Report for 1974 - Part 1

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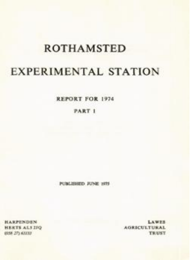

Botany Department

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Introduction

Crop physiology seeks to determine the factors (both internal and external) which determine crop yield and to show how they may be influenced by changes in agronomic practice or by breeding. An understanding of the complex physiology of the whole plant is most likely to be achieved through an integrated approach combining investigations of the physiology and biochemistry of individual plant processes with studies of plant growth. This approach is being most intensively pursued with the cereal crop. A similar but smaller amount of work is undertaken with sugar beet and considerably less with potatoes.

In addition to crop physiology, work in the Botany Department is also concerned with the biology of weeds and in particular of weed species which are not easy to control by selective herbicides.

Cereal crops

Response of spring wheat to large amounts of nitrogen

Growth and photosynthesis. The effects on Kleiber spring wheat of nine amounts of nitrogen (0–200 kg N ha^{-1}) were studied in an experiment similar to those of 1972 and 1973 (*Rothamsted Report for 1973*, Part 1, 89). The objective was to explain why large amounts of nitrogen which increase vegetative growth fail to increase grain yield proportionately.

Dry weight and leaf area at anthesis and the dry weight of straw plus chaff were 25% less than in 1973 because of the dry spring and early summer, but the mean grain yield of 5·3 t ha^{-1} (451 g m^{-2} dry matter) was only 10% less than in 1973. The cool wet weather after anthesis delayed leaf senescence and ripening: the crop was harvested 68 days after anthesis.

Grain yield was increased negligibly by nitrogen, probably because infection with *Fusarium* spp. increased with nitrogen. The weight of healthy ears suggested that, in the absence of *Fusarium*, grain yield would have responded to nitrogen throughout the range and been about 15% greater with 200 kg N ha^{-1} than with no N. By contrast, with 200 kg N ha^{-1}, leaf area and dry weight of the rest of the plant were 40–50% greater than with no N.

Gross photosynthesis (estimated from the uptake of $^{14}CO_2$) per unit area of flag leaf did not decrease with increasing nitrogen; photosynthesis of the leaf below the flag leaf decreased slightly, as did light intensity at the leaf surface. This decrease was more than compensated by an increase in leaf area so that photosynthetic production per unit land area was increased considerably by nitrogen. Nitrogen did not increase stem growth after anthesis. In all three years nitrogen increased dry weight of leaves and stems considerably at both anthesis and maturity but did not affect the change with time between the two growth stages. Leaves changed little in dry weight with time after anthesis until they died. Dry weight of the stems increased until 10–20 days after anthesis and then decreased to the earlier value but there was no influence of extra nitrogen.

Data obtained on the partition of ^{14}C between ear and shoot, after supplying flag leaves with $^{14}CO_2$, indicated that extra nitrogen sometimes decreased movement of carbohydrate to the ear, but usually only temporarily. In 1972 nitrogen had no effect at maturity on the percentage of the ^{14}C recovered in the whole shoot that occurred in the ear: it was 87% when flag leaves were treated six days after anthesis and 97% when treated at 19 days. In 1973 nitrogen decreased the percentage in the mature ear from 87% with no N to 73% with 200 kg N ha^{-1} when the $^{14}CO_2$ was supplied at 10 days after anthesis, but for treatment at 24 days nitrogen had only a temporary effect: the percentage in the ear 24 h after treatment was 70% with no N and 60% with 200 kg N ha^{-1} and 91% for all treatments at maturity. The addition of 200 kg N ha^{-1} also decreased movement of ^{14}C from the leaf below the flag leaf to the mature ear when treated at 10 days in 1973, from 78 to 71%. These effects of nitrogen on distribution of ^{14}C are not necessarily incompatible with the absence of effects on stem dry weight. The accumulation in the stems of carbon assimilated on a particular day may be compensated by increased respiration of assimilated carbohydrate at another time. (Pearman, Thomas and Thorne)

Sugar content of spring wheat. It has been suggested that the synthesis of starch in the grain is related to the level of sucrose in the endosperm, and that, given an adequate supply of carbohydrate to the ear, this level is limited by the capacity of the processes transporting sugar into the grain (Jenner & Rathjen, *Annals of Botany* (1972), **36**, 726–741). Sugar might be expected to accumulate in the ear structures (glumes and rachis) if grain yield were limited in this way with large nitrogen dressings. Plants were taken from the field at the end of a sunny day in 1973, 31 days after anthesis when the grains were growing rapidly, and total levels of sucrose and reducing sugars measured. Nitrogen fertiliser in the range 0–200 kg N ha^{-1} had no effect on sugar concentrations in the grains, ear structures, flag leaf or top internode, and the concentrations were much lower than those reported to occur when transport is limiting. The mean concentrations of sucrose plus reducing sugars, expressed as mg reducing sugar g^{-1} fresh weight were: grain 17·1, ear structures 35·6, flag leaf 34·8, top internode 52·4. As the weights of the leaves and stems were bigger in the plants grown with large nitrogen dressings, the total amount of sugar in these tissues was larger. (Thomas)

Effect of nitrogen on photo- and dark-respiration of wheat. Some plants growing in paper pots sunk in the ground in the field plots receiving different amounts of nitrogen fertiliser were dug up and brought into a growth room with day/night temperatures of 18/14°C, humidity of 70/90% RH, 16 h day and 125 W m^{-2} visible radiation.

The CO_2 compensation point and the release of CO_2 into CO_2-free air, measured on the flag leaf during the day, were unaffected by nitrogen except that at 13–16 days after anthesis the addition of 200 kg N ha^{-1} decreased the compensation point by 7 vpm. Measurements were also made of the release of CO_2 into CO_2-free air from flag leaves of plants growing in the field. The average values, $\simeq$2·55 mg CO_2 dm^{-2} h^{-1} (i.e. 4·08 mg CO_2 g^{-1} dry wt. h^{-1}), were similar to those measured in the growth rooms and no effect of nitrogen was detectable. Dark respiration rates of the stem plus leaves and of the ear at night were unaffected by nitrogen and decreased with age. Mean values at 13–16 days were: shoot 0·37, ear 0·84; at 27–30 days: shoot 0·30, ear 0·50 mg CO_2 g^{-1} h^{-1}.

The activity of phosphofructokinase, an enzyme reported to regulate the glycolytic pathway of respiration, was measured in extracts of the flag leaves and top internodes. The activity remained constant when assayed at intervals from anthesis to 35 days later. Mean values at 25°C were 19·1, 23·2 and 24·9 μmol substrate g^{-1} fr. wt. h^{-1} at 0, 100 and 200 kg N ha^{-1} respectively. If all the substrate were ultimately converted to CO_2 in respiration maximum rates of release would be 14, 17 and 18 mg CO_2 g^{-1} dry wt. h^{-1}– values greatly in excess of those actually measured. (Pearman and Thomas)

Effect of late nitrogen sprays on spring wheat. Nitrogen fertiliser applied to the leaves after ear emergence delayed leaf senescence and increased yield when tested 21 years ago (Thorne & Watson, *Journal of Agricultural Science* (1955), **46**, 449–456). When leaf-area index is declining an increase in leaf area may increase grain yield even if without effect at the beginning of the grain growth period (*Rothamsted Report for 1973*, Part 1, 95). To test the effects of late applications of nitrogen on a modern, high-yielding crop, eight amounts of nitrogen were applied as 'Nitro-Chalk' at sowing to Kleiber spring wheat and compared with the same amounts of nitrogen applied half as 'Nitro-Chalk' at sowing and half as a spray two days after anthesis. The sprays were various concentrations of urea up to a maximum of 470 g $litre^{-1}$ applied at 345 litre ha^{-1} (30 gal $acre^{-1}$), or at 690 litre ha^{-1} when supplying 87·5 or 100 kg N ha^{-1}. All solutions supplying more than 50 kg N ha^{-1} scorched the crop.

At total rates exceeding 150 kg N ha^{-1} the split dressings gave smaller grain yields than the same amount of nitrogen applied at sowing because the scorch decreased leaf area and grain size. At 25 and 50 kg N ha^{-1} the split dressing gave about 0·3 t ha^{-1} more grain than the spring application. The split dressing delayed leaf senescence and increased ear number, apparently by preventing the death of some ear-bearing shoots that occurred with the spring applications. (Pearman, Thomas and Thorne)

Effects of light, CO_2 and nitrogen on grain growth and carbohydrate metabolism of wheat. To investigate the effects of differences in nitrogen content on growth and carbohydrate metabolism after anthesis, Kolibri spring wheat grown in pots in controlled environment rooms was given 0·5 g N as NH_4NO_3 ten days before anthesis and the production of late tillers was prevented. In addition, in order to alter the balance between the supply of carbohydrate for grain filling and the capacity of the grains to absorb carbohydrate, two light intensities (56 and 112 W m^{-2} visible radiation) and two atmospheric CO_2 concentrations (425 and 970 vpm) were combined factorially with the nitrogen treatment starting six days after anthesis. Daylength was 16 h and day/night temperatures and humidities were 19/14°C and 75/93% respectively.

Senescence of all leaves, including the flag leaf, was delayed by extra nitrogen and slightly hastened by extra light and CO_2. The rate of ear growth and final grain dry weight were increased by extra nitrogen and light. Nitrogen increased the number of grains per ear and light increased grain size. Extra CO_2 increased ear dry weight up to 33 days after anthesis similarly to extra light, but thereafter the difference disappeared and CO_2 did not affect grain yield. Dry weight of the rest of the shoot was unaffected by nitrogen. It increased faster with extra light or CO_2 until maximum weight was reached at 14–24 days after anthesis; thereafter the larger shoots decreased in weight faster than the smaller ones so that there was no difference at maturity. These changes in dry weight, and the distribution of ^{14}C within the shoots 24 h after it was supplied to flag leaves, showed that at 14 days after anthesis the ear was an inadequate sink for carbohydrate in conditions favouring photosynthesis or when there were few grains because of lack of nitrogen. The percentage of the total ^{14}C in the shoot found in the ear was decreased by increasing the light intensity or CO_2 concentration and increased by increasing the nitrogen supply; it ranged from 61% with bright light, high CO_2 concentration and low nitrogen to 85% with dim light, low CO_2 concentration and high nitrogen. This inadequacy of the ear as a sink was only temporary. By maturity 95% of the ^{14}C in the plants treated at 13 days was in the ear irrespective of treatment: most of that previously accumulated in the stem had moved to the ear and the rest had been lost by respiration. Also, when flag leaves were given $^{14}CO_2$ 32 days after anthesis, neither the percentage recovered in the ear after 24 h (77%) nor at maturity (96%) was affected by treatment. (Pearman, Thomas and Thorne)

Certain enzyme assays were made on flag leaves on ten occasions from nine days before anthesis to 39 days after. The activities of ribulose biphosphate carboxylase at anthesis were 666 and 1014 μmol CO_2 fixed g^{-1} fr. wt. h^{-1} (i.e. 123 and 188 mg CO_2 dm^{-2} h^{-1}) for no extra nitrogen and extra nitrogen respectively, and at 32 days after anthesis were 214 and 546 μmol CO_2 g^{-1} fr. wt. h^{-1} respectively. The corresponding figures for ribulose biphosphate oxygenase were 59·7 and 83·9 μmol O_2 consumed g^{-1} fr. wt. h^{-1} at anthesis and 15·8 and 39·2 μmol O_2 consumed g^{-1} fr. wt. h^{-1} 32 days later. There was no significant difference in the ratio of the activities of the two enzymes with nitrogen treatment. The activities at the two nitrogen levels declined in parallel throughout the period of the experiment.

The activities of ribulose bisphosphate carboxylase were of a similar order to those measured in a field-grown crop of spring wheat in 1973 (*Rothamsted Report for 1973*, Part 1, 91). As in 1973 there was no evidence that the higher rates of carboxylase with extra nitrogen led to higher rates of photosynthesis; all rates of photosynthesis were far less than the maximum activity of the carboxylase.

The increase in enzyme activities with extra nitrogen is correlated with higher levels of protein in the leaves. The protein content of the flag leaves (measured with bovine serum albumin as standard) was 44·0 mg protein g^{-1} fr. wt. before anthesis; it decreased until anthesis and was then maintained at a fairly constant level for 32 days at 35·8 mg g^{-1} fr. wt. in leaves from plants given extra nitrogen and 25·7 mg g^{-1} fr. wt. in those given no extra nitrogen. The chlorophyll content of the flag leaves followed a similar pattern. Some of the extra carbon fixed in photosynthesis in plants grown with extra nitrogen may be used to maintain the higher concentrations of these compounds rather than to provide carbohydrate for grain growth.

The only effect of light and CO_2 on the activities of ribulose bisphosphate carboxylase and oxygenase, and protein and chlorophyll content was that the levels decreased less rapidly, when the light intensity or CO_2 concentration was less, consistent with the delay in senescence observed.

Light intensity had no effect on the distribution of ^{14}C in early products of photosynthesis. Extra nitrogen at the lower CO_2 concentration increased the incorporation into glycine from about 2 to 5% seven days after anthesis, with a fall in incorporation into phosphoglyceric acid from 36 to 32%. The only other consistent effect of nitrogen was an increase in the incorporation into alanine (e.g. from 1 to 2% at seven days after anthesis). Carbon may move into glycine more rapidly in plants given extra nitrogen, but confirmation of this requires more extensive analysis of the rate of movement of radioactivity through individual compounds. The greater incorporation into glycine and alanine may be the result of larger pools of nitrogen-containing compounds in the plants given extra nitrogen. Increasing the concentration of CO_2 to 970 vpm decreased the incorporation of ^{14}C into serine (from 3 to 1%) and into glycine (to 1% in flag leaves from plants at both levels of nitrogen). Incorporation into phosphoglyceric acid was increased to 41%. The results are consistent with a decreased flow of carbon through the intermediates of photorespiration at high concentrations of CO_2 which may contribute to the increased growth observed. There was no evidence for a change in the relative activities of the oxygenase and carboxylase at the higher concentration of CO_2. (Thomas)

General conclusions. The main reason why grain production did not increase proportionately to the increase in gross photosynthetic production caused by additional nitrogen fertiliser is probably that the respiratory loss of carbon was greater due to a greater dry weight and concentration of proteins. For example, respiration of the larger shoots produced in 1974 by the addition of 200 kg N ha^{-1} represents the loss of about 74 g m^{-2} of dry matter during the whole of the grain filling period, or about 16% of the observed grain yield. Better methods of determining respiratory loss of carbon using ^{14}C are being sought. (Thomas and Thorne)

Photorespiration as a factor in crop growth; a comparison of maize and wheat. Plots of Kleiber spring wheat were sown on 4 April and 2 May, and Pioneer maize on 3 May, at Rothamsted, to compare growth and photosynthetic rates. Measurements of photosynthetic rate using $^{14}CO_2$ (*Rothamsted Report for 1973*, Part 1, 89) for leaves at the top of the canopies showed that except at light intensities above 1700 μE m^{-2} s^{-1} (approx. 460 W m^{-2}) of photosynthetically active radiation or temperatures above 30°C wheat had faster rates per unit leaf area than maize. At 15°C the mean photosynthetic rates found were 29 and 20 mg CO_2 dm^{-2} h^{-1} for wheat and maize respectively; at 25°C the corresponding values were 34 and 28. Rates of release into CO_2-free air at 25°C and light intensities of 1000 μE m^{-2} s^{-1} were estimated as 0·2 and 2·0 mg CO_2 dm^{-2} h^{-1}, for maize leaves and flag leaves of wheat respectively. Rates of release into CO_2-free air are related (but not simply) to rates of photorespiration. The reaction probably responsible for CO_2 evolution in photorespiration, the conversion of glycine to serine, was catalysed more rapidly by extracts of wheat leaves (up to 40 μmol serine formed g^{-1} fr. wt. h^{-1}, 3·4 mg glycine C converted dm^{-2} h^{-1} or 3·1 mg CO_2 released dm^{-2} h^{-1}) than by extracts of maize leaves (up to 3 μmol serine g^{-1} fr. wt. h^{-1}). The activity in extracts of wheat leaves was at a maximum at full expansion and declined as the leaf senesced; for each successive leaf the maximum rate was greater and persisted longer so that highest activities were observed in the whole of July.

An attempt was made to measure rates of conversion of glycine to serine *in vivo* by measuring changes in amounts of glycine and serine present when leaves were suddenly darkened. Amounts in wheat before darkening varied from 7 to 15 μmol glycine g^{-1} dry wt. and from 6 to 10 μmol serine g^{-1} dry wt. The amounts present in maize leaves ranged from 5·5 to 8·8 and 5·5 to 8·6 μmol g^{-1} dry wt. of glycine and serine respectively. In wheat, glycine decreased initially at a rate of 13·2 mg glycine dm^{-2} h^{-1} in darkness; equivalent to a rate of CO_2 production double the measured rate of CO_2 evolution into CO_2-free air.

In other experiments, $^{14}CO_2$ in air was supplied to leaves of the wheat and maize for

10 seconds. Malate and aspartate became strongly radioactive in maize with little activity in glycine and serine, consistent with a slow rate of photorespiration in maize. In wheat leaves, much ^{14}C was incorporated into glycine and serine. These amino acids became labelled rapidly but during subsequent photosynthesis in air this label was lost only slowly; indicating a small active pool transferring to a larger, less active pool.

The data indicate that the rate of release of CO_2 in photorespiration in maize is less than one-tenth that in wheat. But at temperatures below 25°C wheat leaves still achieved a greater net rate of photosynthesis per unit area. (Bird, Cornelius and Keys)

Carbon metabolism in wheat leaf segments. Kolibri spring wheat was grown in a constant environment room at 20°C with 16-h days and 50 W m^{-2} visible radiation. After two weeks, 4 cm segments of the first leaves were excised. Samples of five leaf segments were selected and enclosed in leaf chambers (16 cm^3) so that the cut bases were immersed in water or a 2% aqueous solution of isonicotinyl hydrazide (INH). Air (430 cm^3 min^{-1}) containing 150 or 320 vpm CO_2 was passed through the leaf chambers while the leaf segments were illuminated by tungsten lamps (light intensity 150 W m^{-2}) at 20°C. When a steady rate of photosynthesis had been reached the gas mixture was changed to one containing $^{14}CO_2$ of known specific activity at the same concentrations as before. Subsequently, the composition of gas mixtures was again changed to either 0, 150, 320 or 1000 vpm $^{12}CO_2$ in 21 or 1% oxygen. Samples of leaf segments were killed and extracted. INH decreased incorporation of ^{14}C into serine and sucrose. When the gas mixture containing $^{14}CO_2$ was changed to one containing $^{12}CO_2$ in the absence of INH, ^{14}C decreased in glycine and increased in sucrose and respired CO_2; in the presence of INH the amount of ^{14}C in glycine, serine and sucrose remained almost constant, and evolution of $^{14}CO_2$ was negligible. These results are consistent with our view that conversion of glycine to serine is responsible for CO_2 evolution during photorespiration and suggest that much sucrose is made from glycine and serine.

Without INH, rates of incorporation of ^{14}C during steady state photosynthesis into glycine and serine, respectively, were equivalent to 12·5 and 4·8 (150 vpm CO_2) and 18·2 and 4·2 (320 vpm CO_2) μg C dm^{-2} min^{-1}. Total assimilation of ^{14}C was equivalent to 33·5 (150 vpm CO_2) and 63·2 (320 vpm CO_2) μg C dm^{-2} min^{-1} (2·0 and 3·8 mg C dm^{-2} h^{-1}). As both glycine and serine probably exist in two pools with different activities the above rates of incorporation provide only minimum estimates of the flow of carbon. After 15 min photosynthesis in $^{14}CO_2$ the pools of glycine and serine were almost saturated with ^{14}C. Initial changes in the amount of ^{14}C in glycine and serine, when the composition of the gas mixture was changed, were used to calculate rates of loss of carbon. In CO_2-free 1% oxygen there was a decrease in glycine (39 μg C dm^{-2} min^{-1}) and increase in serine but an insignificant release of $^{14}CO_2$. Similar results for sunflower leaves were considered by Atkins, Canvin and Fock (in: *Photosynthesis and Photorespiration*, Wiley Interscience, 1971, p. 497) to show that CO_2 in photorespiration was not derived from glycine. But $^{14}CO_2$ was evolved in 1% oxygen with 1000 vpm $^{12}CO_2$ present; so that the results previously obtained in the absence of CO_2 probably result from photosynthetic refixation of any $^{14}CO_2$ evolved. This conclusion was confirmed by the rapid loss of ^{14}C from phosphate esters with 1000 vpm $^{12}CO_2$ but persistence of ^{14}C in phosphate esters when CO_2 was absent. Refixation of $^{14}CO_2$ has a further effect; by supplying ^{14}C to the photosynthetic intermediates (phosphate esters) it allows synthesis of [^{14}C] glycine to continue so the net rate of decrease of ^{14}C in glycine in CO_2-free 1% oxygen is slower than with 1000 vpm $^{12}CO_2$. The effect is more marked in 21% oxygen where glycollate synthesis is rapid; calculated minimum rates of carbon flow from glycine were 16, 23 and 75 μg C dm^{-2} min^{-1} for 0, 320 and 1000 vpm $^{12}CO_2$ following photosynthesis in 320 vpm $^{14}CO_2$. In 1000 vpm CO_2 when glycollate synthesis is thought to be slower (Lee & Whittingham, *Journal of Experimental Botany* (1974), **25**, 277–287), and refixation of photorespired $^{14}CO_2$ is prevented, the initial rate of decrease in ^{14}C in glycine (75 μg C dm^{-2} min^{-1}) probably closely represents the rate of carbon flow through glycine during photosynthesis in 320 vpm CO_2. It is to be noted that the rates of carbon flow out of glycine can exceed the total rate of C assimilation from 320 vpm CO_2 (63·2 μg C dm^{-2} min^{-1}; see above). Further experiments concerned changes in ^{14}C in glycine and serine when 15 min photosynthesis in $^{14}CO_2$ were followed by a period in the dark. The further metabolism of serine and refixation of CO_2 are both light-dependent so that loss of ^{14}C from glycine was accompanied by a nearly stoichiometric increase in serine and CO_2 output; the calculated rates were 36, 29 and 9·7 μg C dm^{-2} min^{-1} (means of ten estimates) for decrease of glycine and increases of serine and CO_2 respectively. In this experiment the rate of assimilation of $^{14}CO_2$ during the 15 min photosynthesis corresponded to 43·4 μg C dm^{-2} min^{-1} (equivalent to 9·5 mg CO_2 dm^{-2} h^{-1}). It was concluded that nearly all of the carbon assimilated at 320 vpm CO_2 may be metabolised by the glycollate pathway and most, if not all, of the CO_2 evolved in photorespiration is derived from conversion of glycine to serine. (Kumarasinghe and Whittingham)

The role of the glycollate pathway in sucrose synthesis. The final reactions of sucrose synthesis do not occur to a significant extent in the chloroplast (*Rothamsted Report for 1973*, Part 1, 92). Either assimilation of CO_2 or addition of a keto acid results in synthesis of [^{14}C] sucrose and production of $^{14}CO_2$ from [^{14}C] serine added to leaf segments. Hence sucrose synthesis can occur via glycollate and serine under conditions of active synthesis. When glycollate synthesis is decreased by high CO_2 or low oxygen in the atmosphere it is likely that much of the sucrose is made directly from phosphate esters originating in the chloroplast. We still wish to determine the amount of sucrose made directly from sugar phosphate intermediates of photosynthesis compared with that made from intermediates of the glycollate pathway; also to what extent the chloroplasts may be involved in converting serine to sugar phosphates.

The intramolecular distribution of ^{14}C in the hexose units of sucrose following short periods of photosynthesis by pea leaves in $^{14}CO_2$ at concentrations of 150 and 1000 vpm was investigated. The method for degrading the hexose (Rognstad & Woronsberg, *Analytical Biochemistry* (1968), **25**, 448–451) gave the sums of ^{14}C in carbons 3 + 4, 2 + 5 and 1 + 6. After 30 seconds in 1000 vpm $^{14}CO_2$ when 1·5 g pea leaflets had assimilated 2·5 μmol CO_2, the 3 + 4 carbons contained 73% of the total ^{14}C in sucrose; after 30 seconds in 150 vpm $^{14}CO_2$, when the same weight of pea leaflets had assimilated 0·5 μmol CO_2 the 3 + 4 carbons contained only 44% of the total ^{14}C in sucrose. By the time 2·5 μmol CO_2 had been assimilated at 150 vpm CO_2 radioactivity in carbons 3 + 4 was about 50% of the total. In 1000 vpm CO_2 less carbon should be metabolised by way of glycollate than at 150 vpm. Glycollate, glycine and serine made during photosynthesis in $^{14}CO_2$ have all their carbon atoms equally radioactive at the shortest times that can be studied. Therefore, when much of the sucrose is made from carbon metabolised by the glycollate pathway the carbons of sucrose should be equally labelled (i.e. with 33% of the total ^{14}C in carbons 3 + 4). When much of the sucrose is made from carbon coming directly from photosynthesis it may be expected to be predominantly 3 + 4 labelled. The results of this preliminary investigation are consistent with more sucrose being made from intermediates of the glycollate pathway during photosynthesis in low compared to high CO_2 concentrations. (Bird, Cornelius, Keys and Whittingham)

Root growth of barley at different seed rates and with different N and P fertiliser. The effects on root growth of a wide range of seed rates and their interactions with nitrogen and phosphorus fertiliser was investigated. Barley, var. Julia, was sown on 2 April on the light, sandy silty loam overlying sand in Stackyard Field, Woburn, at eight seed rates increasing in approximately equal steps from 34 to 269 kg ha^{-1}. Fertilisers supplying 100 kg P_2O_5 ha^{-1} (worked into the seedbed) applied to half the plots and supplying 50 or 100 kg N ha^{-1} (applied at sowing) were combined factorially with seed rate in a single replicate. K_2O (120 kg ha^{-1}) and 60 kg MgO ha^{-1} were worked in before sowing to all plots. Plant numbers were counted on 29 April, and crop samples from approximately 0·5m^2 were taken on 6 May, 28 May, 24 June and 29 July. Also six soil cores 7 cm in diameter and up to 1 m deep were taken from random positions in each sample area and separated into layers 15 or 25 cm deep for root estimation. Sub-samples of clean roots were photographed for later length estimation on the Quantimet image analysing computer and all roots dried and weighed. Grain and straw yield were taken from approximately 2 m^2 samples on 20 August. Soil samples were analysed at the beginning and end of the experiment to measure any depletion of plant nutrients. Measurements of soil moisture were made with a neutron moisture probe three days before and four days after each root sampling on plots sown at 34, 135 and 235 kg ha^{-1}.

The plant numbers estimated for each seed rate at seedling emergence were 71, 122, 192, 248, 297, 350, 388 and 456 m^{-2}; final grain and straw yields were not significantly affected by seed rate, or by phosphorus fertiliser, averaging 4·0 t grain and 4·2 t straw ha^{-1} and 5·1 t grain and 5·2 t straw ha^{-1} at the lower and higher N rates (at 85% dry matter; S.E. grain: 0·09, straw: 0·11 t ha^{-1}).

When the barley had three expanded leaves (6 May), roots extended to 30–45 cm deep and total root dry weight, like shoot dry weight and leaf-area index, increased linearly from 15 g roots m^{-2} to 85 g m^{-2} from the lowest to the highest seed rate, indicating little competition between plants. Neither N nor P treatments significantly affected shoot or root dry weights, but the higher N rate decreased the proportion of roots below 15 cm deep. By 28 May the relationship between total root weight and seed rate was markedly curved, with root weights increasing from 23 g m^{-2} at a seed rate of 34 kg ha^{-1} to 50 g m^{-2} at 135 kg ha^{-1} but with little increase above that seed rate. Increasing seed rate also increased the proportions of total roots at depths below 30 cm, while below 60 cm the weight of roots, although small, continued to increase up to the highest seed rates. Thus denser crops favoured development of root systems at greater depths. At this stage nitrogen had little effect on root weights, but phosphorus stimulated root growth at low seed rates in the top 15 cm of soil, while depressing root growth at high seed rates in soil layers below 30 cm.

At the first sampling, although there were from six to nine times as many roots in the top layer, only three times as much water was depleted from the 0–15 cm soil layer as from 15–30 cm with little loss from the 30–45 cm layer and none from below 45 cm. Water loss increased with root density at higher seed rates, but not proportionately. At the second sampling water depletion at increasing depths of soil was in the proportions 10 : 20 : 15 : 10 : 3, compared with roots in the proportions 74 : 20 : 5 : 1 : (trace). No loss occurred below 75 cm. Water uptake from the top layer was evidently restricted by the drying soil. Water loss increased at high seed rates only in the 60–75 cm layer. Further data are still to be analysed. (Taylor and Welbank)

Carbohydrate metabolism of detached ears. Studies have continued on the effects of growth substances on the accumulation of starch in developing wheat grains. As described in previous reports growth substances were applied to the individual grains on wheat ears which were subsequently detached and incubated with their stalks in ^{14}C-sucrose solution. The previously described effects of chlormequat chloride (CCC), GA_3 and the GA precursor entkaurene on the amount of radioactivity accumulated in the starch of the grains were found on several occasions, but in other experiments these responses did not occur. It now seems unlikely that the substances tested are important regulators of starch accumulation.

It is proposed to discontinue these experiments. In future work the influence of certain growth substances on grain ripening and the cessation of starch accumulation will be investigated. (Radley)

Endogenous gibberellins in developing wheat grains. Wheat grains at different stages of development were examined for the presence of gibberellin-like compounds suitable for isolation and identification by combined gas chromatography–mass spectrometry.

Wheat seeds (var. Kolibri) were planted at weekly intervals and harvested on a common date (30 August). The acidic gibberellin-like substances were extracted, purified by thin-layer chromatography and assayed by the barley endosperm test.

The gibberellin content per grain reached a maximum four weeks after anthesis corresponding to the period of highest grain fresh weight but declined as the grain started to ripen although dry matter was still accumulating. Essentially similar results were obtained with plants harvested (5 July) up to four weeks after anthesis. The experiments were preliminary to investigations to determine the influence of gibberellins on grain growth and development. (Lenton)

Effects of aerial pollutants on cereal growth. In addition to experiments at Woburn Experimental Farm, additional sites were obtained in 1974 at Manor Farm, Ampthill and at Elstow, Bedfordshire. Under normal conditions the site at Elstow suffers severe pollution. Due to the closure of two brickworks and the introduction of short-time working at others, pollution was severely restricted in 1974 and there was only one episode at Elstow when average day levels of 200 $\mu g\ m^{-3}$ SO_2 were exceeded.

At Manor Farm, spring barley, var. Julia, was grown in two plastic houses through which was blown ambient field air or ambient air filtered through a dust filter followed by an active charcoal filter. Mean SO_2 level in the filtered house was less than 3 $\mu g\ m^{-3}$ against an ambient air value of 60 $\mu g\ m^{-3}$. The crop showed no signs of visible injury in the polluted air and there was no evidence of yield loss; indeed plants growing in the filtered house gave a slightly smaller yield than those in the unfiltered house. Both the temperature and the humidity in the houses exceeded that outside. Analysis of the plant material for sulphur and fluoride showed high levels of both elements in plants from the non-filtered as compared to the filtered house, but sulphur levels in plants from outside the chambers were lower than those from inside the filtered house. This difference may be related to the difference in temperature and humidity. Fluoride levels of outside plants were greater than those of plants in the house.

In an attempt to overcome the difference in temperature and humidity inside the chambers and outside, a type of open top chamber was developed and underwent trials at Woburn. There was little difference in relative humidity, temperature or soil moisture between the inside of the chamber and outside. A significant reduction was obtained in the level of pollutants within the chamber but in preliminary experiments a consistent difference could not be maintained. However, it was observed again that barley growing in the filtered chamber had a lower yield than in the unfiltered chamber. Further developmental work on the design of the open top chamber is being undertaken during the winter and trials will be undertaken next summer on a polluted site. (Brough, Parry and Whittingham)

Carbon metabolism of polluted leaves. The mechanism of inhibition of photosynthesis by SO_2 is still uncertain but is unlikely to be due simply to an effect on stomatal movement. An apparatus was constructed in which detached leaves or leaf segments from cereals could be exposed to variable illumination and SO_2 concentration. Temperature and humidity of the gas stream were constant and provision was made for supplying $^{14}CO_2$ to the leaf chambers. Concentrations of SO_2 up to 3250 μg m^{-3} were used, much higher than those found in the field, but exposure times were short. Barley, cv. Julia, used at the two-leaf stage showed reduced inhibition of photosynthesis after 5 min exposure. The decreased rate was accompanied by a fall in the percentage of ^{14}C incorporated into PGA (3-phosphoglyceric acid) and hexose phosphates with corresponding small increases in sucrose, aspartate and malate and larger increases in alanine, serine and glycine. At some concentrations of SO_2 an initial stimulation of photosynthesis occurred, accompanied by a sharp rise in the percentage ^{14}C in sucrose and corresponding falls in PGA and hexose phosphates. Prolonging the fumigation or increasing the SO_2 concentration caused inhibition of photosynthesis. This is consistent with an initial stomatal opening induced by SO_2.

The method is potentially useful as a rapid screening method to test barley varieties for variations in susceptibility to SO_2. (Kendall and Whittingham)

Sugar beet

Water relations. Growth room experiments in which air and soil moisture were varied under otherwise constant conditions showed that sugar beet photosynthesised and grew faster under conditions of high humidity (*Rothamsted Report for 1973*, Part 1, 98–99). In 1974 a field experiment investigated whether application of water as a mist over a crop would increase the moisture content of the air around its leaves sufficiently to increase plant growth and yield. Water was applied either as mist irrigation between 08.00 h and 20.00 h according to the evaporative demand measured by an electronic leaf sensor, or as trickle irrigation to maintain the soil water deficit within 12 mm of the potential deficit calculated from meteorological data, or the same amount of water as applied to the mist plots given as trickle-irrigation to the soil. The three treatments were applied for six weeks either to the young crop (starting 6 June) or to the mature crop (starting 24 August).

1974 was a bad year for sugar beet. Dry weather early in the season delayed the germination and establishment of the crop. There was also high incidence of virus yellows disease. Virus infection was particularly severe on some of the misted plots in the young crop resulting in yield loss. Weather was particularly dull and wet during the late irrigation treatments to the mature crop. Overall, no beneficial effect of any irrigation treatment was observed.

A secondary objective of the experiment was to obtain information on the development and magnitude of water stresses in field-grown sugar beet and to determine how these affected the photosynthetic activity.

When there was a large soil moisture deficit under the unirrigated crop (100 mm) and solar radiation was low (daily visible radiation = 377 J cm^{-2}), leaf water potentials in the unirrigated crop decreased from -8 bar at 06.00 h to -15 bar during the afternoon. Both trickle irrigation and mist irrigation kept leaf water potentials around -10 bar for most of the day; consequently stomatal resistances were lower (3 seconds cm^{-1} cf. 10 seconds cm^{-1} during the afternoon) and photosynthetic rates higher (15 mg $^{14}CO_2$ dm^{-2} h^{-1} cf. 8 mg $^{14}CO_2$ dm^{-2} h^{-1} during the afternoon) than in the unirrigated plants.

On days of high insolation (daily visible radiation = 945 J cm^{-2}) when soil moisture was plentiful there were no differences in behaviour between the unirrigated and trickle irrigated plants. Leaf water potentials in both decreased from -5 bar at 05.00 h to -15 bar in the afternoon. Leaf water potentials in mist-irrigated plants were similar in the morning but decreased to only -10 bar in the afternoon. Stomatal resistances and photosynthetic rates were the same in all treatments during the morning (3 seconds cm^{-1} and 25 mg $^{14}CO_2$ dm^{-2} h^{-1}) but stomatal resistances increased to 16 seconds cm^{-1} during the afternoon in unirrigated and trickle-irrigated plants and photosynthesis decreased to 12 mg $^{14}CO_2$ dm^{-2} h^{-1} whereas stomatal resistances increased only slightly and photosynthetic rates hardly changed in mist-irrigated plants.

At low insolation the vapour pressure deficit of the air under mist was 15·3 mbar compared with 14·8 mbar without mist, equivalent to relative humidities of 90 and 86% respectively. At high insolation the vapour pressure deficits were 15·5 mbar (68% relative humidity) and 16·4 mbar (65% relative humidity) respectively. Thus there was no appreciable effect of mist-irrigation on the moisture content of the air. On sunny days leaf temperatures of unirrigated plants averaged 22·5°C, 0·4°C cooler than the surrounding air, whereas leaf temperatures of mist-irrigated plants averaged 19·6°C, almost 4·0°C cooler than the surrounding air. On dull days leaf temperatures of mist-irrigated plants were similar and within 0·5°C of the air temperature.

These observations suggest that water applied as a mist to the leaves of sugar beet is directly evaporated and, by reducing the radiant energy load on the leaf, enables the plant to maintain lower leaf temperatures and greater leaf water potentials. This physiological effect of mist-irrigation was measurable only on days of high insolation, so effects on overall growth and yield of the crop depend on the number of such days occurring during the growing season. In 1974 these were particularly few. (Milford)

Application of growth regulators

Growth substances and bolting. Cold treatment of sugar-beet plants causes bolting during subsequent growth in warm conditions and long days. It is known that application of gibberellic acid will cause stem elongation in the absence of cold treatment. In other biennial rosette species elongation is accompanied by an increase in the endogenous gibberellin concentration. Therefore experiments are being carried out with the object of (a) measuring the changes in endogenous gibberellins and other growth substances, in sugar beet during chilling and bolting to establish a correlation with morphological changes, and (b) controlling bolting with various growth retardants, especially those inhibiting gibberellin biosynthesis.

The endogenous gibberellin in the bud and young leaf tissue of large plants grown outside through the winter was measured by bioassay. The gibberellin concentration decreased sharply after mid-December and increased at the beginning of April as bolting commenced, reaching a high concentration by late April. There was no evidence of any qualitative changes in the gibberellins.

Young seedlings of Sharpe's Klein Monobeet in 8-in. pots were placed outdoors on 7 January three days after receiving 100 mg in 100 ml chlormequat chloride (CCC) as a soil drench. The treatment was repeated after six weeks. For some weeks the treated plants had dark leaves and short petioles, and the gibberellin content on 15 February was lower in the treated plants than in the controls. By 5 April the gibberellin content was no longer different and by 8 May stems were several centimetres long in half the plants of both control and treated groups. Eventually almost all the plants bolted. Hence treatment with CCC applied during vernalisation did not prevent bolting. The time of application has now to be varied in relation to temperature and/or daylength changes. (Radley)

'Ethrel'. Earlier experiments at Rothamsted showed little effect of spraying 'Ethrel' on sugar-beet plants (*Rothamsted Report for 1969*, Part 1, 118 and *1970*, Part 1, 104) but recent work (Freytag & Akeson, *Plant Physiology* (1973), **51** (suppl.), 30) prompted a re-investigation.

Seedlings growing in soil in 5-in. pots were treated with a soil drench of 'Ethrel' three times at two-week intervals and were harvested two to three weeks after the final treatment. In the first experiment 20 ml of 1000 mg $litre^{-1}$ 'Ethrel' significantly increased the fr. wt., but not the dry wt., of the roots whereas 100 and 5000 mg $litre^{-1}$ had no effect; all three concentrations gave a smaller dry wt. of the tops.

In a second experiment in 8-in. pots, carried out later in the season, there was a stimulatory effect on root fr. wt. with all treatments (50 ml of 200, 600, 1000 mg $litre^{-1}$) the effect being greater with the higher concentrations. Root dry wt. was also affected, but proportionately less than fr. wt., so that percentage water content was significantly greater at 1000 mg $litre^{-1}$ than in control plants. The tops were unaffected. Further experiments are in progress. (Radley)

Gibberellins. Gibberellic acid (GA_3) can promote root growth of sugar-beet seedlings growing in sand culture, especially when applied to the roots (*Rothamsted Report for 1972*, Part 1, 99) and when applied as a microdrop to the base of the petioles of expanded leaves of clonal plants growing in 'Eff' compost (*Rothamsted Report for 1973*, Part 1, 100). This year GA_3 was applied to seedlings of Sharpe's Klein Monobeet growing in soil to test the practical significance of the previous observations.

Plants were grown in 5-in. pots in John Innes compost No. 1 or in sand treated with slow-release fertiliser. Half the plants in each batch were treated four times with 20 ml of 10 mg $litre^{-1}$ GA_3 applied as a soil drench at weekly intervals, commencing at the 3–4 leaf stage and harvested a week after the final treatment. The treatment caused a significantly greater increase in fresh and dry weight of all parts of the plants growing in sand. (Control dry wt. roots 1·27 g, leaves 2·99 g.)

There was no effect of the treatment on the plants grown in soil, which grew to a larger size at the same leaf number (dry wt. roots 3·45 g, leaves 7·35 g).

In other experiments GA_5 was applied as microdrops to leaves of plants grown in different size pots. Plants grown in 8-in. pots of John Innes Potting Compost No. 1 were treated once with either 5 or 50 μg GA_3 at the 10-leaf stage and harvested after two or four weeks. There was an increase in root dry matter at the highest gibberellin level after two weeks (50 μg GA_3, 3·78 ± 0·83 g) compared with the control (2·97 ± 0·84 g) but this was not statistically significant; furthermore no differences in root weights at the second harvest were observed (50 μg GA_3, 20·67 ± 4·58; control 20·87 ± 4·85 g).

A positive response to applied gibberellin was only obtained when plant growth was restricted by poor growing conditions or restricted pot size. The differential response to applied gibberellin under 'poor' and 'good' growing conditions may be reflected in differences in endogenous gibberellins. Preliminary results show that the concentration of endogenous gibberellin-like substances is ten times higher (170 pg GA_3 equiv. g^{-1} fr. wt) in shoots of Sharpe's Klein Monobeet plants grown in 'Eff' compost compared with previously reported results for plants at a similar stage of development grown in sand culture (*Rothamsted Report for 1973*, Part 1, 101). (Lenton and Radley)

Endogenous growth regulators

Gibberellins. The acidic gibberellin-like compound present in leaves of Sharpe's Klein Monobeet seedlings was shown to be less polar than GA_1 when chromatographed on silica gel-impregnated glass fibre sheets using $CHCl_3$:CH_3COOH:H_2O (60 : 5 : 40, by vol.) as solvent system and using the wide range partition columns of Sephadex LH20 recently described by MacMillan and Wels (*Journal of Chromatography* (1973), **87**, 271–276). The search for other biologically active gibberellin-like compounds in sugar-beet roots has proved unsuccessful. The second substance referred to in the *Rothamsted Report for 1973*, Part 1, 101, has not been detected in seedlings. A new thin-layer chromatography system has been developed which separates $GA_{4/7}$ from abscisic acid

(ABA), a known inhibitor of gibberellin responses, but gibberellin-like activity similar to $GA_{4/7}$ has only been detected once in an extract from vernalised seed. No further gibberellins have been detected using the dwarf rice assay, which responds to a wider range of gibberellins than the barley endosperm test. Acidic hydrolysis and β-glucosidase treatment of purified butanol fractions from sugar-beet roots did not release any active substances. Relatively large scale extracts of young seedling roots, developing seeds and phloem sap collected as aphid honeydew are in the process of purification to obtain sufficient material for the isolation and identification by combined gas chromatography–mass spectrometry of the major biologically active gibberellins. (Lenton)

Cytokinins. Last year several compounds influencing cell division were found in a basic and neutral ethyl acetate fraction from leaves and roots of young sugar-beet plants (*Rothamsted Report for 1973*, Part 1, 101). A cytokinin was subsequently detected in a butanol fraction from the roots. The active compound eluted between zeatin riboside and zeatin on reverse phase columns of Sephadex LH20 using 35% (v/v) ethanol as developing solvent. The compound breaks down slowly on storage at −20°C into a non-polar but biologically active compound. The level of butanol-soluble cytokinin in leaves was much lower than that in roots and the activity was confined to compounds similar to zeatin, zeatin riboside and a more polar compound. The butanol-soluble cytokinin present in phloem sap consists mainly of the more polar compound and smaller amounts of the compound with polarity similar to zeatin. (Lenton)

Betaine. The oat-leaf chlorophyll retention assay for cytokinins was the one used to assay beet extracts for betaine. It was found that glycine, methionine and urea were ineffective in this assay at concentrations similar to those effective with betaine (10^{-2}–10^{-1}M), but chlorophyll was retained also after treatment with choline chloride, ammonium nitrate and CCC. Betaine was found to be inactive in several other cytokinin assays, i.e. anthocyanin production in *Amaranthus* seedlings, enlargement of excised radish cotyledons, and soybean callus growth. Betaine stimulates enlargement of excised sugar-beet cotyledons and also causes retention of chlorophyll in sugar-beet leaf discs.

Betaine was measured in a succession of leaves from sugar-beet plants harvested in the autumn. Every fifth leaf was taken, and the laminae were extracted by maceration. The concentration was about 9 mg g^{-1} fr. wt. in all leaves except the youngest, in which it was 20 mg g^{-1} fr. wt.

The results suggest that betaine may be involved in leaf expansion and leaf senescence. In preliminary experiments betaine has been applied to young sugar-beet seedlings but effects have only been observed with plants grown from washed seeds and not from dry seeds. (Wheeler)

Auxin. The sequence of sugar-beet leaves tested for betaine were also examined for auxins, using the wheat coleoptile section assay. An auxin which was probably indole-3-acetic acid (IAA), increased in amount per leaf with increasing leaf age (1–72 ng). The highest concentration (21 g kg^{-1} fr. wt.) occurred in the 20th leaf. Another auxin, which may be indole-acetonitrile (IAN), occurred in both acidic and non-acidic fractions. This was variable in amount, but the highest concentrations (16–17 g IAN kg^{-1} fr. wt.) occurred in the youngest leaves (30th and 35th).

An acidic inhibitor, which may be abscisic acid, was present in all leaves. The amount, measured by the wheat coleoptile section assay, was greatest per leaf in the oldest leaves, but in highest concentration in the 30th and 35th leaves.

IAA (10^{-7}–10^{-4}M) stimulates the elongation of segments cut from young sugar-beet petioles, whereas IAN does not do so up to 19 h incubation. After 43 h IAN has an effect possibly because the IAN has been converted to IAA in the detached petiole segments. This possibility is being examined. (Wheeler)

Potatoes

Investigations on the growth and metabolism of potatoes have been undertaken by a research grant and a studentship supported by the Potato Marketing Board with the objective of relating the process of tuber formation and growth to the photosynthetic activity of the plant. According to one view, tuber formation is a direct consequence of a high carbohydrate level in the stolon and after the initiation of tubers the photosynthetic activity of the plant increases in response to the increased demand for carbohydrate. An alternative view is that the formation of tubers is controlled by the balance of growth hormones. For example, treatment of leaves with gibberellins has been shown to inhibit tuber initiation even when plants are grown under short days which normally induce their formation.

The measurement of photosynthetic activity of two sets of plants of variable leaf area, differing only in the presence or absence of tubers, produced little evidence that the rate of photosynthesis was regulated by the presence of tubers. Some evidence was obtained that carbohydrates were stored in the stem and then remobilised for subsequent tuber growth. Tuber initiation was related to factors which influenced photosynthetic activity in the period prior to tuberisation and there was no marked change in hormone or enzyme activity at the period of tuberisation. The influence of day length indicates control by a hormone system but our results suggested that this operates by modifying the natural change in pattern of metabolism which accompanies plant development.

Experiments have begun in the present year to investigate the metabolic changes which result from the bruising of potato tubers. The oxidation of tyrosine and to a lesser extent of *o*-diphenols to form the brown black pigment melanin ('black spot') is indicative of marked changes in the overall metabolism of the tuber. Susceptibility to bruising depends in part on the conditions under which the tubers are grown, e.g. potassium-deficient crops are more susceptible to bruising and in part to conditions under which mechanical impact takes place, i.e. low temperatures increase the amount of bruising. The work being undertaken is aimed to determine those characteristics of the tuber which are important in controlling the degree of bruising and to consider possible means to prevent the bruising mechanism developing following mechanical impact. (Frier, McIlroy and Whittingham)

Weed biology

Classical experiments

Broadbalk. In *winter wheat* terbutryne applied in autumn controlled autumn-germinating blackgrass (*Alopecurus myosuroides*) and other species. Following a mild, damp winter the soils became severely capped in spring. Harrowing failed to break up the cap in hollows, and this and the drought discouraged spring-germinating species. Knotgrass (*Polygonum aviculare*) seedlings were stunted and black medick (*Medicago lupulina*) and scarlet pimpernel (*Anagallis arvensis*) emerged later than usual. Some germination of blackgrass occurred in spring by which time the terbutryne was no longer effective, so sprayed plots contained some plants at harvest, but they were fewer and later-flowering than on the unsprayed section.

The stubble on continuous wheat plots sprayed with terbutryne in autumn and dicamba/mecoprop/MCPA mixture in spring was again remarkably free of dicotyledonous annual weeds and many rotation plots which were also sprayed had fewer than five weed plants. Perennial weeds, especially field horsetail (*Equisetum arvense*), couch grass (*Agropyron repens* and *Agrostis gigantea*) and field bindweed (*Convolvulus arvensis*) were prevalent on all sprayed sections despite autumn spraying of continuous wheat plots with aminotriazole. Potatoes appeared in wheat plots where they were planted last two years ago.

On the unsprayed plots with higher rates of N, autumn-germinated blackgrass was so dense that it almost suppressed other weeds. The current year's crop of blackgrass seeds started to germinate on the surface of the unploughed stubble in a wet period between 11 and 15 September.

Wild oats (chiefly *Avena ludoviciana*) were hand-pulled as usual. Although less abundant than in the 1940s, persistent and thorough hand-pulling has not eradicated them. The worst infestations now are on the more fertile plots where a dense crop makes hand-roguing difficult.

In *spring beans*, the spring cultivations prevented the soil capping noted in wheat, but in May the small weed-seedlings were hidden among the clods. Black medick was more abundant in beans than in wheat, and there were many ground-keeping potatoes. Knotgrass plants were numerous but small, presumably the continued effect of spring drought. Scarlet pimpernel was more abundant in beans on plot 10 (N2 only) which is favourable to it, than in wheat.

In *potatoes*, the plots were almost weed-free in early May, even before spraying with linuron/paraquat. By mid-September, although most annual weeds were still scarce, horsetail was rampant on low-N plots, black bindweed (*Polygonum convolvulus*) on no-K plots where the potatoes were weak, and creeping thistle (*Cirsium arvense*) on plot 17 but not on plot 18 now receiving identical treatment (N2 + ½ rate PK, Na, Mg annually).

Weed-seed content of soil under different cropping regimes and with different fertilisers. Duplicate, composite soil-samples were taken from the wheat and bean stubble before ploughing on seven sections of seven plots, to see whether the introduction in 1969 of rotations (wheat/potatoes/beans and wheat/wheat/fallow) had affected the weed-seed content of the soil, compared to continuous wheat with and without herbicides. Samples were concentrated by washing and the remaining soil containing all the weed-seeds kept moist in earthenware pans in a cool glasshouse. Weed seedlings will be removed, identified and counted and the soil thoroughly cultivated at approximately six-week intervals for three years.

Up to 14 November, by which time germination of non-dormant blackgrass should be almost finished, the mean number of blackgrass seedlings per pan in the rotation wheat and bean sections was two, compared with seven for wheat in the fallow cycle, 58 for continuous wheat with herbicides and 278 for almost continuous wheat (fallowed 1963 and 1972) without herbicides. Thus repeated spraying with terbutryne had decreased non-dormant blackgrass seeds in the soil by 79% and a three-course rotation with two spring-planted crops by a further 20%.

The numbers of non-dormant blackgrass seeds in soil were also greatly affected by fertilisers given to the crop. In plots receiving PK, N0 had only eight seedlings per pan, N1 had 72 and N2 had 45, showing a similar N response to that of plant dry weights (*Rothamsted Report for 1968*, Part 2, 207). Blackgrass seedlings were most numerous (84 and 95 per pan) in two plots receiving N2PK0, where wheat yields are depressed by K-deficiency. This agrees with the results of pot experiments showing that unbalanced fertilisers favour the growth of blackgrass in competition with wheat. In a previous pot experiment (*Rothamsted Report for 1971*, Part 1, 116) blackgrass grown alone did not respond to added K.

Hoosfield. Wild oats (*Avena fatua*) were only occasional in the spring barley, from which they are hand-rogued annually, but occurred in some of the bean plots in the rotation section of the field.

After six years of constant N levels on the same quarter-plots of continuous barley, it was decided to rotate them annually starting in 1974, N0 being followed by N3, to see if crop competition would discourage weeds, especially horsetail. One of the four plots previously infested under N0 showed no change in the amount of horsetail under N3, and on the other three the density increased. A former N1 plot, receiving N0 this year, now has a small patch of horsetail not previously recorded, and another shows increased density. Apparently it is more difficult to suppress horsetail that is already present, than to prevent it from entering a plot.

The general weed scores in barley stubble, made up mainly of numerous annual species, showed clearly the pattern of this year's N application, with more weed-cover on N0 than on plots given N, although the plots previously with N would have fewer weed-seeds in the soil than those previously receiving none. Scentless mayweed (*Tripleurospermum maritimum* ssp. *inodorum* was one of the main weeds on N0 plots. Others were fluellen (*Kickxia elatine*) and groundsel (*Senecio vulgaris*). (Thurston)

Park Grass. Visual surveys have shown that liming during 1965–68 has changed the botanical composition of subplots that were previously unlimed (*Rothamsted Report for 1973*, Part 2, 67–73) but also that changes have occurred in other plots with unchanged treatments since the last hay analysis in 1949. To quantify some of these changes samples of grass were taken in June from the *c* (recently-limed) and *d* (permanently unlimed) subplots of plots given ammonium sulphate, i.e. 2, 4^2, 9, 10, 11^1, 11^2 and 18.

Subplots *d* of plots 1 (48 kg N ha^{-1} annually) and 18 (96 kg N, 225 kg K, 15 kg Na and 10 kg Mg ha^{-1}) continue to be dominated by *Agrostis tenuis* but *Anthoxanthum odoratum* has increased, particularly on 18*d*, where it contributed 17% to the yield of the first cut in 1973. On 1*c*, lime has decreased the percentage of *A. tenuis* from 84 to 20 and increased *Festuca rubra* from 3 to 49%; on 18*c* the corresponding changes have been from 83 to 52% and from less than 1 to 14%. Leguminosae (mainly *Trifolium pratense*) contribute 2% to the yield of 1*c*, and other dicotyledons 17% on 1*c*, and 6% on 18*c*. Major changes have occurred on the unlimed sections of plots 4^2 (96 N and 35 P kg ha^{-1}), 9 (96 N, 35 P, 225 K, 15 Na and 10 Mg kg ha^{-1}) and 10 (as 9 but excluding K). More than 70% of the herbage on these subplots now consists of *A. odoratum* compared to 10% on 4^2 and 10 and less than 1% on 9 in 1948–49. Recent lime has decreased *A. odoratum* on subplots *c* to 5–10%. On 4^2c, *A. odoratum* has been replaced mainly by *F. rubra*, on 9*c* mainly by *Holcus lanatus*, and on 10*c*, by both. *Poa pratensis* now contributes 7–16% to the yield of these subplots. Leguminosae, Umbelliferae and *Taraxacum officinale* contribute 10% to the yield of 9*c*; they were previously absent on this subplot and continue to be so on 9*d*. The unlimed subplots of 11^1 and 11^2 (144 kg N ha^{-1} and P, K, Na and Mg as 9) are still dominated by *H. lanatus*. Recent lime has decreased *H. lanatus* from 97 to 33% and replaced it with *Arrhenatherum elatius* (29%), *P. pratensis* (12%), *Alopecurus pratensis* (8%), *Dactylis glomerata* (6%), *Poa trivialis* (5%) and *F. rubra* (3%) and dicotyledonous weeds (1–2%). (Williams)

Biology and control of perennial weeds

***Equisetum arvense* (Field Horsetail).** Observations were continued at Woburn and Rothamsted on the trials started in 1972 and 1973 respectively (*Rothamsted Report for 1972*, Part 1, 105–106; *Report for 1973*, Part 1, 104–106). To test for residual effects of chlorthiamid at both sites, half-plots were sown with winter wheat (cv. Cappelle-Desprez) in autumn 1973 and with barley (cv. Julia) in spring 1974. At Woburn, the establishment of winter wheat on the plots treated with chlorthiamid in May 1972 was only slightly inferior to that on the rest of the site and later there was no visible difference because of increased tillering in the thinner areas; spring barley established equally well on all plots, showing that the herbicide had disappeared completely by April 1974. At Rothamsted, establishment of both winter and spring barley was severely inhibited on plots given a large amount (9·2 kg a.i. ha^{-1}) of chlorthiamid in March 1973; and was variable with the smaller amount (4·6 kg ha^{-1}).

The *Equisetum* infestation was much lighter at both sites than in the previous seasons, partly because of increased crop competition. At Woburn the plot treated with chlorthiamid remained free of the weed for the third successive season and at Rothamsted the plots treated with the larger amount of the herbicide also remained uninfested. The other chemical treatments and rotary cultivation gave little control.

Soil cores were taken at Woburn at the end of the growing season. In 1974 the dry weight of rhizomes were 42, 16, 2 and 3 g m^{-2} in the 0–25, 25–50, 50–75 and 75–100 cm depth zones compared to 192, 20, 15 and 6 in 1973. In 1974 there were 522 tubers compared to 795 m^{-2} in 1973 with a reduction from 712 to 362 between 0 and 25 cm. Tuber weights decreased from 76 to 35 g m^{-2}.

Thus *Equisetum* can be controlled by large amounts of chlorthiamid but a prolonged fallow is required before crops can establish satisfactorily afterwards. During such a fallow most of the rhizomes and tubers are formed in the plough layer so that when the land is cropped with a competitive cereal the infestation is decreased even without use of herbicide.

The growth of *Equisetum* from tubers was studied in competition with wheat in the glasshouse. Competition decreased the growth of *Equisetum* when the wheat was ripe. With a smaller amount of nitrogen (54 against 162 kg ha^{-1}) *Equisetum* dry weight was decreased from 30 g to 6 and 3 g respectively at a lower and higher crop density, and with the larger amount of nitrogen few *Equisetum* plants survived. At the lower density of wheat and with the smaller amount of nitrogen new tuber growth contributed 46% to the total dry weight compared to 16% when the weed was growing alone. Under conditions of competitive stress the species evidently partitions relatively more of its assimilate into tubers than into rhizomes.

Observations in pots indicated that the tubers formed during 1973 remained attached to the rhizomes and dormant throughout the period March–July 1974 but germinated readily when detached. The mean weight of tubers remained constant from the end of March until after the emergence of vegetative shoots in early May, so that shoot emergence is not at the expense of tuber reserves. In the field, tubers are most likely to be detached from the rhizomes by cultivations in the uppermost 25 cm; tests made in pots indicated that as many shoots were capable of emerging from tubers from 25 cm as from shallower depths. (Williams)

***Agropyron repens* and *Agrostis gigantea*.** Further experiments (*Rothamsted Report for 1972*, Part 1, 107–108 and *for 1973*, Part 1, 103–104) were done to evaluate how planting time, the type of cereal, its seed rate and nitrogen supply (none *v* 45 kg ha^{-1}) may influence the development of infestations by seedlings of *Agropyron* and *Agrostis*.

In winter wheat delaying planting of the weed seedlings until the spring almost completely prevented rhizome formation; in spring wheat and barley the effects of delaying planting by two weeks varied greatly; it decreased the rhizome weight of *Agrostis* in barley without nitrogen ten-fold but *Agropyron* in wheat given nitrogen only two to three-fold. Halving the sowing rate allowed the weed seedlings to form much more rhizome (0·85 cf. with 0·33 g m^{-2}) in spring cereals and in winter wheat given nitrogen (1·8 cf. 1·0 g m^{-2}) but had much less effect when nitrogen was not given (1·3 cf. with 1·1 g m^{-2}). Added nitrogen doubled the rhizome weight of *Agropyron* but halved that of *Agrostis* at both seed rates in winter wheat, but in the spring cereals it usually markedly decreased rhizome weight except for *Agropyron* in thinly-sown wheat, which is greatly increased. Nitrogen often had a differential effect on shoot and rhizome growth: for example, although it halved rhizome growth of *Agrostis* in winter wheat, and *Agropyron* in spring wheat, it greatly increased shoot growth in both instances. (Williams)

Blackgrass (*Alopecurus myosuroides*)

Germination

Effect of fertilisers applied to parent plant. No further germination occurred in pans of seed from the 1971 pot experiment (*Rothamsted Report for 1971*, Part 1, 115–116) so the results can now be summarized.

Seeds germinating before the end of 1971 were classed as non-dormant. The rates and combinations of N, P and K given to the parent plants had no great effect on viability or dormancy of the seeds produced. Viability in individual treatments was 75–82% of the seeds sown. Treatment-means for viability were within 4% of each other, and dormant seeds were only 12–16% of those sown, but in individual treatments dormancy ranged from 8% in N4P2K0 to 23% in N2P0K2, showing no regular trends in response to fertilisers.

Interaction of crop competition with fertilisers given to the parent plant. Scarcely any germination occurred in 1974 in pans of seeds from the 1972 pot experiment (*Rothamsted Report for 1972*, Part 1, 104–105). The greatest total was only 16% (blackgrass alone with P2N2) so treatment-differences would not show up clearly. However, germination was slightly less where P was given and when blackgrass competed with wheat rather than other blackgrass plants.

Effect of fertilisers and crop competition on plant growth. The pot experiment described in *Rothamsted Report for 1972*, Part 1, 104–105, was repeated but with winter wheat var. Cappelle-Desprez sown on 2 November 1973. The object was to see if autumn-sown plants which represent probably two-thirds of the total population responded in the same way as spring-sown to fertilisers and competition. Comparison with the results of the spring-sown experiment (*Rothamsted Report for 1972*, Part 1, 105) shows that both blackgrass and wheat are heavier at all levels of fertiliser and on both harvest dates (8/9 April; 7 July) after the longer growing-period following autumn sowing, but this is more obvious in April than later.

Responses to N and P follow the same pattern as before. (Thurston)

Staff and visiting workers

T. O. Pocock joined the department to investigate the effect of growth regulators in relation to the sugar-beet crop. He replaced Dr. J. F. Garrod, who left to undertake work in a commercial agricultural chemical research laboratory. P. Hoskin left the department to join ADAS and P. J. Dawson returned to university as a full-time student for a higher degree. The work on pollution is now being undertaken by M. A. Parry and Alison Brough. The work on the physiology of potatoes supported by the Potato Marketing Board has been reduced following C. J. Taylor's appointment to a post at the University of the Witwatersrand, Johannesburg, and Vivienne Frier to a post at Imperial College, London. D. W. Lawlor has spent one year at the University of Trier-Kaiserslautern, Germany, studying some aspects of photorespiration in relation to drought.

Sandwich students who worked in the department were Stephen Hall, Tony Keevan, Stella Roberts, Malcolm Rodger and Christina Tyson.

Short-term visitors to the department included Mr M. Zima, a British Council East Europe Exchange Scholar from the Department of Plant Biology, University of Agriculture, Nitra, Czechoslovakia, who is spending six months studying the photosynthesis of crop plants.

C. P. Whittingham attended the 37th Winter Congress of the Institut International de Recherches Betteravieres in Brussels and took the Chair at the Physiology Symposium. Together with S. Kumarasinghe he also attended the 3rd International Congress on Photosynthesis in Israel.

A. J. Keys attended the FAO/IAEA discussion meeting in Vienna concerning the use of tracer techniques in plant breeding.

Joan Thurston was present at the 12th British Weed Control Conference at Brighton and organised an informal session of the Annual Grass Weeds Group of the European Weed Research Council.

R. W. Soffe at the invitation of the NFU attended the Vienna International Horticultural Exhibition in April and assisted in arranging a display of fruit, flowers and vegetables, for which the NFU received the Salzburg award.

Publications

BOOK

1 WHITTINGHAM, C. P. (1974) *The mechanism of photosynthesis.* London: Edward Arnold, 125 pp.

GENERAL PAPER

2 WELBANK, P. J. (1974) Soil conditions affecting root distribution. In: Soil type and land capability. Ed. D. Mackney. *Soil Survey Technical Monograph* No. 4, 91–98.

RESEARCH PAPERS

3 GARROD, J. F. (1974) The role of gibberellins in early growth and development of sugar beet. *Journal of Experimental Botany* **25**, 945–954.

4 KEYS, A. J. (1973) Biochemical aspects of the conversion of inorganic nitrogen into plant protein. In: *Biological efficiency of protein production.* Ed. J. G. W. Jones. 69–82.

5 LEE, R. B. & WHITTINGHAM, C. P. (1974) The influence of partial pressure of CO_2 upon carbon metabolism in the tomato leaf. *Journal of Experimental Botany* **25**, 277–287.

6 THOMAS, S. M. & THORNE, G. N. (1975) Effect of nitrogen fertiliser on photosynthesis and ribulose 1,5-diphosphate carboxylase activity in spring wheat in the field. *Journal of Experimental Botany* **26**, 87–97.

7 WAIDYANATHA, U. P. DE S., KEYS, A. J. & WHITTINGHAM, C. P. (1975) Effects of oxygen on metabolism by the glycollate pathway in leaves. *Journal of Experimental Botany* **26**, 100–106.

8 WAIDYANATHA, U. P. DE S., KEYS, A. J. & WHITTINGHAM, C. P. (1975) Effects of carbon dioxide on metabolism by the glycollate pathway in leaves. *Journal of Experimental Botany* **26**, 106–110.