ROTHAMSTED RESEARCH

Report for 1980 - Part 1

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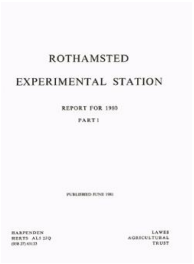

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Introduction

Vacancies arising by the resignation of several members of staff have been reassigned to the extended research programme on photosynthesis. This programme has been given national priority by the Agricultural Research Council and in future we intend to increase the proportion of our resources applied to research on photosynthesis at the molecular, biochemical and physiological levels. Unfortunately this transfer of posts has made two of the existing research programmes no longer viable. Thus, the present year is the last in which any work will be undertaken on the effects of aerial pollutants on arable crops. The previous 5 years' work had established a frequent significant yield loss but further investigation of the problem would require an extended and more fundamental approach. In addition the small programme of work on potato crop physiology, started 3 years ago, is to be discontinued.

The Department is continuing its long-term interest in studies of the crop physiology of cereals and sugar beet and is also contributing to the multidisciplinary investigations to study the factors which limit yield of cereal crops. That part of the work in which P. J. Welbank is collaborating is reported in the Report of the Soils and Plant Nutrition Department (p. 243).

Following the retirement of Miss J. M. Thurston work on weed biology has now been discontinued at Rothamsted; much of the work is now incorporated into the programme at the Weed Research Organisation.

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Studies on photosynthesis

RuBP carboxylase/oxygenase. A more extensive purification procedure for RuBP carboxylase/oxygenase from leaves has been developed. Protein precipitating between 35 and 55% saturation with ammonium sulphate was dissolved in buffer and layered on to sucrose gradients in cellulose nitrate tubes. The tubes were centrifuged at 215 000 *g* (av.) in an angle rotor for 2·5 h (Ellis, *Trends in Biochemical Sciences* (1980), **4**, 241–244) and the enzyme recovered from the sucrose gradients and chromatographed on a DEAE Sephacel column. Fractions containing the enzyme were desalted and freeze-dried from buffered 1 mM-dithiothreitol (Machler, Keys & Cornelius, *Journal of Experimental Botany* (1980), **31**, 7–14). Up to the commencement of freeze-drying the purification took 30 h. In the solution before freeze-drying gel electrophoresis confirmed that the RuBP carboxylase/oxgenase was essentially free from other proteins. After freeze-drying the specific activity of the protein was unchanged although additional protein species were present in small amounts. Whilst the specific activity increased during the first stages of purification from wheat and barley, it subsequently declined; similar changes in specific activity during purification from spinach leaves were observed by Andrews, Lorimer and Tolbert (*Biochemistry* (1973), **12**, 11–18). Although the final specific activity of our most active preparations was 0·9 mol mg^{-1} protein min^{-1}, we believe this to be less than the maximum value obtainable. The freeze-dried enzyme from wheat required 3–5 h incubation with Mg^{2+} and CO_2 at 25°C and pH 8·2 to reach maximum activity. Addition of thiols to the solution used to activate the enzyme or a change in pH did not shorten the time required for full activation. Raising the temperature during activation to 45°C gave maximum activity in 25 min and the specific activity attained was greater than that achieved at 25°C. A comparison has been made of the relative affinity for CO_2 and O_2 of RuBP carboxylase/oxygenase from various crops and other plant species including carboxylases from diploid and tetraploid ryegrasses reported to have widely different K_m (CO_2) values (Garrett, *Nature, London* (1978) **274**, 913–915). No significant differences between the K_m (CO_2) values were found. The carboxylases from wheat, barley, sugar beet, potato, sunflower, cress and ryegrass all have K_m (CO_2) values between 10·5 and 14·4 μM. These values were arrived at by a computer calculation based on the statistical method of Wilkinson (*Biochemical Journal* (1961), **80**, 324–332). Standard errors were small for individual estimates but occasion to occasion variation was such that we cannot yet be certain that the K_m (CO_2), for example, of barley carboxylase, which was usually estimated to be near to 10·5 μM, is truly different from the K_m (CO_2) of ryegrass which was usually nearer to 14·4 μM. Our measurements of sensitivity to oxygen do not suggest any major variation between the different enzymes studied. With a view to investigating whether larger differences in K_m (CO_2) exist, experiments with enzymes from species other than agricultural crops are to be initiated. (Bird, Cornelius and Keys)

Inhibition of RuBP carboxylase from wheat with pyridoxal phosphate. Paech and Tolbert (*Journal of Biological Chemistry* (1978), **253**, 7864–7873) reported that pyridoxal phosphate inhibited RuBP carboxylase from spinach by reacting first with eight lysyl residues at the catalytic site resulting in up to a 90% decrease in activity. In a second slower phase a further eight lysyl residues could be substituted, probably at the activating site, after which the enzyme became totally inactive. With carboxylase from wheat leaves there was an initial phase in which ten molecules of pyridoxal phosphate were added with the loss of 85% of the activity. In a slower second phase, a further 20 pyridoxal phosphates were added and decreased the activity by a total of 95%. Thus more pyridoxal residues were required for wheat than for spinach and complete inhibition was not attained. Pyridoxal phosphate reacted more rapidly with the enzyme from wheat when it was fully activated

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in solution with Mg^{2+} and CO_2. However, Mg^{2+} and CO_2 should compete with pyridoxal phosphate in the second phase of inhibition if this involves the activating site. (Holbrook)

Photosynthesis by protoplasts and chloroplasts. To investigate biochemical factors limiting the rate of photosynthetic carbon metabolism, studies have been made using protoplasts and chloroplasts from young barley and wheat leaves. In particular, we re-investigated whether the affinity for CO_2 of intact systems was greater than that of the RuBP carboxylase isolated from them. We confirmed the finding (Robinson, McNeill & Walker, *FEBS Letters* (1979), **97**, 296–300), that the carboxylase activity which is released when chloroplasts are ruptured is more than sufficient to account for rates of CO_2 assimilation by intact chloroplasts and protoplasts. The affinity for CO_2 of the leaf proved more difficult to estimate because of variable kinetics but measurements indicated that affinities were not significantly greater than for the purified carboxylase. Future studies will seek to establish the potential specific activity of the carboxylase in chloroplasts and whether effects of oxygen on photosynthesis by protoplasts and chloroplasts can be wholly accounted for by effects on the carboxylase. (Thomas and Holbrook)

Effects of temperature on photosynthetic and photorespiratory metabolism. Studies have continued to examine why decreased oxygen concentrations fail to stimulate photosynthesis at lower temperatures in detached wheat leaves. Measurements of the relative distribution of radioactivity in products of photosynthesis from $^{14}CO_2$ (*Rothamsted Report for 1978*, Part 1, 39–40) showed increased activity of hexose monophosphates at decreased temperatures. The increase was especially marked at 5°C when the CO_2 concentration was increased from 320 to 380 vpm. Treated leaf samples were freeze-dried, finely ground and fractionated into chloroplast rich and chloroplast depleted samples by centrifugation in non-aqueous solvents (Stocking, *Plant Physiology* (1959), **34**, 56–61). Glucose-6-phosphate and fructose-6-phosphate were estimated by specific enzyme methods; total phosphate and orthophosphate were estimated colorimetrically and the relative distribution of the phosphates between the chloroplasts and the rest of the cell calculated (Heber & Willenbrink, *Biochimica et Biophysica Acta* (1974), **82**, 313–324). The amounts and distributions of orthophosphate and of total phosphate were not significantly affected by temperature. When the temperature was decreased and CO_2 concentration raised the increase in absolute amounts of hexose phosphates occurred in both chloroplast and nonchloroplast fractions of the leaf. Thus the increase was not caused by slow transport of phosphate esters from the chloroplasts. Irrespective of temperature and CO_2 concentration, the ratio of glucose-6-phosphate to fructose-6-phosphate in the chloroplast was different from that in the rest of the cell suggesting a highly active phosphohexose isomerase in the cytoplasm that established equilibrium but a less active enzyme in the chloroplast that was insufficient to ensure equilibrium. Preliminary studies of the concentration of ribulose bisphosphate in leaves did not suggest that decreased regeneration of this compound from hexose phosphates caused the latter to be increased in concentration at 5 and 10°C. We conclude that the rate of conversion of hexose phosphates to sucrose probably became rate-limiting at low temperatures. (Arrabaca)

CO_2 compensation concentration (Γ) of ryegrass cultivars. Garrett (*Nature, London* (1978), **274**, 913–915) observed differences in air between isogenic diploid and tetraploid ryegrasses and between diploid and tetraploid non-isogenic cultivars. Tetraploids had a lower CO_2 compensation point (Γ) than diploids (52 compared to 62 μl CO_2 l^{-1}); and this was associated with a smaller rate of CO_2 release in the post-illumination burst, a lower K_m for CO_2 of RuBP carboxylase and a lower K_i for CO_2 in the RuBP oxygenase

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reaction. Because of the importance of these observations and the value of such genetically related but physiologically contrasted material, we obtained material from Dr Garrett and attempted to confirm the original observations.

Excised ryegrass shoots, consisting of a fully expanded and an expanding leaf and 1·5 cm of green leaf base/sheath were sealed with the cut end in water in a glass photosynthesis chamber. Leaves were arranged to avoid self-shading. The chamber was connected to an infrared gas analyser and air circulated through a closed circuit system. Water vapour was removed with magnesium perchlorate. An absorbant for CO_2 could be switched into the system so that Γ could be measured from increasing as well as decreasing CO_2 concentrations. Illumination was by Quartz halogen lamps.

Temperature markedly affected Γ. For cultivars 2837 and 4617 (respectively low and high Γ) it increased from 25μl CO_2 l^{-1} at 15°C to 38 μl CO_2 l^{-1} at 20°C and 53μl CO_2 l^{-1} at 28°C. The tetraploid (640–38–1–312) and diploid (640–38–50–308) also gave similar values at these temperatures. Irradiance influenced Γ. At 20°C and with irradiance less than 150 μE m^{-2} s^{-1} (photosynthetically active radiation), no steady state concentration was attained but Γ was 40 μl CO_2 l^{-1} at 350 μE m^{-2} s^{-1} and remained almost constant up to 800 μE m^{-2} s^{-1}. At 10°C Γ was again not measurable below 25 μE m^{-2} s^{-1} but from 25 to 350 μE m^{-2} s^{-1} was 30 μl l^{-1}; at still greater irradiance it was 25μl l^{-1}.

Values of Γ of 50–60 μl CO_2 l^{-1} were measured at 30°C and irradiance of 350 μE m^{-2} s^{-1} or more; again at lower irradiance no steady state was attained. There were no significant differences in Γ in response to light and temperature between cultivars. For No. 4993 (alleged high Γ) and No. 1572 (alleged low Γ), the values (averaged over all irradiances above 350 μE m^{-2} s^{-1}) were $35{\cdot}2 \pm 2{\cdot}1$ and $37{\cdot}6 \pm 3{\cdot}5$ μl CO_2 l^{-1} respectively. The mean values for isogenic tetraploid and diploid lines were $36{\cdot}5 \pm 2{\cdot}9$ and $41{\cdot}6 \pm 3{\cdot}3$ μl CO_2 l^{-1} at 20°C and irradiance greater than 350 μE m^{-2} s^{-1}.

Repeated measurements made at 20°C and 800 μE m^{-2} s^{-1} failed to show consistent differences between the strains; the mean was 35 μl with a range of 33–41 μl CO_2 l^{-1}. The failure to attain steady state conditions at lower irradiances and at all temperatures has not been explained but changes in dark respiration are probably involved. It is possible that desiccation, which causes a rapid rise in Γ, may be important and result from a low chamber humidity. The ploidy levels of the cultivars were not checked. (Lawlor and Young)

Effects of respiratory substrates upon CO_2 compensation concentration (Γ) of barley. Oliver and Zelitch (*Plant Physiology* (1977) **59**, 688–694) reported that tobacco leaves fed with glutamic acid had a lower rate of photorespiration than those fed with water only. In previous work on water-stressed sunflower leaves (Lawlor & Fock, *Journal of Experimental Botany* (1977), **28**, 320–328) it was suggested that when the net fixation of carbon was small sucrose might be used as a substrate for photorespiration. A preliminary examination of the effects of some intermediates on photorespiration was made, using the compensation concentration as an indicator of change in the relative rates of photorespiration and photosynthesis.

Shoots of 3–4 week old barley (cv. Magnum) consisting of the second (mature) leaf and emerging third leaf, were placed with the cut end in either water, 0·1 M-sucrose, 0·1 M-glyoxylate or 0·1 M-glycine. Plants were kept at 20°C in the light (800 μE m^{-2} s^{-1}) and normal atmosphere and the effect of length of time of exposure to the solution measured.

Treatment with sucrose significantly increased Γ; averaged over all determinations, Γ was 39·8 μl CO_2 l^{-1} in water and 46·6 μl CO_2 l^{-1} in sucrose. The increase was detectable after 2 h exposure to the solution and persisted for 24 h. Neither treatment with glycine nor glyoxylate resulted in a significant change in Γ. The possibility that mitochondrial respiration is stimulated by sucrose remains to be examined. (Lawlor and Young)

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Barley mutants. We have sought mutants of barley defective in specific enzymes of photorespiratory metabolism using a screening procedure previously used successfully for selection of mutants of *Arabidopsis thaliana* (Somerville & Ogren, *Nature, London* (1979), **280**, 833–835; *Nature, London* (1980), **286**, 257–259). Seed (cv. Maris Mink), was provided by the Biochemistry Department after treatment with the mutagen sodium azide. It was grown in a constant environment room in a CO_2-enriched atmosphere. After 3 weeks mutants with pigment and other defects were discarded. Then the CO_2 concentration was decreased to 300 vpm and plants which failed to grow satisfactorily were marked and immediately or later returned to CO_2-enriched conditions. Those that recovered were propagated vegetatively by tiller cuttings and allowed to produce seed. From an original total of 18 176 seedlings, nine mutants that grew reasonably well in >1000 vpm CO_2 but not in 300 vpm CO_2 were selected. Of these nine plants, five lines have survived. Study of the distribution of radioactivity in products of photosynthesis in $^{14}CO_2$ did not suggest any major defect in enzymes directly involved in photorespiration. Also, measurements of glutamine synthetase and GOGAT activity and of ammonia concentrations in the leaves, did not indicate any impaired ability to re-utilise ammonia produced by photorespiration (*Rothamsted Report for 1978*, Part 1, 40–41). Recently we have obtained evidence that one mutant has a low catalase activity and another, showing rather a similar pattern of radioactivity distribution probably accumulates an oxidant in normal air, perhaps indicating a defect preventing destruction of superoxide radicals in the chloroplasts. (Kendall and Keys, with Lea, Biochemistry Department)

Tracer experiments and compartmental modelling in analysis of plant metabolism. Radioactive carbon is used as a tracer to measure fluxes of carbon between storage and grain in cereals or to estimate the contribution of assimilation by particular leaves to storage or to grain filling.

We have examined this approach as it is applied to complex systems to determine whether the flux of carbon can be accurately deduced from the behaviour of tracer alone. Experimentally the distribution with time of radioactivity within the plant is readily measured but it is often difficult or impossible to measure the specific activity of the substance being transported.

The differential equations describing material fluxes are non-linear whereas those for specific activity are linear. The flux of material between pools can be estimated only if both the amount of tracer and total pool size are known or if the rate of movement and the specific activity of the material being transported are known. Only then can the true fluxes be calculated accurately. As the system becomes more complex interactions become important and the amount of information required for a full analysis increased. Measurements of the distribution of radioactivity alone provides only qualitative estimates of the material fluxes, together with accurate estimates of the time at which fluxes occur. (Lawlor, with Pearlman, Statistics Department)

Cereals

Development of winter wheat. The correct timing of application of nitrogen fertiliser, as well as of growth regulators and weedkillers, requires a knowledge of crop development (*Rothamsted Report for 1979*, Part 1, 41). Little is known about how development is affected by the early sowing that is becoming common, or how it is controlled in the field by environmental factors. Development of the varieties Maris Huntsman and Hustler sown on five dates between 20 September and 15 November 1979 was studied on small plots next to the multifactorial experiment assessing factors limiting yield (p. 18). Sowings made in and after December unfortunately failed to establish.

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The two varieties behaved similarly. The difference of 56 days between the first and last sowing resulted in a difference of 91 days in emergence, 53 days in reaching 'double ridges' (ear initiation), and only 8 days in anthesis. Tillering always ceased close to the date of reaching double ridges. A mechanistic model using standard meteorological observations was developed that accounted for the timing of emergence, double ridges and anthesis in these crops and in 15 other crops of Maris Huntsman grown at Rothamsted and Sutton Bonington between 1974 and 1979. Development was shown to depend principally on temperature, vernalisation and photoperiod. (Gallagher, Taylor and Thorne)

Factors determining grain size and number in wheat. The response to removing the top half of the ear 5 days after anthesis was used to estimate the potential capacity of ears to accumulate assimilates. In field experiments in 1979 this treatment increased dry weight per grain by 23% in ears of the semi-dwarf varieties Hobbit, Hustler and Sentry and the taller varieties Flanders and Armada. Grains in ears of Maris Huntsman increased negligibly, as in previous years (*Rothamsted Report for 1979*, Part 1, 41). In the semi-dwarf varieties, but not in the taller ones, halving ears also increased the number of grains in the lower half of the ear. So semi-dwarf varieties, which usually have more grains per ear than tall varieties, have the potential to set still more. Nitrogen content of the grain in the lower ear was increased by halving similarly in all varieties, including Maris Huntsman, and relatively more than dry matter (DM). Hence the movement into the grain of nitrogen and carbohydrate may be controlled independently. The lower grains absorbed most of the nitrogen that was normally absorbed by the upper grains; uptake of nitrogen into the shoot between anthesis and maturity was unaffected by halving the ear.

These results suggest that the frequent observation of inverse correlations between increasing DM per grain or nitrogen percentage DM and the number of grains per ear are not inevitable. (Thorne)

Factors controlling barley grain size. Differences in temperature are often held responsible for differences in barley grain size between seasons and districts. To quantify the effect of temperature on grain size, buckets containing 9 kg of dry soil and peat and 12 spring barley plants (cv. Porthos) were transferred at awn emergence from a glasshouse to controlled environment rooms set at the following 18 h day/6 h night temperatures: 13/7, 17/11, 21/15, 25/19°C. These temperatures span the range experienced from a cool summer in Scotland to a hot summer in South-east England. The relative humidity was 70% giving vapour pressure deficits of 0·20, 0·54, 0·77 and 0·93 kPa. The plants were exposed to irradiance of either 560 or 380 E m^{-2} s^{-1} (bright or dim) equivalent to either a bright or a dull summer. Plants in each treatment were irrigated either with an amount of water equal to the evaporative loss from well-watered pots or with half that amount (wet and dry). Harvests were taken at intervals of 100 degree days (°C d) when the DM and green area of plant parts were measured. The pattern of increase in the mean mass per grain of main stem ears was studied using logistic curves.

Warm temperatures decreased the numbers of grains per ear but the effect was significant only on tiller ears. Mean mass per grain decreased linearly from 49 mg at 13/7°C to 36 mg at 25/19°C, a rate of decrease of roughly 1 mg $°C^{-1}$. Analysis showed that this was associated with a significant and linear increase in development rate with temperature that was compensated for only partially by an increase in grain growth rate. Extrapolation indicated a base temperature of about 2°C for development rate. The results suggest that grain growth rate is a quadratic function of temperature, grain growth ceasing at about 2°C and reaching a maximum rate at about 30°C.

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Dim light decreased mass per grain by about 4 mg due to a slightly slower growth rate and a slightly faster development rate. There was an interaction with temperature, the effect of dim light being much greater at 17/11 and 21/15°C than at cooler or warmer temperatures. The dry treatment increased the distance from the flag leaf ligule to the collar of main stem ears, an effect typical of drought in the field. Otherwise dryness only decreased the number and dry mass of late tillers. (Gallagher and Pearman)

Effect of glume removal on wheat grain development. It was reported (*Rothamsted Report for 1979*, Part 1, 45) that grain growth was much reduced when the glumes and lemmas were removed. To test whether this effect was due partly to desiccation after removal of the grain's protective covering, deglumed ears were enclosed in either clear or black plastic bags. The water content and DM increase of the grains were similar to those of unprotected grains with the lemma removed. In other experiments the reduced growth of the grain in the third floret of the spikelet, after removal of its subtending lemma, was partly or wholly reversed by removal of the grains in the two lowest florets of the spikelet. These results suggest that it is not desiccation but a decreased uptake into the grain which is affected by glume removal. (Radley)

Pre-harvest sprouting susceptibility. The grains of wheat cultivars susceptible to pre-harvest sprouting have been claimed to contain more indoleacetic acid (IAA) than resistant cultivars. The free form of IAA was present in larger amounts in Hustler (susceptible) than in Hobbit (resistant) as ripening commenced but decreased to trace amounts in both cultivars when they were almost ripe. A bound form of IAA subsequently increased for a short time in both cultivars but to a greater extent in Hustler. Similar and constant amounts of tryptophan were found in both cultivars, a transient increase occurring in both at the same time as the increase in bound IAA. (Radley)

Grain growth in cultured wheat ears. Grain growth and development is being investigated under defined nutritional and environmental conditions using a detached wheat ear culture technique (Donovan & Lee, *Plant Science Letters* (1977), **9**, 107–113). Initial experiments with the awned spring wheat, cv. Highbury, grown on a medium containing filter-sterilised L-glutamine as a nitrogen source showed a similar pattern of DM accumulation to that of intact plants but premature awn senescence. The latter could not be reversed by addition of 6 benzylaminopurine (10^{-6}M) to the culture medium. Replacement of L-glutamine with inorganic nitrogen gave a similar pattern of DM accumulation and improved grain water balance without premature senescence. It was adopted as the nitrogen source for the basal medium.

Intact plants of spring wheat, cv. Highbury (awned) and Sicco (awnless), were grown in controlled environments under the same temperature conditions (18·2° day/13·4° night) as detached ears. Grain DM accumulation was identical (1·4 mg d^{-1}) in intact and detached ears of Highbury from 12 to 30 days after anthesis. Grain from intact ears of Sicco grew at the same rate as those from Highbury but from detached ears at a slower rate (1·1 mg d^{-1}). Grain water content reached a similar broad optimum (23 days post-anthesis) in intact plants of both varieties. Grain of detached ears of Highbury accumulated water at a faster rate for a longer period whereas grain of detached ears of Sicco ceased accumulation sooner than grain of intact plants. The lack of awns in Sicco may have reduced water and nutrient uptake in detached ears resulting in slower grain growth. Removal of the awns of Highbury made the grain growth pattern closer to that of Sicco. The calcium content, taken as a measure of water uptake, was similar in grains of intact and detached ears of Highbury but removal of awns reduced grain calcium content particularly in detached ears.

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The functional significance of the accumulation of auxin and gibberellins in developing wheat grains (*Rothamsted Report for 1979*, Part 1, 45–46) is being investigated by the detached ear culture method in an attempt to separate the effects of growth substances and assimilate supply on grain and development. The auxin content, determined as indole-α-pyrone, of grain from intact and detached ears of Highbury showed a similar pattern of increase over the initial period of accumulation (23–30 days post-anthesis) but was greater in grain from intact than detached ears. Other experiments showed an increase in grain auxin in detached ears at the onset of senescence. The gibberellin content of grain of intact and detached ears of Sicco showed a similar pattern of accumulation and decline of biologically active compounds over the period 16–30 days post-anthesis. It would appear that grains of detached ears are capable of independent gibberellin synthesis but that tryptophan released from senescing tissues may alter the pattern of accumulation of free and bound auxin in grains of intact and detached ears. (Lenton and Radley)

Aerial pollution and barley growth. During the last 8 years the growth and yield of barley grown in carbon filtered and ambient field air has been compared at sites around the brickworks in the Marston Valley, Bedfordshire. A similar experiment to that at Thrupp End in 1979 (*Rothamsted Report for 1979*, Part 1, 40) was repeated in 1980.

The mean level of sulphur dioxide during the growing period was 52 $\mu g\ m^{-3}$; the highest concentrations of SO_2 occurred between the emergence of the plants and the onset of tillering and just before anthesis. The mean level of fluoride was 0·15 $\mu g\ m^{-3}$ (0·13 gaseous and 0·02 $\mu g\ m^{-3}$ particulate fluoride) and the pattern of peak concentrations closely followed that of SO_2. The pollutant concentration in the filtered chambers was 37% of that in the unfiltered chambers whilst the concentration in the unfiltered chambers was 92% of that outside.

The yield of plants grown in the chambers was lower than that of plants grown in the open and their development was accelerated by 7–8 days. The most important factor in reducing grain and straw yield was the reduction in tiller number in the chambers. However the mass per grain was 16% heavier in the chambers thus partly compensating for the reduced number of ears. The reduction in tiller number may be due to increased apical dominance resulting from the slightly higher temperature in the chambers.

TABLE 1

Effect of filtration and open-topped chambers on yield and fluoride content at maturity

	Ears (m^2)	Straw dry wt ($g\ m^{-2}$)	Grain wt ($g\ m^{-2}$)	1000 Grain (wt g)	Grains per ear	F Content ppm by wt
Filtered chambers	715	569	560	42·4	18·9	29
Unfiltered chambers	709	475	518	42·0	17·4	43
Unenclosed plots	955	675	631	35·0	19·1	111

At anthesis and maturity straw dry weights were substantially greater (17%) in the filtered compared to unfiltered chambers whilst grain yield, 1000 grain weights and grain number per ear were also greater although the increase was not significant.

These results are consistent with our earlier experiments. A main effect of the chambers (filtered or unfiltered) is to reduce yield by reducing tiller production and ear number. This contrasts with the effect of filtration which has little effect on ear number but increased yields by increasing the size of the shoots and grains. Thus, whilst frequently in our experiments the yield of barley grown in carbon filtered air in chambers has been less than that of a crop grown in the field, the characteristic effect of the chambers and filtration has been on different yield components. We suggest that the difference observed

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between filtered and unfiltered chambers indicates a specific effect of aerial pollutants on grain growth. (Buckenham, Parry and Young)

Sugar beet

Temperature and leaf development. Leaf development and growth is being studied in controlled environments and in the field. During the last three seasons (1978–80) the times of appearance and the rates of expansion of individual leaves were measured on the crop productivity study areas at Broom's Barn and the influence of temperature, water and nutrients examined. In 1978, three crops were sown on 7 April, 24 April and 18 May. Early in the season there were considerable variations in the weekly mean air temperatures which allowed comparison of the growth of leaves when they were produced at similar positions on the plant but initiated or expanded at different temperatures.

The two crops sown in April grew slowly at first and by mid-July had reached a leaf area index (L) of between 2·0 and 2·4, and early in August L had reached 3·3. Leaf growth of the May-sown crop was slower and by mid-July L was only 0·5, but between mid-July and mid-August leaf area expanded rapidly and from then until October all three crops maintained an L of more than 3·0. The differences in rates of formation of leaf canopy produced differences in the quantities of radiation intercepted by the crops and consequently in their yields of total DM and sugar (*Rothamsted Report for 1978*, Part 1, 64).

By mid-July plants of the two earliest-sown crops had 21 and 23 leaves respectively and plants of the May-sown crop, 19 leaves. When harvested in October plants from the early, middle and late sowings had 48, 49 and 44 leaves respectively. In the constant conditions of controlled environments, leaf appearance was shown to be linear with temperature above 2°C (*Rothamsted Report for 1979*, Part 1, 46–47). Leaf appearance in the field was also linear with accumulated thermal times (°C d) above the base temperature of 2°C but the rates of appearance of early and late leaves were different. Each leaf up to leaf 20 required 26°C d to be accumulated before it unfolded from the apex and the requirement was the same for all three crops. More thermal time was needed before each subsequent leaf appeared; in the two April-sown crops 36°C d were required and in that sown in May, 43°C d. Thus, accumulated temperature accounted for much of the variation in rates of leaf appearance within the season.

L depends on how fast, long and large individual leaves grow and how long they survive. The areas of leaves successively produced by the three crops increased until the twelfth leaf and thereafter decreased. Leaves grew larger because they grew faster and not because they continued to expand for a longer time. Averaged over the whole of their growth, leaves up to the twelfth expanded at increasing rates from 5 to 16 $cm^2\ d^{-1}$ but the time taken by all to complete their growth was 27 ± 2 days. This progression in rate of expansion and size of successive leaves must be controlled by factors within the plant such as size of the leaf primordia and competition between them for assimilate, mineral nutrients, hormones and space on the growing apex.

The fifth to twelfth leaves of the crop sown on 24 April were smaller than those of the crop sown on the 7 April and subsequent leaves were larger. By contrast, leaves up to the sixth were larger in the crop sown on 18 May than that sown on 7 April, leaves 8–14 were smaller and subsequent leaves were again larger. There was no obvious evidence that the differences between crops in rates of expansion of these leaves was caused by differences in temperature during the main period of their expansion as these varied by only 2–3°C and not consistently with changes in rate. Variations in temperature when leaves are being initiated seem more important in determining final sizes of sugar-beet leaves than temperature differences during expansion (*Rothamsted Report for 1978*, Part 1, 46). Differences in the final sizes of comparable leaves in the three crops grown in 1978 were

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highly correlated with the mean air temperatures under which they were initiated. Leaves of the crops sown on 24 April and 18 May were 30% smaller than their counterparts in the 7 April crop when they were initiated at temperatures 1–2°C lower, and 50% larger when they were initiated at temperatures 2–3°C warmer. (Milford)

Root growth and sugar accumulation. Sugar-beet crops can partition their DM differently, so that the amount of sugar produced from similar amounts of radiation intercepted varies. The partitioning of DM within cells between sugar and non-sugar components was measured in roots from the two main treatments of the Crop Productivity Group's 1979 study area at Broom's Barn: namely, nitrogen applied at 125 kg ha^{-1} with irrigation; and no additional nitrogen or irrigation. The relationship between water content, sugar content and residual DM per cell all with cell volume was determined in July, August, September and November.

Water content per cell was linearly related to cell volume with no difference within a treatment although cells from the irrigated treatment had more water per unit volume. Residual DM per cell (i.e. after extraction with 80% ethanol) constitutes mainly cell wall material and was more related to cell surface area than volume. Estimated cell wall thickness increased with volume to a maximum at a cell volume of $40–50 \times 10^4$ μm^3 thereafter remaining constant. Cells from the nitrogen treatment consistently had thinner walls for a given cell volume except in November when wall thickness increased. The relationship between cell volume and sugar content per cell was curvilinear. The linear coefficient of a fitted quadratic regression can be used as a measure of the potential sugar storage capacity of the cell and the largest values observed for plants grown in a range of conditions are between 2·0 and 2·5 ng sucrose 10^4 μm^{-3}. However, early in the season only the smallest cells had accumulated sugar to this extent. As the season progressed, more of the larger cells accumulated sugar to their potential capacity and by November all cells had achieved it, so the relationship between sugar content and cell volume became linear. Because water content was also linearly related to cell volume this maximum sugar storage capacity represents a maximum fresh weight concentration of sucrose within the cell of 21–23%.

Giving additional nitrogen produced less total DM per cell within the root even though shoot and root weights were increased. This implies that there were more root cells competing for assimilate which resulted in thinner walls and a slower accumulation of sugar except in November when shoot growth had ceased and more assimilate was available to the root. Then cell wall thickness increased and cells accumulated sugar to maximum capacity. Despite the competition between cells for assimilate, partitioning between sugar and non-sugar components was constant in all but the smallest cells from August onwards.

The pattern of sugar accumulation within cells and the level at which partitioning between sugar and non-sugar becomes constant may reflect a balance between assimilate supply to the root and competition within the root for that assimilate (determined by both cell numbers and rate of cell expansion). The maximum potential storage capacity of the cell may be determined by its osmotic status and involve other osmotically-active components. (Pocock)

Hormonal control of storage root development in sugar beet. The patterns of early storage root development were studied in relation to total DM production and its distribution in three subspecies of *Beta vulgaris* (sugar beet, mangold and chard) grown in controlled environments. All three subspecies produced leaf area and DM exponentially over the sampling period (40–60 days after sowing) and relative growth rates for both leaf area and DM were similar.

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Storage root growth (increase in DM) increased linearly with total DM production in all three subspecies. Similar proportions of total DM were partitioned to the storage root in sugar beet and mangold but only one third as much in chard. The pattern of storage root development differed in the three subspecies in relation to increasing root DM. The number of secondary cambia initiated per unit DM decreased in the sequence chard > sugar beet > mangold. The extent of cell division and expansion in cells derived from the cambia (measured as mean ring width) in roots of similar DM decreased in the sequence mangold > sugar beet = chard. Previous work has shown that the increased ring width in mangold is due to the production of fewer but larger cells compared with sugar beet (*Rothamsted Report for 1979*, Part 1, 48).

Auxin concentration and content, measured as indole-α-pyrone, increased with root DM and were the same in storage roots of sugar beet and mangold of similar weight. Concentrations ranged from 100 ng IAA g^{-1} DM in roots of 0·5 g DM to 180 ng IAA g^{-1} DM in roots of 4·0 g DM. It has proved difficult to causally relate changes in auxin concentration or content to the processes of cambial initiation and activity in these two subspecies. Roots of sugar beet initiated more cambia than mangold at the same auxin concentration. Conversely, on the same basis, cell expansion was greater in mangold than sugar beet. A comparison involving chard which initiates more cambia per unit root DM than sugar beet but has similar cambial activity is proceeding. (Lenton and Milford, with Webster, CASE student)

Potatoes

Effects of lodging on radiation interception and yield. Potato yields are related to the total amount of solar radiation intercepted by the leaves through the growing season. Larger seed, closer spacing and higher fertiliser rates increase yields either through increased leaf cover or by maintaining leaf cover for longer times. However, they may also cause stems to lodge, which might then decrease radiation interception and hence growth and yield. The effects of lodging were studied in crops of cv. Pentland Crown in 1979 (*Rothamsted Report for 1979*, Part 1, 49) and 1980. Smaller or larger seed (20–40 and 70–100 g in 1980) was planted at 25 or 51 cm spacings within the row. The stems were either held erect with a string mesh, lodged early during rapid haulm growth (late July) or lodged late after haulm growth had ceased (late August).

Early growth was greater and complete leaf cover attained earlier with larger seed and/or closer spacing, but once leaf cover was complete and radiation interception at the maximum growth rates were similar for all crops. Plants from larger seed or at closer spacing started to senesce earlier and by harvest in early October the yield advantages were either lost or greatly decreased (total tuber yields: large seed 78·6, small seed 77·7 t ha^{-1}; close spacing 80·1, wide spacing 76·1 t ha^{-1}). Radiation interception decreased after early lodging, but the crop rapidly re-established complete leaf cover, mainly by re-orientation of the stems and leaves, and over the 14 days after lodging radiation interception was only 3–4% less than for unlodged crops. The plants were unable to recover after late lodging. The leaves did not re-orientate, but senesced faster and the decrease in radiation interception for the 14 days after lodging was about 12%. Over the whole season the effects of lodging were small. The early-lodged crops soon recovered, and at the time of late lodging leaf areas and solar radiation were already declining. For both lodging treatments the amount of radiation intercepted was 3–5% less than that for the unlodged crops and yields were similar (unlodged 79·2, early lodged 77·1, late lodged 78·1 t ha^{-1}). The effects of lodging were slightly greater with large seed closely spaced, but the yield loss was still only about 6%. Lodging had little effect on the cv. Pentland Crown which produces large haulms and has a long growing season, but may be a problem with

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second early varieties or varieties which produce small haulms. (Wood, Antoniw and Taylor)

Staff and visiting workers

Joan M. Thurston retired on 31 January 1980 after 38 years' work at Rothamsted, mainly concerned with aspects of plant biology with special reference in later years to weed biology.

Susan M. Thomas and Linda D. Antoniw both resigned during the year and J. N. Gallagher left to take up an appointment at Lincoln College, Canterbury, New Zealand. Anne H. Buckenham has now moved to the University of Nottingham to continue further studies for the Ph.D. degree.

Frances A. Boyle joined the Department on 1 October 1980 as an ARC Research Student to study for the Ph.D. Degree of London University. CASE students who worked in the Department during the year were Brian Newton (University of Essex), Kevin Walker (University of Newcastle upon Tyne) and David Webster (Leicester Polytechnic).

In 1979 A. J. Keys became the OECD United Kingdom Correspondent and Co-ordinator for the theme on effects of the environment on the metabolism of sugars, amino acids and organic acids for the programme on photosynthesis.

C. P. Whittingham, A. J. Keys, G. P. Holbrook and Mrs Celeste Arrabaca all attended the 5th International Congress on Photosynthesis held in September at Halkidiki, Greece. C. P. Whittingham gave a talk and Mrs Arrabaca, with C. P. Whittingham and A. J. Keys, presented a poster on 'Effects of Temperature on Photosynthetic and Photorespiratory Metabolism'. A. J. Keys and C. P. Whittingham also attended the 2nd Congress of the Federation of European Societies of Plant Physiology (FESPP) in Santiago de Compostela, Spain, in July, where A. J. Keys gave a paper entitled 'Purified RuBP Carboxylase and effects of Carbonic Anhydrase on Carboxylation'.

D. W. Lawlor visited Wageningen in November at the invitation of the British and Dutch Plant Growth Regulator Groups to give a talk entitled 'Photorespiration and its Control'.

Gillian N. Thorne, with F. V. Widdowson (Soils and Plant Nutrition Department) and R. D. Prew (Plant Pathology) visited France in June at the invitation of the Institut Technique des Cereales et Fourrages (ITCF) to inspect their experiments on winter wheat and barley.

Publications

General Papers

1 Lenton, J. R. (Ed.) (1980) Gibberellins—chemistry, physiology and use. *British Plant Growth Regulator Group Monograph* No. 5, 139 pp.

2 Keys, A. J. & Whittingham, C. P. (1981) Photorespiratory carbon dioxide loss. In: *Physiological processes limiting plant productivity*. Ed. C. Johnson. London: Butterworths, pp. 137–145.

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5 WHITTINGHAM, C. P. (1979) Photorespiration: its mechanism and significance. *Agronomia Lusitana* **39**, 115–129.

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6 DAY, W., LAWLOR, D. W. & LEGG, B. J. (1981) The effects of drought on barley: soil and plant water relations. *Journal of Agricultural Science, Cambridge* **96**, 61–77.

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13 PEARMAN, I., THOMAS, S. M. & THORNE, G. N. (1981) Dark respiration of several varieties of winter wheat given different amounts of nitrogen fertiliser. *Annals of Botany* **47**, 535–546.

14 RADLEY, M. (1980) Effects of abscisic and gibberellic acids on grain set in wheat. *Annals of Applied Biology* **95**, 409–414.

15 RADLEY, M. (1981) The effect on wheat grain growth of glume removal and of abscisic acid treatment of glumes. *Journal of Experimental Botany* **32**, 129–140.

16 WHEELER, A. W. (1980) Auxin-like growth activity of 3-phenylpropionitrile from water cress (*Nasturtiam officinale*, R. Br.). *Annals of Botany* **46**, 1–5.

17 WHEELER, A. W. (1980) Effects of removing ears and leaves on responses of barley and wheat to chlormequat chloride and gibberellic acid. *Annals of Botany* **46**, 379–381 (Short communication).

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