corporation, as 1·7% a.i. solution at 66 ml m^{-2}. Each regulator was applied as a single foliar spray either in mid-June at the eight-leaf stage or later in the season (late July) at the 30-leaf stage, except GA_3 which was applied only at the eight-leaf stage. Those plants sprayed at the eight-leaf stage were harvested after 2½, 7 and 14 weeks; those sprayed in July were harvested once only after seven weeks.

None of the chemicals had any lasting effect. GA_3 and 'AC 99524' increased both petiole and root weight and GA_3 increased leaf number 2½ weeks after early treatment but the effects were lost after seven weeks. 'AC 92803' and 'AC 23380' increased total leaf number after seven weeks but again the effect was lost soon after. By mid-September root fresh weights were significantly lower than controls in all treatments except GA_3 where there was no difference. A late application of 'AC 92803' and SM3 significantly reduced water percentage dry weight of the root by about 40% and SM3 at both applications increased water percentage dry weight of the shoot by 80%. The only morphological change was caused by 'AC 99524' which caused, as observed previously at Broom's Barn, increased internodes and very fibrous roots. In general the response to all these regulators throughout the season was negligible. These beet were grown under optimum conditions of soil-type, foliar regime, spacing and water supply and had mean root fresh weights of 0·9–1·0 kg. (Pocock)

Potatoes

Bruised and unbruised tissue from several varieties of potato was studied with the transmission electron microscope. Bruising appeared to result in the rupture, by physical shock, of a membrane within the cell which in the intact tissue isolates the enzyme polyphenol oxidase from its substrate tyrosine. The bruising potential of tubers from plants fertilised with low levels of potassium was related to the concentration of a number of chemical constituents, but for tubers grown with higher levels the susceptibility to bruising correlate at best with percentage dry matter. (McIlroy)

Weed Biology

Classical experiments

Broadbalk. The unusual weather throughout the year affected the weed-flora. None of the wheat could be sprayed with terbutryne in the wet autumn of 1974 and blackgrass was abundant on all wheat sections in 1975. Section six (after fallow) was almost as severely affected as section eight (unsprayed). Section two (after potatoes and beans) had less blackgrass, though even there the density on most plots was at least 1 plant m^{-2}. The mild winter allowed autumn-germinated wild oats (*Avena fatua*) to survive and this species formed a higher proportion than usual of the wild oats (predominantly *A. ludoviciana*) hand-pulled in July. Spring-germinating dicotyledons were scarce due to waterlogged soil and cold dry air, followed by the summer heat-wave, and many plot-sections had less than five weed-seedlings on them. Red bartsia (*Odontites verna*) was scarce, the few plants being in beans. In contrast, the perennials field bindweed (*Convolvulus arvensis*) and field horsetail (*Equisetum arvense*) flourished. *Convolvulus* flowered freely, which it seldom does on Broadbalk.

Soil samples were taken from selected plots and sections for the second year of a three-year investigation of the weed-seed content of soil under different cropping regimes (*Rothamsted Report for 1974*, Part 1, 39). The hard-baked soil slowed down sampling but the resulting samples were easy to concentrate and no seeds germinated before the

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prepared samples were put into pans. Phenomenally high numbers of blackgrass seedlings have been removed from these pans already but final totals are not yet available. (Thurston)

Park Grass. Botanical analyses were continued on samples of hay taken in 1974 from the a (limed once every four years) and b (where the pH is being raised to six under the new liming scheme) sub-plots of plots 4^2, 9, 10, 11^1 and 11^2. The object of these analyses is to see what changes have occurred since the last analyses in 1948–49 on sub-plots with unchanged treatment, to quantify changes brought about by the first phase of the new liming scheme (Warren, Johnston & Cooke, *Rothamsted Report for 1964*, 226) and to provide a base for the study of future changes on those a sub-plots whose pH will be raised to seven in the next phase of the same scheme.

The results showed that percentage of Meadow Foxtail (*Alopecurus pratensis*) had decreased greatly, and that, with the exception of sub-plot 4^2a, percentage of False Oat-Grass (*Arrhenatherum elatius*) had increased markedly on sub-plots with unchanged treatment. In 1948–49 there was five times as much *Alopecurus* as *Arrhenatherum* on these plots but in 1974 twice as much *Arrhenatherum* as *Alopecurus*. Since 1948–49 there has been a decrease in Cocksfoot (*Dactylis glomerata*) and Smooth-Stalked Meadow Grass (*Poa pratensis*) on plots receiving K (9, 11^1 and 11^2) but an increase in *P. pratensis* on those without K (4^2 and 10). On plots receiving K, Cow Parsley (*Anthriscus sylvestris*) and Hogweed (*Heracleum sphondylium*) have increased slightly but they continue to be absent on plots without K. Meadow Vetchling (*Lathyrus pratensis*) has increased on 9a as has Yorkshire Fog (*Holcus lanatus*) on this and on 11^1a and 11^2a. Changes in species composition due to recent lime have been smaller than those due to natural succession. As might be expected, they have been largest on those plots which have needed most lime, i.e. on sub-plots 11^1b, 11^2b and 9b. On these sub-plots, recent lime has halved the contribution of *Alopecurus* and increased that of *Arrhenatherum*, decreased the amount of *Holcus* and further increased *Lathyrus* on 9b. Rough-Stalked Meadow Grass (*Poa trivialis*) has increased on 11^2b. In contrast, on sub-plots 4^2b and 10b, where only a small increase in pH was needed, the only significant change has been an increase in the amount of Hairy Oat-Grass (*Avena pubescens*) on 4^2b. (Williams)

Annual weeds

***Effect of propionic acid on viability of wild oat* (A.fatua *and* A.ludoviciana *seeds.*)** Germination-tests on wild oats from grain-stocks treated with propionic acid for storage had suggested that propionic acid decreased viability of the wild oats, but untreated stocks were not then available for comparison (*Rothamsted Report for 1972*, Part 1, 104). Samples of both species of wild oats removed from barley before treatment in 1974 and one day and one year after treatment, were received from Drayton EHF. Before treatment, 92·5% of *A. fatua* seeds were viable and 27·5% dormant, suggesting that they may not have been completely ripe when treated (*Rothamsted Report for 1962*, 236). First seeds of *A. ludoviciana* were 85% viable, 10% dormant and the smaller second seeds 84% viable, 73% dormant. All treated seeds were dead. Feed-stocks treated with propionic acid at the manufacturers' recommended rate are therefore free from viable wild oats. (Thurston)

Perennial weeds

Equisetum arvense (*Field Horsetail*). The plot treated with chlorthiamid at Woburn in 1972 (*Rothamsted Report for 1972*, Part 1, 105) remained free of *Equisetum* but in 1975 the weed was sparse on adjacent untreated plots. At Rothamsted, chlorthiamid at 9·2 kg

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a.i. ha^{-1} eradicated the weed in one block of the trial but not in another (where reinfestation may have occurred from the adjacent hedgerow); 4·6 kg a.i. ha^{-1} chlorthiamid or rotavation every three weeks greatly decreased but did not eradicate the weed. Glyphosate at 4 or 6 kg a.i. ha^{-1} was ineffective. In another experiment, glyphosate was sprayed at the same concentrations in August 1974 on to plants which had been established in pots for six or 18 months. By mid-June 1975, sprayed younger plants had few new shoots and the dry weight of living rhizome per pot was decreased from 24 to 1·5 g. The number of variable tubers was decreased from 379 to 1·5. With older *Equisetum* the dry weight of shoots was decreased by 80% and that of living rhizome and the number of viable tubers were approximately halved. There was little difference between the two rates of glyphosate. (Williams)

Agropyron repens *and* Agrostis gigantea (*The Couch grasses*)

Seed germination and longevity. The experiments begun during autumn 1971 (*Rothamsted Report for 1972*, Part 1, 106 and *for 1973*, Part 1, 102) were continued during 1974 and 1975. From autumn 1973 all plots in the field experiment were given the same treatment (Treatment 2) viz. rotary-cultivation during early autumn, ploughing in late autumn and tine-cultivation in spring, except that in 1974 wet soil conditions prevented rotavation and delayed ploughing until January.

Seedlings of both species continued to emerge during the third and fourth year after sowing. *Agrostis* seeds were more persistent than *Agropyron*: during the second, third and fourth years, 17, 8 and 5 seedlings appeared compared to 12, 4 and 1 m^{-2}. The effects of the earlier cultivation regimes persisted. *Agropyron* seeds were most and *Agrostis* least persistent where they remained on the soil surface for six weeks before being ploughed in during November 1971 (Treatment 1), whereas the reverse was true where the plots were frequently cultivated in autumn 1971 but not in the following spring (Treatment 3). Very few seedlings appeared following spring cultivations in 1975 and this was probably in part due to the dry soil conditions. Further germination of *Agrostis* after rain in September confirmed this. In a glasshouse investigation of germination in Rothamsted and Woburn soils cultivated with different frequencies, germination of *Agrostis* incorporated in the soil at the outset was protracted and incomplete after four years; as in the field it was slowest in the absence of spring cultivations.

In another field experiment weed seeds were sown on the soil surface in mid-September 1974 and then given one of three cultivation treatments:

(1) ploughing immediately after sowing;
(2) ploughing about six weeks later; and
(3) rotary-cultivation immediately after sowing.

In March 1975 all plots were power-harrowed to cereal seed-bed condition, rotary-cultivated in early September and ploughed in late October. In treatment (1) where seeds were deeply buried, no seedlings of either species appeared during the first year; in treatment (2), 40% of the *Agrostis* and 5% of *Agropyron* seeds gave seedlings before ploughing in 1974 and none since. In treatment (3), germination occurred throughout most of the year with peaks following cultivation in autumn and spring; 6% of the *Agrostis* and 10% of the *Agropyron* seeds gave seedlings during the first year. The experiment is being continued. (Williams)

Staff and visiting workers

Vivienne Frier and Saliya Kumarasinghe were awarded the Ph.D. Degree of London University. Saliya Kumarasinghe has now returned to the Botany Department, Colombo Campus, University of Sri Lanka.

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Dr. E. V. de sa Barreto Sampaio of Empresa Brasileira de Pesquisa Agropecuaria, Recife Pe, Brasil, is spending eight months in the Department studying the effects of temperature on respiratory metabolism under the auspices of the British Council. Professor Dr. A. E. Klar of Departamento de Engenharia Agricola, Faculdade de Ciencias Medicas e Biologicas de Botucatu, São Paulo, Brasil, and supported by the Research Foundation of the State of São Paulo, is working on the environmental factors controlling water loss from and the water potentials of cereal leaves.

Sandwich course students who worked in the Department were: I. Bolt, Stella Roberts and T. Warner. In addition N. Hall of Bradford University spent the first six months of his three-year period studying for the Ph.D. degree under the CASE award scheme.

C. P. Whittingham and T. O. Pocock attended the 38th Winter Congress of the Institut International de Recherches Betteravieres in Brussels.

Drs. Lenton, Welbank and Whittingham attended the XIIth International Botanical Congress in Leningrad.

Joan Thurston organised a session of the International Symposium of the European Weed Research Society in Paris and has been elected to the Committee of the Society.

Publications

Theses

1 Frier, V. (1975) Some factors which influence tuber growth in potatoes. Ph.D. Thesis, University of London.

2 Kumarasinghe, K. S. (1975) Glycollate metabolism in detached wheat leaves. Ph.D. Thesis, University of London.

Research Papers

3 Ford, M. A. & Thorne, G. N. (1975) Effects of variation in temperature and light intensity at different times on growth and yield of spring wheat. *Annals of Applied Biology* **80,** 283–299.

4 Ford, M. A., Pearman, I. & Thorne, G. N. (1976) Effect of variation in ear temperature on growth and yield of spring wheat. *Annals of Applied Biology* **82,** 317–333.

5 Lawlor, D. W. & Foch, H. (1975) Photosynthesis and photorespiratory CO_2 evolution of water-stressed sunflower leaves. *Planta* **126,** 247–258.

6 Lawlor, D. W. & Milford, G. F. J. (1975) The control of water and carbon dioxide flux in water-stressed sugar beet. *Journal of Experimental Botany* **26,** 657–665.

7 Milford, G. F. J. (1975) Effects of mist irrigation on the physiology of sugar beet. *Annals of Applied Biology* **80,** 247–250. (Short communication)

8 Milford, G. F. J. & Lawlor, D. W. (1975) Effects of varying air and soil moisture on the water relations and growth of sugar beet. *Annals of Applied Biology* **80,** 93–102.

9 Milford, G. F. J. & Pearman, I. (1975) The relationship between photosynthesis and the concentrations of carbohydrates in the leaves of sugar beet. *Photosynthetica* **9,** 78–83.

10 Radley, M. E. (1976) Effect of variation in ear temperature on gibberellin content of wheat ears. *Annals of Applied Biology* **82,** 335–340.

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11 THORNE, G. N. (1975) The source-sink concept in relation to productivity of cereals. *Proceedings of International Symposium on Breeding and Productivity of Barley*, Kromeriz, Czechoslovakia. 26–30 June 1972, pp. 414–416.

12 WILLIAMS, E. D. (1975) Growth of seedlings of *Agropyron repens* (L.) Beauv. and *Agrostis gigantea* Roth. in cereal crops. *Weed Research* **15,** 299–306.

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