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Report for 1979 - Part 1

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Botany Department

C. P. Whittingham

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Introduction

The Botany Department has continued to concentrate attention on three main arable crops—cereals, sugar beet and potatoes. Further studies of the effects of aerial pollution on cereal growth in Bedfordshire showed a statistically significant improvement both in grain yield and plant growth when the crop was grown in filtered, as compared with unfiltered, air. The work on sugar beet has continued in collaboration with Broom's Barn and is particularly concerned with the relationship between crop development and environmental conditions. The investigation of source/sink relationships in the potato in relation to tuber growth and photosynthetic activity of leaves has continued.

Some work on ribulose bisphosphate (RuBP) carboxylase, a most important enzyme in photosynthesis, is reported in the current year and in future, research on this subject will receive greater attention as part of the ARC Priority Programme on Photosynthesis.

The Department is collaborating in the interdisciplinary experiments on factors determining the yield of cereals and an account of that work is given in another section (p. 17). The Department has also contributed to the work on plant response to water stress reported in the account of the work of the Physics Department (p. 159).

Cereal crops

Atmospheric pollution and growth of barley. In the spring and summer of 1979 no major episodes of pollution occurred at Thrupp End Farm, Bedfordshire and no visual damage on barley, or other cereal crops, was observed. The mean concentration of sulphur dioxide during the growing season was $48~\mu g$ m⁻³ but high short-term peaks occurred and on 8 May a Meloy SA285 continuous sulphur analyser recorded an hourly mean concentration of $731~\mu g$ m⁻³.

An experiment was repeated using the same techniques developed in previous years (Rothamsted Report for 1977, Part 1, 39). Spring barley, var. Magnum, was grown inside eight modified open-topped chambers supplied either with ambient field air or with air that had been cleaned using activated charcoal and particulate filters. The concentration of sulphur dioxide in the chambers with filtration was approximately 30% of that outside. The growth and development of the crop was followed by making non-destructive measurements in the period prior to ear emergence and by destructive harvests at 50% anthesis and final harvest. Poor weather conditions meant that the crop was sown late (18 April) and began to lodge soon after anthesis. As in previous years a 'chamber effect' was observed. Plants grown outside tillered faster and produced more shoots than plants in the chambers. Plants grown in the chambers reached anthesis sooner than plants outside, but produced more late tillers resulting in more unripe ears at final harvest. Neither the non-destructive nor destructive harvests showed significant differences in the number of plants in each harvest. Both grain and straw yields were significantly higher in the plants grown in chambers with filtered, as compared with unfiltered, air. The increase in

Yield and fluoride content of spring barley grown in chambers with filtered or unfiltered air and outside

	Grain dry	Straw dry	1000 grain	Leaf
	weight	weight	weight	fluoride
	(g m ⁻²)	(g m ⁻²)	(g)	(ppm, wt./wt.)
Filtered air chamber	489a	470 ^a	43·8a	27·7 ^a
Unfiltered air chamber	308b	345 ^b	37·6b	53·6 ^b
Outside	559a	597°	31·7c	89·4 ^c

Means followed by the same letter within a given variate are not significantly different at the 95% probability level

grain yield was not the result of the production of more ears, or of an increase in fertile spikelet number per ear, but was due to an increase in grain size. Determination of the concentration of fluoride in the plants grown in the chambers showed the filtration system to have effectively cleaned the air. Further experiments will continue next year. (Buckenham and Parry)

Factors limiting yield of winter wheat. A study of the effects of various sowing systems, amount and timing of nitrogen fertiliser applications, and of irrigation on healthy winter wheat, var. Maris Huntsman, in 1978 showed negligible interactions between factors (Rothamsted Report for 1978, Part 1, 36). The increases in grain yield obtained from additional nitrogen were associated with increase in survival of tillers to produce ears, without compensatory decreases in grain size or in number of grains per ear, that often occur when ear number is increased by nitrogen. In contrast, the increase in ear number caused by doubling the sowing rate, which also increased numbers of tillers in April, was entirely compensated by smaller grains and fewer grains per ear. Additional nitrogen that increased shoot survival and grain yield also increased leaf area at anthesis and 47 days

later. Similar increases in leaf area were caused by applying 102 mm of irrigation between 30 May and 28 July. However, grain yield was slightly, but not quite significantly, decreased by irrigation and straw yield was unaffected. The data on nutrient uptake are reported on p. 24.

Further studies of the interactions between factors, including soil type and control of pests and diseases (on only one soil), were done in 1979 and are reported elsewhere (p. 225). Best yields of grain (85% dry matter (DM)) at Rothamsted in 1979 were 10 t ha⁻¹ compared with only 8·4 t ha⁻¹ in 1978. The winter wheat, var. Hustler, used in 1979 was sown earlier and unlike Maris Huntsman in 1978 was well-tillered by December. It also tillered more and produced 620 ears m⁻² compared with 412 in 1978. (Taylor, Thorne and Welbank, with Widdowson, Soils and Plant Nutrition Department)

The response of winter wheat to nitrogen fertiliser applied before initiation of the ear, while the crop was still tillering, was different from that obtained when the nitrogen was applied later (*Rothamsted Report for 1978*, Part 1, 36). With 60 kg N ha⁻¹, early and late applications of nitrogen had similar effects on tiller production, ear number and vegetative growth. With more nitrogen, these attributes were increased more by early than by late nitrogen, but there were no equivalent increases in nitrogen uptake. Time of nitrogen application affected neither uptake after anthesis, which was 40% of the total, nor distribution at maturity (60% in the grain). Nitrogen concentration in the grain ranged from 1·3 to 1·8% dry weight (DW) depending on the amount of nitrogen applied, irrespective of the timing.

The information obtained in 1979 on the interaction between crop development and time of nitrogen application was rather unsatisfactory. A 3-week delay in sowing delayed ear initiation by 4 weeks and seemed to alter the relation between apical development and tillering pattern (p. 18). The experimental design permitted only one date for the single application of nitrogen, so a compromise between the two dates of ear initiation was selected. The interactions between development, tillering and timing and amount of nitrogen fertiliser will be investigated in 1979/80 in two varieties sown over a wide range of dates. (Taylor and Thorne)

Factors determining grain size in wheat. Removing the top half of the ear to increase the supply of carbohydrate per grain increased DW per grain of spring wheat, var. Kleiber, grown in pots by up to 30%. Similar treatments applied in the field in 1976 increased weight per grain of winter wheat, var. Hobbit by 6% and decreased that of Maris Huntsman. In the more favourable season of 1977, ear-halving again failed to increase grain size of Maris Huntsman (Martinez-Carrasco & Thorne, Annals of Applied Biology (1979), 92, 383-393). An experiment in 1978, a season very favourable for grain growth, confirmed the difference between Hobbit and Maris Huntsman. The two varieties were grown in the field with 30 or 120 kg N ha-1. Grain yield was increased by nitrogen and was slightly greater for Hobbit than Maris Huntsman. The mean yield was 7.4 t ha-1 (85% DM). Removing the top half of the ear 5 days after anthesis increased DW per grain of Hobbit by 31 %, from 48 to 64 mg, but that of Maris Huntsman by only 8 %. The number of grains in the lower half of the ear was also increased by halving, considerably in Hobbit and slightly in Maris Huntsman. Both differences between varieties were greater with more nitrogen. Halving also increased the DW of chaff and stem but similarly in the two varieties. The extra growth of the shoot and ear induced by halving the ear was equivalent to 58 % of the grain in the upper half of the ear of Hobbit. In Maris Huntsman, the compensation was only 31%.

The mechanism responsible for the difference between Hobbit and Maris Huntsman and the response to ear-halving of three other varieties were further studied in the field in 1979. (Thorne)

Factors determining grain size in barley. A field experiment in 1978 showed that dry mass per grain was positively correlated with crop DM production after anthesis. The relation was less than directly proportional, because assimilate formed before anthesis was apparently used for grain growth. A further experiment was carried out in controlled environments to examine the response of grain growth to assimilate supply. Plants were grown in bright light (440 μ E m⁻² s⁻¹) with a day/night temperature of 18/12°C, until the terminal spikelet of the main culm was initiated when half the plants were transferred into a lower light intensity (120 μ E m⁻² s⁻¹). At anthesis and 14 days after anthesis plants were transferred between the two light intensities.

Dim light between terminal spikelet and anthesis caused many spikelets to abort, slowed development and prevented imposition of further treatments at the correct stage. Hence studies were confined to the main culm of plants that were in bright light during this phase. These culms did not differ significantly in grain number per ear regardless of

subsequent light conditions.

Dim light between anthesis and anthesis +14 days caused very slow DM growth, only 15% of that in bright light. Grain growth was less affected, being 67% of that of the bright treatment. Thus grain growth occurred at the expense of further growth of the stem and leaves, which lost weight in the dim treatment, whereas they increased in bright conditions.

Between anthesis +14 days and maturity, grain growth depended on both the previous and the current light environment. For culms that had been in dim light previously, increase in grain DM corresponded closely to increase in total culm DM, stem + leaf DM remaining stable. For culms exposed to bright light previously, those in dim light between anthesis +14 days and maturity produced only 20% of the total DM formed by culms in bright light, but 50% of the grain DM. This discrepancy was accounted for by a large decrease in stem+leaf DM during this phase in both treatments, indicating that DM accumulated in the stem+leaves between anthesis and anthesis +14 days was used for grain growth. Stem+leaf DM per culm did not differ significantly between treatments at maturity but was 12% less than at anthesis. The absolute magnitude of the contribution of pre-anthesis assimilate to grain yield was the same in all treatments; the contribution relative to that of post-anthesis assimilate increased as mass per grain fell. (Gallagher)

Carbon dioxide enrichment, growth and yield of wheat. In a previous experiment enrichment of the atmosphere to $1200~\mu l\, l^{-1}$ compared with $400~\mu l\, l^{-1}$ CO₂ increased the grain yield of spring wheat by 16% (*Rothamsted Report for 1978*, Part 1, 39). Maximum DM production of the shoots minus ears (at 18 days after anthesis) was increased by 12%. However, CO₂ fixation by flag leaves was increased by enrichment by a much larger percentage. For example, when measured 14 days after anthesis, main stem flag leaf total CO₂ fixation was $21\cdot3$ mg CO₂ dm⁻² h⁻¹ at $1200~\mu l\, l^{-1}$ CO₂ and $15\cdot7$ mg CO₂ dm⁻² h⁻¹ at $400~\mu l\, l^{-1}$ CO₂ (SED $0\cdot66$), 36% higher. Photorespiration was only 13% of the total CO₂ fixation at $1200~\mu l\, l^{-1}$ CO₂ compared with 29% at $400~\mu l\, l^{-1}$ CO₂, so net photosynthesis was increased by 66%. Flag-leaf area was not significantly increased. Preliminary measurements suggested that respiratory losses from stems and ears were greater in the enriched environment; for example, when measured 35 to 41 days after anthesis, the respiration rate of main stems and ears was $0\cdot58$ mg CO₂ g⁻¹ h⁻¹ at $1200~\mu l\, l^{-1}$ CO₂ compared with $0\cdot46$ mg CO₂ g⁻¹ h⁻¹ at $400~\mu l\, l^{-1}$ CO₂.

These effects were investigated further in a similar experiment in 1979. The details of the experiment were as in 1978 except that the plants were not enriched prior to anthesis whilst growing outside in the glass-roofed cage. One variety, Kleiber, was used, with four levels of irradiance. At anthesis the plants were transferred to controlled-environment

rooms supplied with either 1200 μ l l⁻¹ or 350 μ l l⁻¹ CO₂. In one pair of rooms the mean irradiance was 613 μ E m⁻² s⁻¹ in half (B), increased to 788 μ E m⁻² s⁻¹ in the other half (A) using 4 × 400 W metal halide lamps; in the other rooms the irradiances were 274 (C) and 150 (D) μ E m⁻² s⁻¹.

Carbon dioxide enrichment increased the rate of ear growth more at the lower irradiances, but increased final grain yields by similar proportions at all irradiances. Mean grain DW at 1200 μ l 1-1 CO₂ was 39.4 g per pot; at 350 μ l 1-1 CO₂, 31.9 g per pot (SED 1.6). Ear growth and final grain yield were increased by irradiance up to 613 μE m⁻² s⁻¹. (Mean grain DW at irradiance A, 45·0; B, 45·6; C, 34·2; D, 17·7 g per pot; SED 2.2.) Weight per grain was the yield component significantly increased by both enrichment and irradiance. Enrichment almost doubled the rates of photosynthesis of main stem flag leaves at the three brighter irradiances. The increase was not so marked at the lowest irradiance until 25 days after anthesis, because these leaves had large stomatal resistances until that time. Rates of net photosynthesis of main stem flag leaves 16 days after anthesis at 1200 µl l-1 CO2 were: at irradiance A, 28.3; B, 28.8; C, 15.3; D, 7.3 mg CO₂ dm⁻² h⁻¹: corresponding values at 350 μl l⁻¹ CO₂ were, 14·7; 12·9; 8·2; 5·8 mg CO₂ dm-2 h-1 (SED 2·7). Hence, photosynthesis was increased by irradiance up to 613 μE m^{-2} s⁻¹, but there was no further increase at 788 μ E m⁻² s⁻¹; at high irradiance increasing the CO2 concentration four times resulted in a doubling of the rate of photosynthesis. Some of the extra carbon fixed contributed to the increase in grain yield. But, as in 1978, the increase in grain yield due to enrichment was small compared with the increase in photosynthesis (24% compared with the 92% increase in mean net photosynthesis per unit area, plus à 14% increase in flag leaf area per pot). Measurements in 1978 showed that roots were about 27% heavier in the CO₂-enriched plants, but they only represent a small part of the total plant weight (4% at final harvest). Maximum shoot minus ear weight in 1979 (at 25 days after anthesis) was increased by 5%. Although some of this material may have been redistributed to the ear, shoot weight continued to decline even after the ears had stopped growing, as in 1978. So not all the extra material fixed was available for grain growth. Preliminary measurements of rates of respiration of stems and leaves throughout the period from anthesis to maturity suggest that enrichment either had no effect or increased the rates in main stems and leaves. For example, at maximum shoot weight, the respiration rates were 0.43 mg CO₂ g⁻¹ h⁻¹ at 1200 μl l⁻¹ CO₂ and 0.34 mg CO₂ g⁻¹ h⁻¹ at 350 µl l⁻¹ CO₂ (SED 0.03). In combination with the increased main shoot weights at this stage, respiratory losses from main shoots were increased by 43% by enrichment. Smaller extra losses were shown for every stage to maturity. Thus losses of carbon by dark respiration account for much of the extra carbon fixed during grain growth. (Kendall and Thomas)

Dark respiration. Greatly decreasing the number of grains in the ear of spring wheat, var. Sicco, from the normal 42 to 6 resulted in a small increase in stem DW, greater production of late tillers and an increase in rate of dark respiration by the stem (Rothamsted Report for 1978, Part 1, 39). A similar experiment was done in 1979, except that late tillers were removed every few days. The stems of main shoots having six-grained ears increased in DW until 3 weeks after treatment when they weighed 25% more than untreated; treated stems had a slightly greater respiration rate than untreated ones. During the next 4 weeks stems of both treated and untreated plants decreased in DW and at maturity had the same weight. During this latter period, respiration rate of treated stems ranged from 0.8 to 0.2 mg CO₂ g⁻¹ h⁻¹ and untreated ones from 0.5 to 0.2 mg CO₂ g⁻¹ h⁻¹. Throughout the period of grain growth the growth of roots and of late tillers, which were removed frequently, was greater in plants with treated ears. By maturity this extra vegeta-

tive production was equivalent to 72% of the difference in ear weight between treated and untreated plants.

The nature of the increased respiration was investigated. In many plants there is evidence that the mitochondria contain two oxidases, the usual cyanide-sensitive cytochrome oxidase and an alternate cyanide-resistant oxidase, which is inhibited by salicylhydroxamic acid (SHAM). Oxygen uptake of sections of stems (0.04 g DW) was measured with an oxygen electrode. Significant increases were observed in the treated compared with the untreated stems (4 weeks after treatment: oxygen uptake of the treated stems was 0.33 mg CO₂ g⁻¹ h⁻¹ (SE 0.04); untreated stems, 0.18 mg CO₂ g⁻¹ h⁻¹ (SE 0.03)). SHAM (up to 25 mm) did not inhibit oxygen uptake by either tissue. This suggested that the alternate oxidase was not active in the stem tissue in normal conditions. Potassium cyanide (0.4M) inhibited oxygen uptake by up to 33%. In combination with SHAM this inhibition was increased to 44% in the untreated samples and 50% in the treated samples. The additional inhibition with SHAM suggested that, although not normally active, the alternate oxidase was present in the tissue and could accept electrons when the cytochrome pathway was inhibited. There may be increased capacity of the alternate pathway in treated tissue. However, oxygen uptake was never completely inhibited suggesting that the inhibitors did not reach all the sites of oxygen uptake in the tissues. Thus the differences between untreated and the treated samples in their response to SHAM plus potassium cyanide could have been due to differences in permeability of the tissues rather than the capacities of their alternate oxidase. (Pearman, Thomas and Thorne)

Reversible activation of RuBP carboxylase from wheat leaves. Freeze-dried RuBP carboxylase purified from wheat leaves was inactive when freshly dissolved in buffer at pH 8·6. Reactivation required 5 h incubation at 20°C in a solution of sodium bicarbonate and magnesium chloride and the maximum activation attained depended on the concentrations of CO₂ and Mg²⁺. If, following activation at 20°C, magnesium chloride and CO₂ were removed from the solution, activity was lost in less than 10 min. Activity was quickly restored if the magnesium chloride and CO₂ were added back immediately; prolonged absence of Mg²⁺ and CO₂ resulted in a change in the carboxylase so that once more maximum activation required 5 h incubation at 20°C. Incubation at temperatures below 20°C resulted in a lower final activity. Furthermore, after activation at 20°C, enzyme stored at 0°C lost activity even in the presence of Mg²⁺ and CO₂, the activity being slowly restored if the enzyme was again incubated at 20°C.

Two steps are proposed in the activation of the purified enzyme; a slow change from an inactive form (E) to a potentially active form (E*) dependent on Mg^{2+} and subsequently a rapid gain of Mg^{2+} and CO_2 to produce the active catalyst.

At a given temperature there must be a proportion of potential sites on the enzyme which increases as the temperature is decreased and which cannot combine and be activated by CO_2 and Mg^{2+} . (Mächler, Cornelius and Keys)

Effect of carbonic anhydrase on the carboxylation of RuBP catalysed by RuBP carboxylase. In chloroplasts, RuBP carboxylase and carbonic anhydrase are present together as soluble enzymes in the stroma. Adding carbonic anhydrase to purified RuBP carboxylase had little effect on its carboxylating activity when the substrate, free CO₂, was present in saturating amounts. When less CO₂ was present, as in determinations of affinity, we found a stimulating effect of carbonic anhydrase on carboxylation as measured by ¹⁴CO₂

incorporation into phosphoglyceric acid (PGA). Also, the rate of carboxylation at pH 8·2 remained constant for at least one minute with a non-saturating concentration of CO₂ (supplied by adding 2 mm-bicarbonate) only if carbonic anhydrase was present. In the absence of anhydrase the rate of carboxylation declined with time so that the estimation of initial rate from measurements of the amount of PGA produced even after times as short as 20 s results in a significant under-estimate of the initial rate and an over-estimation of the K_m for CO₂. (Bird, Cornelius and Keys)

Effect of growth substances on wheat grain set. It has been suggested (Evans, Bingham & Roskams, Australian Journal of Biological Sciences (1972), 25, 1–8) that there may be, within a wheat ear, a correlative inhibition of grain set which is hormonal in nature. The effects of applied growth substances on grain set was studied. Microdrops of methanol containing 5 μ g of various growth substances were applied to the glumes of each spikelet. Indoleacetic acid (IAA), napthaleneacetic acid, benzyl adenine and ethephon were all ineffective. Abscisic acid (ABA) inhibited grain set in the upper florets of many spikelets in the cultivars Sicco, Kleiber and Maris Huntsman, but was ineffective (even at 20 μ g per floret) in the semi-dwarf cultivars Hobbit, Hustler and Highbury. The lack of response of the semi-dwarf cultivars may be associated with their highly synchronous development. In the responsive cultivars drought conditions at anthesis might increase endogenous levels of ABA and thus reduce grain set. Gibberellic acid affected both normal and semi-dwarf cultivars, preventing dehiscence and exertion of the anthers, although the stamen filaments apparently extended, remaining coiled up inside the florets. (Radley)

Pre-harvest sprouting susceptibility. Susceptibility to pre-harvest sprouting in wheat varies greatly in different cultivars, white-grained cultivars being especially susceptible. As growth substances are known to affect germination both in ripe and developing grain (Rothamsted Report for 1977, Part 1, 41), the endogenous growth substance content of resistant and susceptible cultivars has been examined. Gibberellins (GAs), ABA and IAA all decreased to a very low concentration during ripening, only IAA remaining in significant amounts and most of this was in a bound form. At ripeness the white-grained cultivar, Minister, was found to contain four times as much IAA in both free and bound forms as the red-grained cultivar, Ranger. Preliminary tests on several red-grained cultivars have indicated differences in IAA content possibly related to their sprouting susceptibility. (Radley)

Effect of glume removal on wheat grain development. A possible effect of glumes on the growth of wheat grains was studied by removing them at different stages of development. When glumes were removed from the ears after most of the increase in grain volume had taken place, a loss of water from the grain adjacent to the glume was detected in 1 to 2 days. The DW increase was much reduced. Five hours after degluming, ¹⁴CO₂ was applied to the flag leaves for 1 min, and the grains harvested 48 h later. The amount of ¹⁴C in the grains was markedly less where the glumes had been removed. If the glumes were treated with ABA there was a marked effect on glume senescence, but the grains were largely unaffected, so glume removal and glume senescence are not comparable.

Removing glumes a few days after anthesis did not prevent the development of the grain but it grew to a smaller size. The effect was similar whether all the spikelets were treated or only a few, indicating little interaction between spikelets. The number and size of aleurone cells were both smaller in the treated grains.

The calcium content at final harvest was used as a measure of the amount of water that had entered the grain during growth (Sofield, Wardlaw, Evans & Zee, Australian Journal of Plant Physiology (1977), 4, 799). Grains developing after glume removal accumulated

much less calcium than control grains, although the results suggest that total water uptake by the grain and final DW are not directly connected. When the lower two grains in a spikelet were removed at an early stage the third grain became much larger, but it did not accumulate more calcium. (Radley)

Identification of gibberellins in developing wheat grain. Initial attempts to identify GA forms in developing wheat grain by combined gas chromatography-mass spectrometry (GC-MS) were hindered by the occurrence of large amounts of other compounds with similar chromatographic properties (Rothamsted Report for 1978, Part 1, 45). These impurities have been tentatively identified, from mass spectral data, as trihydroxyoctadecanoic acids which probably arise via the action of lipoxygenase on the corresponding C₁₈ fatty acids (Graveland, Lipids (1973), 8, 599-611).

Alternative extraction methods have been explored as a means of reducing these contaminants. Comparison of absolute methanol and 0.2M-tris/HCl (pH 7.6) as extraction media showed they were equally effective at extracting GA but more impurities were extracted with tris buffer. Addition of 1.8M ammonium sulphate to tris, either in the grinding medium or at a later stage, reduced the efficiency of extraction of both GA and

impurity to an equal extent.

Methanolic extraction and subsequent GC analysis of grains subdivided into embryo, endosperm and outer layer showed that a large proportion of impurity was associated with the outer layer whereas GA was more equally distributed between the three tissues.

Possible differences in the GA complement of diploid embryo and outer layer (maternal tissue) were compared with triploid endosperm tissue. Grains (var. Maris Huntsman) were harvested from the field over a four-day period up to maximum water content, subdivided into different tissues, extracted with methanol and purified. Gibberellins GA24, GA25 and GA15 and their corresponding C-13 hydroxy compounds GA19, GA17 and GA₄₄ were identified in endosperm tissue by combined GC-MS. In addition to these known compounds the structure of novel 1β-hydroxy derivatives of GA9, GA20, GA4 and GA_1 were deduced from mass spectral data together with 1β , 2β -dihydroxy GA_4 . Two parallel pathways, with and without early C-13 hydroxylation, may occur in wheat endosperm. The occurrence of 1β-hydroxy derivatives of GA9 and GA20 and the apparent absence of free GA4 and GA1, both of which occur in vegetative tissue, suggest that 1β -hydroxylation precedes 3β -hydroxylation in endosperm. The occurrence of 1β , 2β -dihydroxy GA_4 shows that GA deactivation involves 2β -hydroxylation.

Trace amounts of GA19, GA44 and GA20 were detected in embryos by combined GC-MS but problems with large amounts of impurities prevented identification of the less polar GAs in outer layers. Gibberellins GA_{17} , GA_{19} , 1β -hydroxy GA_4 and 1β , 2β-dihydroxy GA₄ were identified in the more polar fraction from outer layers.

The identification of novel GAs in wheat endosperm presents exciting possibilities for biosynthetic work but their relevance to control of developmental processes in grain and their action in relation to the induction of hydrolytic enzymes and premature germination remain the ultimate objectives of the work. (Lenton, with Mr. P. Gaskin and Professor J. MacMillan, University of Bristol)

Sugar beet

Temperature and leaf development. Much of the radiation available in spring is not intercepted by sugar-beet crops because leaf growth is slower at colder temperatures. In an average year, more than 800 MJ m⁻² of solar radiation may be lost before the crop establishes full leaf cover; and each MJ of radiation lost represents 1.8 g of total DM and 0.8 g of sugar (Rothamsted Report for 1978, Part 1, 64). The potential for producing 46

varieties capable of better growth at low temperatures was examined in controlled environments with nine British commercial varieties and 16 European selections (*Rothamsted Report for 1977*, Part 1, 41–42, and *for 1978*, Part 1, 46).

No genotype tested produced, or was able to expand, leaves below 2°-3°C. Above this temperature the rate of expansion of leaf area per plant was faster in Amono, Hilleshog Monotri, Anglo Maribo Polybeet and Sharpe's Klein Megapoly than in Vytomo, Nomo and Sharpe's Klein Monobeet. However, the genetic diversity within varieties resulted in the fastest rate of expansion of leaf area for an individual plant of a variety, being four

times that of the slowest, with the greatest range at low temperatures.

The differences observed between varieties and between individual plants were largely caused by differences in the rates of growth and sizes of individual leaves and not in their number. The relationship between rate and duration of expansion, and temperature, was analysed by fitting generalised logistic equations to the individual growth curves of the first six leaves produced by each plant (Dennett, Auld & Elston, Annals of Botany (1978), 42, 223–232). The first pair of leaves were small in all varieties and contributed little to leaf area. They were probably present as primordia in the seed and likely to have been influenced as much by their history on the mother plant as by the temperature conditions of the experiment. Leaves from the third onwards grew to progressively larger areas; in field-grown plants this continues up to the 11th or 12th leaf. Plants that produced large leaves early continued to do so. Varieties such as Amono, Hilleshog Monotri and Anglo Maribo Polybeet that had more leaf area per plant had larger individual leaves than slower-growing varieties such as Vytomo and Sharpe's Klein Monobeet. Large leaves, whether from different positions on the plant, or from plants of different genotype, were large because they grew faster not because they continued to grow for longer.

The rates of leaf production, the rate and duration of expansion, and final leaf size, were all sensitive to temperature in the range 7°-20°C. The rate of leaf production and the reciprocal of the duration of expansion—a measure of the rate of development—decreased linearly as temperature decreased and the temperatures at which both ceased, obtained by extrapolation, were close to 2°C for all varieties. For individual leaves the rates of expansion were linear above 8°-10°C; below this temperature the relationship increasingly departed from linear so that, although it was likely that leaf expansion also ceased at temperatures close to 2°C, it was more sensitive to temperatures between 2° and 10°C than leaf production or the duration of leaf expansion. Because of this, the increase in duration of expansion of a given leaf as temperature decreased over this range was insufficient to compensate for the decrease in the rate of expansion, so final leaf size decreased with cooler temperatures; at 7°C final leaf area was less than a quarter of the potential area. In this respect sugar beet differs from cereals (Gallagher, Biscoe & Wallace, Journal of Experimental Botany (1979), 30, 657-668). (Milford, with Janet Riley, Statistics Department)

Effect of light quality on leaf growth. Previous studies have shown that extending daylength with a mixture of red and far-red light of low intensity increased plant growth by increasing leaf expansion and petiole growth (*Rothamsted Report for 1976*, Part 1, 42). Preliminary studies on the effect of daylength extension on the developmental anatomy of the leaf showed an increase in cell division early in growth (*Rothamsted Report for 1977*, Part 1, 42). The experiment was repeated with a different sampling regime to improve precision and in addition to the control (12 h fluorescent light) and extending daylength treatments (12 h fluorescent+4 h tungsten), a third batch of plants was transferred from control to extended daylength when the fifth leaf was 10 mm long.

Final areas of the fifth leaf increased from 220 cm² in the control to 320 cm² in extended daylength plants and 280 cm² in transferred plants. Differences in leaf area were due

to differences in rates of expansion with no effect on duration of expansion. The different leaf areas can be accounted for almost entirely by differences in final cell numbers $(110 \times 10^6 \text{ control}; 150 \times 10^6 \text{ transferred}; \text{ and } 190 \times 10^6 \text{ extended daylength})$. Final cell number is a function of the rate of cell division and its duration. The time from $5 \times 10^6 \text{ cells to } 95\%$ final number was similar for all three treatments (20-22 days). Hence differences in cell number were due to different rates of division. In extended daylength plants, cell division increased above that in control plants once leaves had reached 10% final area, and after transfer cell division quickly adjusted to a higher rate. Linear dimensions of cells from semi-thin sections of fully-expanded leaves suggest that, although cell volume is not altered, cell shape contributes to the increase in leaf area, particularly in transferred plants. These plants had leaves with thinner epidermal cells and shorter palisade cells together with a higher proportion of mesophyll air space. The experiment shows that changes in rates and duration of cell division are major determinants of leaf growth and the earlier in development such changes occur the greater is the effect likely to be both on rate of leaf expansion and its final area. (Pocock)

Root growth and sugar accumulation. The partitioning of assimilate in the sugar-beet root between growth and storage depends on the sizes to which the cells of the various root tissues grow and their efficiency in accumulating sugar relative to non-sugar DM. Last year's report (Rothamsted Report for 1978, Part 1, 47) described the anatomical development of three sugar-beet cultivars (Bush Mono G, Vytomo, Rustic 42) and of mangold (cv. Wintergold). This year measurements were made of changes in cell volume and sugar and non-sugar DM per cell in samples of tissues from each ring across the root taken in both August and October.

Sugar concentrations of whole roots of the three sugar-beet types were similar (65% DM) but were lower in mangold (47%). The fresh weight (FW) and DW concentrations of sugar across the root at any one time were similar in the three sugar-beet types. In mangold, DM concentration was similar across the root whereas FW concentration was lower in the parenchymatous zones of each ring. Mean cell volumes in vascular zones of rings did not change between August and October ($10^5 \mu m^3$ in sugar beets and $2 \times 10^5 \mu m^3$ in mangold). In both August and October the mean cell volume in the parenchymatous zones of sugar-beet roots was $3 \times 10^5 \mu m^3$. In mangold, however, the cell volume in these zones increased from 5 to $6 \times 10^5 \mu m^3$ by October. The efficiencies with which the cells of the roots accumulated sugar per unit of cell volume were the same for the three sugar-beet types at any one time but increased from $1.25 \mu g$ to $2.0 \mu g$ sugar per $10^4 \mu m^3$ cell volume between August and October. However, the accumulation of nonsugar DM increased in proportion so that the DW concentration of sugar remained the same. Mangold cells were less efficient at accumulating sugar and increased from $0.7 \mu g$ to $1.0 \mu g$ sugar per $10^4 \mu m^3$ cell volume. (Pocock)

Hormonal control of storage root development in sugar beet. Initiation of cambia and subsequent differentiation of cells derived from them are important determinants of sugar storage capacity in sugar beet. Concentration gradients of auxin (and sucrose) are thought to control the pattern of cambial formation and changes in gene expression leading to cell differentiation (Warren-Wilson, *Proceedings of the Royal Society of London, Series B*, (1978), 203, 153–176; Sachs, *Differentiation* (1978), 11, 65–73).

Changes in cambial activity and auxin concentration were compared initially in two sub-species of *Beta vulgaris*. More cambia with greater meristematic activity were produced in sugar beet than in mangold. The auxin, IAA, was identified by combined GC-MS in a purified extract of sugar-beet roots (21 mm diameter, 150 g DM). A modified spectrophotofluorimetric assay based on the method of Knegt and Bruinsma (*Phytochemistry*

(1973), 12, 753–756) was used to measure IAA in young storage roots (up to 50 mm diameter). During the period when cambial ring number increased to 6·2 in mangold and 8·7 in sugar beet, auxin concentration increased to 140 ng g⁻¹ DM in mangold and 320 ng g⁻¹ DM in sugar beet. Auxin concentration per unit length of cambial tissue was two to three times greater in sugar beet than mangold and this difference may be associated with the increased meristematic activity of cambia in sugar beet. (Lenton, with Webster (CASE Student) and Professor M. C. Elliott, Leicester Polytechnic)

Identification of the auxin phenylacetonitrile in sugar beet. Bioassay of ethyl acetate extracts and steam distillates of sugar-beet plants detected a neutral, auxin-like substance but its identification as phenylacetonitrile (PAN) could not be confirmed by high pressure liquid chromatography (*Rothamsted Report for 1975*, Part 1, 46). Now, PAN, at a concentration of $2.3~\mu g~g^{-1}$ FW of leaves, together with 11 other volatile constituents, have been identified by GC-MS. Assay of sugar-beet steam distillates with wheat-coleoptile sections estimated $8.7~\mu g~PAN~g^{-1}$ FW in seedling leaves decreased to $0.6~\mu g~PAN~g^{-1}$ in mature leaves. The largest concentration of PAN found was a little less than the most effective concentrations ($10-35~\mu g~PAN~ml^{-1}$) which elongated wheat-coleoptile sections.

An earlier examination of water cress by GC-MS identified 3-phenylpropionitrile (PPN) amongst other volatile constituents (MacLeod and Islam, *Journal of the Science of Food and Agriculture* (1975), **26**, 1545–1550). Both steam distillates from water-cress shoots and solutions of PPN (13·1 to $39\cdot3~\mu g$ ml⁻¹) stimulated elongation of wheat-coleoptile sections as effectively as PAN; $108~\mu g$ PPN g⁻¹ FW of shoots was detected by GC-MS and $270~\mu g$ PPN g⁻¹ by wheat-coleoptile sections. (Wheeler, with Dr. V. Gil and Dr. A. J. MacLeod, Queen Elizabeth College, London)

Potatoes

Effects of lodging on radiation interception and yield. Tuber yield is related to the amount of solar radiation intercepted by the crop throughout the growing season (*Rothamsted Report for 1978*, Part 1, 48). With the use of closer spacing, higher fertiliser rates and irrigation, there is a greater tendency for stems to lodge. Since lodging decreases radiation interception it may result in poorer crop growth and tuber yields.

In 1979 crops of var. Pentland Crown were planted at 25.4 or 50.8 cm spacing and either the stems held erect using a string mesh; lodged early during rapid haulm growth (late

July); or lodged late after haulm growth had ceased (end of August).

Although plant density was halved at the wider spacing, compensatory growth occurred and by the beginning of August haulm weight, leaf area index and radiation interception were similar for the two spacings. During the early stages of tuber growth, yields were greater with closer spacing, but by final harvest tuber yields were similar (close spacing 47·5, wide spacing 45·7 t ha⁻¹; SED 1·02), although ware yields were greater with wide spacing (38·6 and 41·3 t ha⁻¹ for close and wide spacing; SED 1·08).

Radiation interception decreased during the two weeks after early lodging, 27 and 6% less radiation being intercepted by the close- and wide-spaced crops respectively. The crops partially recovered due to greater axillary branch growth and reorientation of leaves and by mid-August the early-lodged crops were intercepting a similar proportion of radiation to the control. From early July to the end of September radiation interception by the close-spaced, early-lodged crops was decreased by 17% and tuber yields decreased by 8% (tuber yields 49·8 and 45·6 t ha⁻¹ for control and early-lodged; SED 1·77). Tuber numbers were not affected by lodging but fewer reached the larger size grades. Over the same period the amount of radiation intercepted and yields were the

same for the control and wide-spaced, early lodged-crops (tuber yields 45.6 and 45.3 t ha⁻¹ for control and early-lodged; SED 1.77).

With late-lodging, radiation interception again decreased and no regrowth of the haulm occurred. There was little effect on wide-spaced crops and from early July to the end of September radiation interception decreased only by about 9% and yields by 6% for the close-spaced crops (tuber yields 49·8 and 47·0 t ha⁻¹ for control and late-lodged; SED 1·77).

Hence whilst lodging decreased radiation interception and tuber growth these effects were partly offset by compensatory haulm growth when lodging occurred early in the season. Although compensatory haulm growth did not follow late lodging, the effects on yield were small. (Wood, Antoniw and Taylor)

Investigation of potato source/sink relationships using grafting techniques. Following last year's preliminary experiment (*Rothamsted Report for 1978*, Part 1, 49), further investigations were carried out on paired, grafted leaves (var. Pentland Crown). At the beginning of linear tuber bulking (three weeks after initiation) one stolon system was removed from each of 25 grafted pairs, one haulm removed from each of 50 grafted pairs and 25 grafted pairs left uncut. Half of the haulm-removed plants were grown at a closer spacing than the rest of the plants. Growth analysis measurements were taken until final harvest at complete haulm senescence.

Compared to a single control stolon system, doubling the haulm:tuber ratio resulted in an increased tuber bulking rate and a doubling of tuber yield on the remaining system. Total plant tuber yield (226 g DW) was not significantly different from that of the control (239 g). The increased yield of a single stolon system was not due to increased tuber numbers or maximum size but to an increased proportion of tubers reaching large size. Haulm growth was not significantly different from that of control plants. On removal of one stolon system the bulking rate of the remaining system did not increase to the level of control plants until two to four weeks after treatment. If tuber bulking controls net assimilation rate a decrease would be expected, but none was observed.

Halving the haulm to tuber ratio resulted in a decrease in bulking rate of tubers on both stolon systems and final yield/plant (150 g DW) was 63% of the control. Growth of axillary branches increased after treatment to give a maximum leaf DW of 79% of the control. In 1978 it was suggested that a tuber yield greater than 50% of control was partly due to a reduction of shading following the removal of one haulm. A fourth treatment was included this year in which half of the haulm-removed plants were closely spaced to give similar shading to that of the controls. The final tuber yield of these plants (130 g DW) was 54% of the control, and maximum leaf DW was 67% of control. However, with earlier senescence of the wider-spaced plants, there was no significant difference in final yield between plants at the two spacings. The lower tuber yield of haulm-removed plants was not due to fewer tubers but to a lower proportion growing to large size.

These results suggest that the amount of assimilate made available by the haulm limits tuber bulking and yield, at least when changes in source/sink size of this magnitude are made. However, the possibility remains that photosynthesis may be maintained by sink activity to nullify the effect of small fluctuations in environmental conditions. (Antoniw, Wood and Soffe)

Weed biology

Park Grass. The survey before the first cut was done on 4–5 June, rather early for a belated season. False oat (Arrhenatherium elatius) and downy oat (Helictotrichon pubescens), rough hawkbit (Leontodon hispidus) and cat's ear (Hypochoeris radicata) were only starting to flower. Meadow vetchling (Lathyrus pratensis) shoots were considerably taller 50

than the grasses up which they normally climb and plants of knapweed (*Centaurea nigra*) with large leaves were conspicuous among the retarded vegetation on many plots. Although most of the buttercups were *Ranunculus acris*, some *R. bulbosus* flowers were seen, especially on the unmanured, limed plot 3a (*Rothamsted Report for 1977*, Part 1, 45). By 17 June the rough hawkbit and cat's ear were flowering. Birdsfoot trefoil (*Lotus corniculatus*) was also flowering on plots 3a, 8a and 7d where it had been only vegetative a fortnight previously.

The autumn survey was done on 30–31 August, in good weather. The autumn cut was not taken until early October. White clover (*Trifolium repens*), lady's bedstraw (*Galium verum*) and betony (*Betonica officinalis*) flowered particularly well this autumn, probably because herbage had remained shorter than usual on the plots until the first cut. Restharrow (*Ononis repens*) continued to flourish in the corner of plot 4/1c (*Rothamsted Report for 1976*, Part 1, 48). Fairy rings, of 1–3 m diameter, associated with three types of fungi (*Marasmius oreades, Agaricus arvensis* and *Boletus chrysenteron*) showed up clearly, mainly on plots with short herbage, e.g. *Agaricus* on 2c and 3c (both unmanured).

No hay samples were taken this year for botanical analysis. (Thurston)

Broadbalk

Field surveys. The spring survey of wheat sections was done in mid-May, just after spraying with a mixture of dicamba, mecoprop and MCPA. Grasses, especially blackgrass (Alopecurus myosuroides) and wild oats (Avena fatua and A. ludoviciana) were inspected on 11 July and the stubble was surveyed on 5-6 September. In spite of the long, cold winter the early-germinating speedwell (Veronica hederifolia) was flowering in mid-May. Knotgrass (Polygonum aviculare) was germinating abundantly on the section after beans and potatoes by 20 April, probably stimulated by the cold winter, but was subsequently damaged by ground frosts of -5° C to -9° C and spraying completed the kill of seedlings which had already lost their cotyledons. Orache (Atriplex patula) was abundant on the same section; it germinated late enough to miss both the ground-frosts and the herbicide. Scentless mayweed (Tripleurospermum maritimum ssp. inodorum) plants were numerous before spraying, but very small, usually less than 3 cm diameter, and poppies (Papaver rhoeas and P. argemone) were less abundant than usual.

The unsprayed section 8 was very weedy, especially with autumn-germinated black-grass which withstood the severe winter and was already approaching ear-emergence in mid-May, in contrast to the few small spring-germinating seedlings on the sections sprayed with chlortoluron in mid-October. Shepherd's needle (Scandix pecten) was wide-spread on section 8 and there were a few plants of corn gromwell (Lithospermum arvense) and corn buttercup (Ranunculus arvensis), all species seldom seen on sprayed fields. Red bartsia (Odontites verna) was again almost absent, on account of the frozen soil during its six-week germination period in February-March. Well-established clumps of meadow vetchling (Lathyrus pratensis) were prominent in May on the unsprayed, unmanured plot 3, section 8, but black medick (Medicago lupulina) was at the cotyledon stage and common vetch (Vicia sativa) plants were very small.

Broad-leaved dock (Rumex obtusifolius) retained its place on plot 19, section 8, and fumitory (Fumaria officinalis) still characterised plot 11 but was well controlled by herbicide. Hemp-nettle (Galeopsis tetrahit), originally on plot 19, spread across the field probably by the use of the baler, and allowed to establish by its resistance to the first herbicide used, has now decreased. Scarlet pimpernel (Anagallis arvensis) showed as usual on plot 10 and there were a few plants elsewhere; germinating in late May it escaped both the winter and the herbicide. Fool's parsley (Aethusa cynapium) was much less abundant than last year (Rothamsted Report for 1978, Part 1, 51) except on plot 16, section 8 and dwarf spurge (Euphorbia exigua) was more prevalent on sections 0 and 1 than elsewhere.

Blackgrass is the most widespread annual weed on Broadbalk, occurring on all except one of the 131 plots in wheat in 1979. The mean scores for abundance, omitting the incomplete plots 1 and 20, confirmed previous findings that blackgrass and wheat are both depressed by giving no fertilisers, and that blackgrass responds more than wheat to PK without N or PN without K; the best control of blackgrass is obtained by rotation including a fallow or two spring-planted crops, plus herbicide in the wheat phase. At higher levels of artificial-fertiliser N, or with farmyard manure, competition from wheat prevents further multiplication of blackgrass.

Wild oats remained at the low level of infestation recorded in 1978 (Rothamsted Report for 1978, Part 1, 50). Sterile brome (Anisantha sterilis) was recorded in wheat on Broadbalk for the first time; two plants were seen on plots 12 (N₂ P Na) and one on plot 7 (N₂ P K Mg), both on section 0 near the Wilderness, where sterile brome has grown for years along the boundaries. This may be a chance occurrence, but merits further observation.

Apart from ubiquitous blackgrass, perennial weeds are now the most formidable problems on Broadbalk. Plots (all with sparse wheat-crops) with old infestations of field horsetail (Equisetum arvense) were densely covered for much of their length and 20 other plot-sections had a few shoots which might form the nuclei of new infestations. Creeping thistle (Cirsium arvense) multiplied during the year, especially on the unsprayed section 8, and hand-pulling was done to try to control it. Bent couch (Agrostis gigantea) now affects 12 plot-sections, six of them on the unsprayed section having densely infested areas. They are all plots with non-competitive wheat crops. Plot 19, section 8 is completely covered with bent couch, to the exclusion of creeping softgrass (Holcus mollis) which used to cover the half nearest to the hedge. However, the old severe infestations of bent couch on plots 10 and 11 of section 9 are greatly reduced and the couch (Agropyron repens) on plot 16, section 0, has been eliminated by spraying the stubble with glyphosate. There are, however, small clumps of both perennial grasses on some other plots. Coltsfoot (Tussilago farfara) had very small leaves in May and was neither abundant nor widespread in the stubble, and somewhat surprisingly after such wet soil in spring, rough-stalked meadow grass (Poa trivialis) was not seen, in contrast to 1978 (Rothamsted Report for 1978, Part 1, 51), presumably being controlled by the cold winter.

The potatoes on section 4 were planted on 14 May and by 18 June annual weeds were scarce, apart from black bindweed (*Polygonum convolvulus*) on plots 1 and 11, but perennial weeds especially creeping thistle and field horsetail formed large dense patches. There was a small patch of coltsfoot on plot 16 and a larger one of field bindweed (*Convolvulus arvensis*) on plot 17. The potato haulms were swiped off on 4 September, without warning before growth ceased so the autumn weed survey was of whatever was still visible on the ground the next day. Field bindweed almost completely covered plot 22—the heaviest infestation of this species ever seen on Broadbalk—and eight more plots were less severely affected. Field horsetail was dense on half of plots 3 and 5 and scattered on plot 6. Creeping thistle was abundant on two-thirds of plot 13 and present on seven others, and plots 16 and 18 had patches of coltsfoot. The occurrence of perennial weeds, especially field bindweed and field horsetail resembles that of section 7 in potatoes in 1977 (*Rothamsted Report for 1977*, Part 1, 46). Only two plots appeared to have had any quantity of annual weeds, plot 19 having black bindweed and knotgrass and plot 1 larger but fewer plants of fool's parsley, fat hen (*Chenopodium album*) and scentless mayweed.

Germination of seedlings in pans of soil. The 3-year period for soil samples taken in in 1976 ended in September 1979, and the pans saved for a fourth and a fifth year from 1975 have not been kept longer (Rothamsted Report for 1978, Part 1, 52).

The 1976 pans produced 22 000 seedlings in 3 years, 37% of which were blackgrass. This is similar to 1974, and contrasts with the 1975 set taken without autumn-applied terbutryne (*Rothamsted Report for 1978*, Part 1, 52). Only 5% of the total seedlings appeared in the third year, compared to 8% and 3% in the third years of the 1974 and 1975 sets.

In the five pans from 1974, retained for a fifth year, 17 seedlings of fumitory (Fumaria officinalis), or 25% of the total, appeared between 1 October 1978 and 30 September 1979. This is the second highest yearly germination, the greatest being 49% in the third year. The early part of 1979 was exceptionally cold and there was a weekend failure in the glasshouse heating and field records from Broadbalk show fumitory to be more abundant after a cold winter. Six other species germinated in the fifth year—knotgrass, poppies, common vetch, parsley piert (Aphanes arvensis), red bartsia and shepherd's purse (Capsella bursapastoris), compared with 17 species surviving into the fourth year of either the 1974 or 1975 set. Occurrence of seedlings in the fifth year did not depend on the number of seeds present initially; 26 poppies represented under 1% of the total, one shepherd's purse, 17% one common vetch, 3% and three red bartsia, 7% of the total seedlings of that species recorded in 5 years. (Thurston)

Staff and Visiting Workers

- G. P. Holbrook joined the department on 1 October with an ARC Research Studentship to study the properties of RuBP carboxylase for the Ph.D. Degree. D. P. Webster (CASE student—Leicester Polytechnic) spent 3 months at Rothamsted studying the hormonal control of storage root growth in sugar beet and K. A. Walker (CASE student—University of Newcastle) was with the Department for 2 months studying nitrogen metabolism in leaves.
- C. P. Whittingham became General Secretary/Treasurer of the International Association for Plant Physiology on 1 January 1979.
- Dr. J. N. Gallagher spent 3 weeks from 24 September to 15 October at Blacklands Research Station, Temple, Texas, under the auspices of the United States Department of Agriculture to advise about functional relationships to be incorporated in models of cereal growth and development.
- A. J. Keys attended and gave a paper at the Gordon Research Conference on glycine decarboxylation, serine synthesis and photorespiration at Santa Barbara, California in January and in June Joan M. Thurston visited Yugoslavia as a guest of the Yugoslavian Weed Science Society to attend a symposium on wild oats. She also visited West Germany in October to attend the Council and Symposium of the Research Group of the European Weed Research Society. In November, C. P. Whittingham attended the Council Meeting of the Federation of European Societies of Plant Physiology in Paris.

Publications

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- 1 KEYS, A. J. (1979) Mechanism of carbon dioxide assimilation in photosynthesis. School Science Review 60 (213) 670-677.
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- 3 LAWLOR, D. W. (1979) Effects of water and heat stress on carbon metabolism of plants with C₃ and C₄ photosynthesis. In: Stress physiology in crop plants. Ed. H. Mussell & R. Staples. New York: John Wiley, pp, 304–326.
- 4 POCOCK, T. O. & LENTON, J. R. (1980) Potential use of retardants for chemical control of bolting in sugar beet. *Plant Growth Retardants. Joint SCI/BPGRG Monograph* No. 4, pp. 47–58.

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- 6 GALLAGHER, J. N. (1979) Field studies of cereal leaf growth. II. The relation between auxanometer and dissection measurements of leaf extension and their relation to crop leaf area expansion. *Journal of Experimental Botany* 30, 637–643.
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- 12 (MARTINEZ-CARRASCO, R.) & THORNE, G. N. (1979) Effects of crop thinning and reduced grain numbers per ear on grain size in two winter wheat varieties given different amounts of nitrogen. Annals of Applied Biology 92, 383-393.
- 13 (Martinez-Carrasco, R.) & Thorne, G. N. (1979) Physiological factors limiting grain size in wheat. *Journal of Experimental Botany* 30, 669–679.
- MILFORD, G. F. J. & (RILEY, J.) (1980) The effects of temperature on leaf growth of sugar beet varieties. *Annals of Applied Biology* **94**, 431–443.
- PEARMAN, I., THOMAS, S. M. & THORNE, G. N. (1979) Effect of nitrogen fertilizer on photosynthesis of several varieties of winter wheat. *Annals of Botany* 43, 613–621.
- 16 RADLEY, M. (1979) The role of gibberellin, abscisic acid, and auxin in the regulation of developing wheat grains. *Journal of Experimental Botany* 30, 381–389.
- 17 (WILLIAMS, E. D.) (1979) Studies on the depth distribution and on the germination and growth of Equisetum arvense L. (field horsetail) from tubers. Weed Research 19, 25–32.