ROTHAMSTED RESEARCH

Report for 1978 - Part 1

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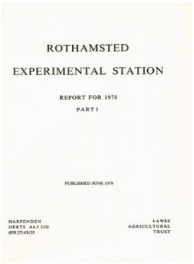

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Introduction

Much of the work in the Department is concerned with the physiology of the cereal crop and extends from experiments in the field on the effect of the time of application of nitrogen fertiliser and the method of drilling and spacing, to metabolic studies in the laboratory on the specific process of photorespiration in the wheat leaf. Considerable attention is given to the effects of water stress both in measurements with the whole crop and with the analysis of the metabolic processes primarily concerned. New work has been initiated on the factors which determine the size of grain in barley supported by a grant from the Home-Grown Cereals Authority.

The work on the effect of aerial pollutants on crop plants has been extended to include a study at the Great House Experimental Husbandry Farm (MAFF) in Lancashire concerning the effects on grass growth in parallel with the continuation of studies on cereal growth in Bedfordshire.

Studies on the physiology of sugar beet undertaken at Rothamsted are now closely integrated with field investigations on the physiology of the crop being undertaken at Broom's Barn; this enables the specialised resources available at Rothamsted, such as controlled environment facilities, to be utilised more directly in elucidation of problems arising from studies on the field crop.

The investigations on the physiology of the potato crop started last year have con-

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tinued and particular attention has been paid to the significance of source/sink relationships.

The annual survey of weeds on Broadbalk and Park Grass were both successfully completed. A review of the botanical analyses of the Park Grass plots from 1856–1976 by E. D. Williams, has now been published and is available from the Librarian at Rothamsted.

Cereal crops

Wheat

Precision sowing, irrigation and nitrogen fertiliser. A study of the effect of sowing practice, water supply and fertiliser on barley in 1977 showed that a seed rate less than normal decreased yields, but row spacing and irrigation were without effect. In 1977/78 a similar experiment was done with winter wheat.

Wheat, var. Maris Huntsman, was sown on 27 October after beans with 314 kg ha^{-1} of 0-20-20 fertiliser in the seed bed. Seed was drilled with a force-feed (Nordsten) drill sowing at 10·5 cm or 21 cm or a precision (Stanhay) drill sowing at 10·5 cm row spacing. Seed rates of 115 or 230 kg ha^{-1} were factorially combined with a spring nitrogen treatment of 90 or 150 kg ha^{-1}, a late (24 May) nitrogen treatment of 0 or 30 kg ha^{-1} and with or without irrigation. Eight extra plots broadcast at the same two seed rates using the Nordsten drill with seed tubes disconnected received early nitrogen treatments only. Other plots drilled with the Nordsten drill at 10·5 cm spacing and the higher seed rate were given nitrogen fertiliser at 0, 30, 60, 120, 150 and 210 kg ha^{-1}. Four plots were sown by hand at the lower seed rate in 10·5 cm rows with a smaller area sown in a 7·3 × 7·3 cm square spacing; they received either the higher or lower rate of nitrogen in April. These extra plots were not irrigated.

Irrigation was applied through trickle lines (at 42 cm spacing with nozzles 30 cm apart) to permit irrigation until the crop was ripe. It was applied when the estimated soil water deficit exceeded 30 mm and was first needed on 30 May; a total of 102 mm was applied between then and 28 July. A total of 273 mm rain fell between 19 April and harvest. Soil water content was monitored using a neutron probe on each of the eight Nordsten-drilled 10·5 cm row plots in the main experiment that received no late nitrogen.

Initial plant populations on 19 December were 154 m^{-1} at the lower seed rate, with no significant differences between drills or row spacing, 267 m^{-1} at the higher rate with the Nordsten drill and 222 m^{-1} with the Stanhay. Broadcast stands were similar to those with the Nordsten drill.

The mean grain yield (at 85% dry matter) with 90 kg N ha^{-1} in April and no late nitrogen was 7·5 t ha^{-1} which was increased by 0·7 t ha^{-1} with an additional 60 kg N ha^{-1} in April and by 0·5 t ha^{-1} with 30 kg N ha^{-1} given in May (SED = 0·18 t). The yields of plots given eight different rates of nitrogen were still increasing up to 210 kg N ha^{-1} and an additional 30 kg N ha^{-1} in May appeared to increase yield similarly to the same amount of extra nitrogen given in April.

Neither drilling method, seed rate, nor irrigation, significantly affected grain yield. Broadcasting yielded a mean of 8·43 t ha^{-1}, not significantly different from the mean of 8·02 t ha^{-1} from plots sown in rows with the same seed rate (or 7·99 t ha^{-1} if precision drilled plots are included). However, hand sowing in rows did significantly enhance the response to the higher rate of April nitrogen by 0·9 t ha^{-1} compared with close row drilling. (Taylor, Thorne and Welbank, with Widdowson, Soils and Plant Nutrition Department)

Rates and times of nitrogen application on winter wheat. Many previous experiments have compared times of nitrogen fertiliser application in terms of dates of application

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rather than stages of plant development. It is considered that nitrogen applied after the ear has initiated and shortly before tillering ceases increases the proportion of tillers that survive, but not their maximum number; nitrogen applied earlier increases tiller number as well as the number that survive. However, there is little experimental evidence that late applied nitrogen increases yield more than earlier applications.

Winter wheat, var. Maris Huntsman, was sown at Rothamsted at 190 kg ha^{-1} after a bean crop with a basal fertiliser (0-20-20) applied at 312 kg ha^{-1}. Three rates of nitrogen fertiliser (60, 120 and 180 kg N ha^{-1}) were applied either before ear initiation (6 March) or a few days after the double ridge stage of ear development (17 April). At the double ridge stage, which is reached shortly before tillering stops, spikelets begin to initiate. The date was determined by dissecting ten main shoots and examining the developing ear under a binocular microscope every week between 16 March and 14 April.

Seedling establishment was only 60% but the mean shoot number was 471 m^{-2} at the first nitrogen application. Maximum shoot number was reached on 16 May. Early nitrogen increased mean shoot number from 559 to 923 m^{-2} (with a range of 702 to 1048 from the lowest to highest application), compared with a smaller increase in the mean to 693 m^{-2} (independent of rate) with late nitrogen treatments.

The time of nitrogen application had no observed effect on the rate of early ear development but the highest rate of late nitrogen delayed anthesis by 1 day.

TABLE 1

Shoot number and dry matter at anthesis in relation to time of application of nitrogen

Date of application	Shoot number m^{-2} N kg ha^{-1}					Shoot weight g m^{-2} N kg ha^{-1}				
	0	60	120	180	Mean	0	60	120	180	Mean
6 March	215	298	396	434	376	386	760	1016	1060	945
17 April		291	358	356	335		762	907	899	856
		SE 7·8			SED 11·0		SE 23·8			SED 33·7

Between 16 May and anthesis shoot number on the early nitrogen plots decreased by 60% but that on the late nitrogen plots by only 50%. At anthesis, plots with the two highest rates of early nitrogen still had significantly more shoots than those with equivalent late nitrogen, although both early and late 60 kg N ha^{-1} produced similar numbers of shoots. All the differences of shoot numbers between treatments were reflected in shoot dry matter yields (Table 1).

Although there was little difference between the leaf area index (LAI) of early and late nitrogen treatments at anthesis (8·1 and 7·6 respectively), the crop with late nitrogen had a flag LAI of 1·13 which was 0·14 more than that receiving early nitrogen. As the crop ripened green leaf area persisted for 1 to 3 days longer on the late as compared with the early nitrogen crop.

The differences in shoot numbers at anthesis persisted until final harvest and were reflected in the final straw yields. The largest straw yield was 10·4 t ha^{-1} with 180 kg early N ha^{-1}.

The late nitrogen treatments produced ears with more fertile spikelets, fewer infertile spikelets and a larger 1000 grain weight than the early nitrogen (16·9 compared with 15·9; 3·27 and 4·14; and 52·4 and 51·2 g respectively). The crop had 36·3 grains per ear (late nitrogen) compared with 32·3 grains per ear (early nitrogen). However, the larger shoot numbers of the two highest early nitrogen treatments meant that the difference in grain yields with early and late nitrogen was quite small, although still statistically significant (Table 2).

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TABLE 2

Yields (t ha^{-1}) of winter wheat given nitrogen early or late

Date of application	Nitrogen application, kg ha^{-1}				
	0	60	120	180	Mean
6 March	4·31	6·12	7·34	7·54	7.00
17 April		6·34	7·43	8·13	7·30
		SE 0·099			SE 0·15

Lodging was more severe with the two highest rates of early nitrogen (particularly 180 kg N ha^{-1}) than with equivalent late nitrogen treatments and could have depressed yields. Lodging did not occur with 60 kg N ha^{-1}, but late application still produced a 4% greater grain yield than early application. The larger and more persistent green flag leaf with late nitrogen treatments was reflected in a significantly larger 1000 grain weight.

Further conclusions about the efficiency of nitrogen use must await chemical analysis of the plant material from the anthesis and final harvests. (Taylor, Thorne and Welbank)

Distribution of photosynthate in wheat. The distribution of ^{14}C-labelled photosynthate is being studied every year on six of the highest-yielding plots on Broadbalk, to provide a background against which values obtained in a single season can be judged. Distribution patterns obtained in 1976 and 1977 were similar to those already reported for three varieties of winter wheat by Makunga, Pearman, Thomas and Thorne (*Annals of Applied Biology* (1978), **88**, 429–437). In 1978, ^{14}C supplied to either of the top two leaves 14 days before anthesis behaved as before—about 50% of ^{14}C remaining at maturity was in the ear and only 16% in the grain. But when ^{14}C was supplied 9 days after anthesis, the amount reaching the ear was 70%, considerably less than observed previously. Unusually this was no less when the $^{14}CO_2$ had been absorbed by the leaf below, rather than the flag leaf. Parallel observations on Maris Huntsman and Hobbit not yet analysed should show whether patterns in 1978 are generally different from those in previous years.

Nitrogen fertiliser did not affect the distribution of ^{14}C in spring or winter wheat either 24 h after exposure to $^{14}CO_2$ or at maturity but did increase the concentration of sugars in the glumes, rachis and top internode of plants gathered late in the day (*Rothamsted Report for 1977*, Part 1, 33). To understand this anomaly, sugar concentrations and relative ^{14}C contents were determined in parts of wheat shoots harvested at dusk following morning exposure of the top two leaves to $^{14}CO_2$. The experiment was done 14 days after anthesis in 1977 with Maris Huntsman given up to 210 kg N ha^{-1}, enough to double grain yield. Nitrogen did not affect the proportion of the ^{14}C absorbed that reached the top internode or ear structures by dusk. For ^{14}C absorbed by the flag leaf, 14% was in the top internode and 5% in the ear structures (27% in the grain, 38% still in the flag leaf, 16% in the rest of the shoot). Only 5% of the ^{14}C from the leaf below the flag leaf had reached the top internode, and 2% the ear structures; more than 60% was still in the leaf exposed to $^{14}CO_2$. In contrast, nitrogen increased the concentration of soluble reducing and non-reducing sugars in the top internode whether measured at dusk or after 24 h. The concentrations in the top internode from plants grown with 30 kg N ha^{-1} were 37·9 (SE 2·7) and 37·1 (SE 3·5) mg g^{-1} fresh weight at dusk and 24 h respectively. For plants grown with 210 kg N ha^{-1}, the corresponding figures were 50·0 (SE 3·2) and 50·1 (SE 2·8) mg g^{-1} fresh weight. There were no differences in the sugar concentrations in the ear structures either with nitrogen or time. These data suggest that current photosynthate does not accumulate in the larger pool of carbohydrates present in the stems with extra nitrogen. (Thomas and Thorne)

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Dark respiration. Earlier measurements in a controlled environment showed that ears of semi-dwarf varieties had a slower rate of dark respiration than the ears of Maris Huntsman (*Rothamsted Report for 1977*, Part 1, 34). A similar difference was found in 1978 when CO_2 exchange of ears was measured in the field. The mean respiration rates for the period 12 to 49 days after anthesis were: Hobbit 0·46, Maris Huntsman 0·49 mg CO_2 per g dry weight h^{-1} (SED 0·005). In this experiment Hobbit produced 0·5 t h^{-1} more dry matter in the grain than Maris Huntsman.

There is considerable circumstantial evidence indicating that respiration rates in cereal plants during grain growth can increase without any concomitant increase in growth. To obtain more direct evidence, an experiment similar to that of Nösberger and Thorne (*Annals of Botany* (1965), **29**, 635–644) was done in a growth room using spring wheat var. Sicco. Shortly after anthesis the number of grains per ear was reduced from the normal 42 to six. Plants with only six grains in the ear showed a decreased rate of photosynthesis, a small increase in stem dry weight, increased production of late tillers and an increased rate of dark respiration per g dry weight of stem. The latter persisted throughout the grain-filling period, including after late tillers were removed at 35 days after anthesis. (Pearman and Thorne)

CO_2 enrichment, growth and yield in wheat. A previous experiment in which spring wheat var. Kleiber was grown in an atmosphere containing a high concentration of CO_2 gave no increase in yield (*Rothamsted Report for 1977*, Part 1, 39). Other varieties were used in this year's experiments. Two experiments were undertaken one on a small scale using winter wheat and a much larger spring wheat experiment. The plants were grown outside in a glass-roofed cage, in 20 cm pots. From emergence, air or air enriched with CO_2 (1200 $\mu l\ l^{-1}$ CO_2), was supplied as described in last year's report.

Of the two varieties used in the winter wheat experiment, Hobbit produces more grains per ear, has lower straw weight and higher grain yield than Cappelle-Desprez (Makunga *et al.*, *Annals of Applied Biology* (1978), **88**, 429–437). Samples were taken at anthesis, anthesis + 16 days and at maturity. There was no evidence of any variety × CO_2 interaction. At final harvest CO_2 enrichment had increased grain yield (mean for two varieties, 47·2 g per pot, compared with 41·8 g; SED 2·7). Total dry matter was also increased (96·4 g per pot, compared to 87·2 g; SED 5·1).

In the spring wheat experiment, Kleiber and Sicco—a new higher-yielding variety—were used. At anthesis all the plants were transferred to controlled environment rooms. Two rooms were enriched to 1200 $\mu l\ l^{-1}$ CO_2 during the 16 h light period, the other two rooms were maintained at 400 $\mu l\ l^{-1}$ CO_2. Mean irradiance for half of each room was 635 $\mu E\ m^{-2}\ s^{-1}$, and for the other half 250 $\mu E\ m^{-2}\ s^{-1}$. Samples were taken for growth analysis at anthesis, then weekly up to maturity. Rates of gross and net photosynthesis and rates of dark respiration were measured. There were no interactions. At final harvest CO_2 enrichment had increased grain yield (43·9 g per pot, compared with 37·7 g, SED 2·0) and total dry matter (93·5 g per pot, compared with 82·2 g, SED 4·2). The higher irradiance had increased grain yield (47·4 g per pot compared with 34·2 g, SED 2·0) and total dry matter (94·0 g per pot compared with 81·6 g, SED 4·2). Kleiber yielded more grain and more total dry matter than Sicco (Grain: Kleiber 45·1 g per pot; Sicco 36·5 g per pot; SED 2·0; Total dry matter: Kleiber 95·4 g per pot; Sicco 80·2 g per pot; SED 4·2). Detailed consideration of results awaits further statistical analysis. (Kendall and Thomas)

Effects of temperature on photosynthesis and respiration. The effect of photorespiration on net photosynthesis by wheat leaves at various temperatures was assessed by measuring net CO_2 exchange in 2 and 21 % oxygen. At 25°C higher oxygen inhibited at both 314·5

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and 380 μl l^{-1} CO_2. At 10°C, when the concentration of CO_2 was 314·5 μl l^{-1}, photosynthesis was significantly faster in 2 compared to 21% oxygen, but with 380 μl l^{-1} CO_2 the reverse was true. If the effects of decreased oxygen concentration were the result solely of reduced oxygenase activity of ribulose bisphosphate (RuBP) carboxylase/oxygenase, oxygen should have inhibited at both CO_2 concentrations and to a greater extent if the *in vitro* kinetics are applicable. In other experiments $^{14}CO_2$ was supplied to leaves during steady photosynthesis with or without a further period of 1 min in 1000 μl l^{-1} $^{12}CO_2$ in the light or in 350 μl l^{-1} $^{12}CO_2$ in darkness. Analysis of the distribution of ^{14}C in various products showed that the flux of carbon through the glycollate pathway was essentially as predicted by the known properties of RuBP carboxylase/oxygenase. However, relatively more ^{14}C was found in phosphoglyceric acid (PGA) and hexose monophosphates (HMP) at lower temperatures, without corresponding increases of ^{14}C in uridine diphosphoglucose or RuBP. The rate of sucrose synthesis appears to become limiting at low temperatures causing the accumulation of HMP which may then directly inhibit synthesis of RuBP or reduction of PGA, or affect the carboxylase/oxygenase activities, and hence net photosynthesis. Evidence for a slight inhibition of photosynthesis in 2% compared to 21% O_2 (not significant $P = 0{\cdot}05$) in the presence of 380 μl l^{-1} CO_2 was observed in the above experiments; similar observations have been reported by Jolliffe and Tregunna (*Canadian Journal of Botany* (1973) **51**, 841–853) and Mächler and Nösberger (*Oeceologia* (Berlin) (1978) **35**, 267–276). An inhibition might occur since, when photorespiratory metabolism is decreased in 2% O_2, hexose phosphates would be synthesised more rapidly and any feed-back effect increased. Sucrose synthesis takes place in the cytoplasm (*Rothamsted Report for 1973*, Part 1, 92) so the accumulation of hexose phosphate also may be in the cytoplasm rather than in the chloroplast. Although free exchange of phosphate esters across the chloroplast envelope is thought to take place via triose phosphates, further investigation of the site of accumulation of HMP at low temperature would be valuable in relation to studies of the regulation of photosynthesis. (Arrabaca)

Fate of ammonia produced during photorespiration. Most photorespired CO_2 is produced in the glycollate pathway during the conversion of two molecules of glycine to one of serine. This reaction, which takes place in the mitochondria, gives rise to ammonia in equimolar amounts to CO_2 and serine. Calculations from published rates of photorespiration and nitrate reduction suggest that the former process may produce ten times more ammonia in leaves than the latter. Detached flag leaves accumulated ammonia when supplied with methionine sulphoximine (MSO), a specific inhibitor of glutamine synthetase. When these leaves were supplied with [^{15}N] glycine as well as MSO, 50% more ammonia accumulated and because of its ^{15}N content this ammonia was clearly derived from the added glycine. Similar experiments with protoplasts from pea leaves also showed accumulation of ammonia-N derived from glycine in the presence of MSO. The results suggest that ammonia produced by photorespiration, like that produced from newly-assimilated nitrate (Miflin & Lea, *Phytochemistry* (1976), **15**, 873–885), reacts first with glutamate to form glutamine catalysed by glutamine synthetase; it is not reacted directly with 2-oxoglutarate to form glutamate catalysed by glutamate dehydrogenase in the mitochondria. Glutamine synthetase is absent from mitochondria but present in the cytosol and in chloroplasts (see Biochemistry Department Report, p. 21). To confirm the rôle of glutamine synthetase rather than glutamate dehydrogenase [^{15}N, 1-^{14}C] glycine was supplied to mitochondria obtained from spinach leaves by the method of Douce, Moore and Neuberger (*Plant Physiology* (1977), **60**, 625–628). Almost equimolar amounts of CO_2 and ammonia were released whether or not 2-oxoglutarate was supplied with the glycine. Thus, nicotinamide adenine dinucleotide (NAD) in the

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mitochondrial matrix reduced during the oxidation of glycine, was not used to reductively aminate 2-oxoglutarate catalysed by the endogenous glutamate dehydrogenase. When, instead of 2-oxoglutarate, adenosine triphosphate (ATP), glutamate and a purified preparation of glutamine synthetase was added, the conversion of glycine to serine and CO_2 was stimulated but little ammonia was evolved. The stimulation of glycine oxidation is to be expected because adenosine diphosphate (ADP) produced from ATP during synthesis of glutamine provided the acceptor for oxidative phosphorylation that accompanies conversion of glycine to serine (*Rothamsted Report for 1971*, Part 1, 108–109). We conclude that ammonia produced in leaves because of photorespiration is assimilated by the action of glutamine synthetase and glutamine 2-oxoglutarate amino transferase (GOGAT). (Bird, Cornelius and Keys, with Miflin, Lea and Wallsgrove, Biochemistry Department)

Protoplasts from wheat flag leaves. Huber and Edwards (*Plant Physiology* (1975), **35**, 203–209) readily isolated protoplasts with a high capacity for photosynthesis from young wheat plants. Leaves from older plants yielded few protoplasts and these had little photosynthetic activity. We have attempted to obtain active protoplasts from wheat flag leaves in order to extend studies of the photosynthetic mechanism during grain-filling.

Satisfactory protoplasts were obtained if, instead of cutting the leaves into segments before treating with macerase and cellulysin (Calbiochem), the under-surface of the leaves was gently abraded with emery paper. The yield was improved by stripping away the remains of the lower epidermis following digestion for 1 h. The epidermis and underlying stereome fibres resisted digestion so that if they were not removed they prevented release of protoplasts. Leaf tissue treated with macerase alone released the mesophyll tissue as structures which are single elongated cells with several lobes; no cell walls were visible between lobes and following use of the Feulgen stain only a single nucleus was observed. When subsequently treated with cellulysin the cell wall is removed but the protoplast within does not change much in shape and is not easily disrupted mechanically. From studies of longitudinal sections and of partly digested leaf tissue we conclude that the mesophyll of flag leaves of wheat, and that of several common grasses, consists entirely of these elongated lobed cells. They are arranged within the leaf with their longitudinal axes parallel to the vascular bundles. The cells isolated by the treatment with macerase alone have either been killed during isolation or are cells that have already died within the leaf. Active protoplasts, isolated in low yield by the combined action of macerase and cellulysin are spherical in shape but the maximum size observed is equivalent to only 25% of the total volume of the lobed mesophyll cells. We conclude that, once the support of the cell wall is lost, the protoplasts of the lobed cells rupture. The spherical bodies are portions of the larger protoplast around which the membrane has re-sealed. (Roberts, Keys and Bird)

Barley

Effects of water stress on growth and grain production of spring barley. Both field and laboratory studies have shown that developing cereals, particularly those sown in spring, are sensitive to water stress, especially before the roots have penetrated to deeper zones. Soil water potentials of less than one bar in the top 25 cm of soil cause a large decrease in leaf area and restrict tillering, thereby slowing the rate of ear development and decreasing the number of ears formed per unit ground area. This, together with smaller ear and grain size, decreases the potential yield irrespective of conditions later (*Rothamsted Report for 1976*, Part 1, 34).

To examine the effects of stress on growth and to test methods of measuring water

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potential and plant function barley plants were grown in large pots under a polythene shelter to keep off rain, but otherwise normal atmospheric conditions. The pots, containing 75 kg of Geescroft clay soil, were planted with 24 seeds of barley, var. Julia, on 23 May and fully watered. Tensiometers and psychrometers were installed at 15, 30 and 60 cm depth. One week (early stress) or 6 weeks (later stress) after emergence some pots were not watered and the development of stress was followed. Conditions were cold and humid; after 1 week the surface 15 cm of soil had almost reached −0·7 bar whilst the lower soil was still at potentials greater than −0·4 bar. During this time the crop grew similarly in both wet and dry pots. When the soil temperature was below 6°C at mid-day leaf extension stopped but the rate was about 2 mm h^{-1} between 8 and 20°C. Leaf morphology was unaffected and no other factors were significantly different.

After 2 weeks' drying the soil water potential at 30 cm depth was −0·5 bar and in the bottom layer −0·3 bar. Leaf extension was slowed by 20 to 30% on main stems. Tillers were markedly affected by stress. The first tiller had developed to about the same stage in both wet and dry pots but subsequent tillers were small and had fewer leaves. Only three tillers were formed in dry, and up to nine tillers in wet, pots.

Once the soil throughout the pot had a water potential of less than −0·4 bar for several days the effects on the crop became more obvious. When wilting started, the older leaves yellowed rapidly; some leaves and young tillers died. Chlorophyll measurements showed that the younger mature leaves had similar chlorophyll content and ratio of chlorophyll a to b.

The leaf water potential of control plants was −10 to −15 bar for most of the early stress period and for the dry plants −15 to −20 bar. The osmotic potential was about −20 bar at the start of the experiment, falling to −30 to −40 bar in the wet and −40 to −50 bar in the dry treatment later, so that turgor was large but not sufficient to maintain growth. Relative water content changed little during early stress; only at soil water potentials of less than −0·8 to −1·0 bar did it change more than 15% from the control values.

Plants which had been irrigated early and had formed much leaf and stem material developed a smaller water and osmotic potential and relative water content when subjected to stress, than the earlier stressed crop. Soil water content and potential became lower than in the longer stressed treatment, the leaves died faster and had less chlorophyll, stomatal resistance was larger, and photosynthesis was decreased. All this despite better exploitation of soil in the pot by later stressed plants compared with early stress plants. In many respects the later stress in pots resembled late stress in the field. Early stress, developed over a period, appears to cause changes in the plant which enable it to adjust more satisfactorily to an adverse environment.

Ear growth in the early stressed plants was greatly affected. The fewer ears produced under dry conditions had only 16 grains compared to 24, even when stress was relieved during grain filling. Water stress caused death of two to three grains at the base and up to eight grains at the tip of the ear when water potential in the leaves reached −20 bar, for a period of 1–2 weeks. The remaining grains in the ear were smaller although those in the sixth to tenth position tended to be much larger than those at base or tip. Grain weight was also smaller in droughted plants. One interesting, if unexplained, result of the experiment was the large grain produced, 46 mg average in control and 36 mg in early dry treatments and 34 mg in later stress. Possibly the assimilate supply in the plants at crucial times was much greater than normal in the field because of the better exposure to light. (Lawlor)

Factors determining barley grain size. Heavy applications of nitrogen fertiliser can increase barley yields considerably but are often associated with an increased proportion

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of small grains making the sample unsuitable for malting. The physiological factors which control grain size and which underlie the increased production of small grains were investigated. Barley grain size is thought generally to be controlled by post-anthesis assimilate supply but recent work has indicated that environmental conditions before anthesis are important in determining grain size (Prince, *New Phytologist* (1976), **76**, 377–389). The importance of growth conditions during the phases of ear growth (maximum primordial number to anthesis), endosperm cell division (approximately the 14 days after anthesis) and linear grain growth in determining final grain size was examined in sub-plots of a spring barley crop, var. Porthos, receiving 0, 50 and 100 kg N ha^{-1}. Growth was stimulated during ear growth and endosperm cell division by removing alternate rows (thinning). One sub-plot of each treatment was shaded during linear grain growth with 'Lobrene' netting which decreased the photosynthetically-active radiation by 60%. Preliminary analysis of ears borne on main stem and first leaf tillers indicated that thinning during ear formation did not increase dry mass per grain (M_g) significantly. Thinning during endosperm cell division increased M_g by an average of 10% for crops which received nitrogen and had formed about 14 000 grains m^{-2} but had no effect on the crop which received no nitrogen and had only formed about 10 000 grains m^{-2}. These results suggest that the period shortly after anthesis is particularly important in determining grain size in crops which have formed many grains and which have a large yield potential. To determine whether thinning at anthesis exerted its main effect by increasing endosperm cell numbers and consequently grain growth rate or, simply by increasing the supply of assimilate available for grain growth will require future experiments in controlled environments. (Gallagher)

Effects of aerial pollutants on barley growth and yield. A site in the Bedfordshire brickfields midway between the brickworks of Stewartby and Ridgmont was made available by the London Brick Company. Spring barley, var. Porthos, was grown in both open and closed houses. The experimental design was as in previous years (*Rothamsted Report for 1977*, Part 1, 39). The open-topped chambers had been modified by fitting a collar and baffles to reduce contamination of the air inside the chamber by incursions of ambient air. Modifications to the air distribution system produced a more uniform distribution of air around the plants.

The mean level of sulphur dioxide during the growth period was 50 $\mu g\ m^{-3}$ but there were peaks in excess of 500 $\mu g\ m^{-3}$ that lasted for several hours. Filtration reduced the average level of SO_2 by 90% in the closed and 65% in the open chambers. The efficiency of the open chamber in reducing pollutant concentrations decreased after anthesis. This is thought to be due to the increasing barrier to air diffusion offered by the growing crop. Analysis of the leaves for fluoride showed that concentrations within the filtered chambers remained low throughout the season.

The yield of plants grown in the modified open-topped chambers was close to that of outside plots and compared favourably with results from previous experiments using unmodified chambers. Development of plants in the closed chambers was 10 days ahead of those grown in the open chambers which were again 7–10 days ahead of those grown outside.

Significant differences in total dry weight and straw weight at anthesis and final harvest were observed but differences in grain yield were not significant. (See Table 3.)

In 1979 the experiment will be repeated on the same site but using eight open-topped chambers only to increase replication and improve precision. By increasing the height of the chambers and growing a shorter-strawed variety it is hoped to reduce contamination of the air in the filtered chambers after anthesis.

A similar experiment, using modified open-topped and closed chambers has been set

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TABLE 3

Final harvest for barley plants grown in Bedfordshire

	Open chambers		Outside plots
	+filter	−filter	
Straw wt., g m^{-2}	593***	387***	492
Ear dry wt., g m^{-2}	692	528	588
F levels, ppm w/w	68***	110***	197***

N.B. Straw weights and fluoride levels, filtered and unfiltered, are significantly different at 5% level (***).

up at Great House Experimental Husbandry Farm in Lancashire. Its purpose is to determine the effect of ambient levels of pollution on the growth of a native and an imported population of S23 ryegrass. (Buckenham and Parry)

Effect of temperature on the growth of native C_3 and C_4 grasses. *Spartina townsendii* (*sensu lato*) is exceptional amongst known C_4 species in being native to cool temperate regions (*Rothamsted Report for 1977*, Part 1, 38). The growth of *S. townsendii* was compared with that of a 'native' C_3 grass *Lolium perenne*, for plants from the seedling stage to 80 days of growth. Plants were grown in controlled environment rooms at temperatures of 10, 15, 20 and 25°C and a photon flux density of 600 μE m^{-2} s^{-1} during a 14 h day length. In addition, some plants were transferred from 20 to 10°C and returned to 20°C after 3 days. After 30 days at 25°C, *S. townsendii* had the higher relative growth rate (RGR), 125 g kg^{-1} d^{-1}, compared with 75 g kg^{-1} d^{-1} for *L. perenne*. This difference largely reflects a difference in net assimilation rate (NAR). In contrast, at 10°C RGR of *L. perenne*, 57 g kg^{-1} d^{-1}, was very much greater than that of *S. townsendii*, 18 g kg^{-1} d^{-1}, due to a lower value of both leaf area ratio (LAR) and NAR. At the intermediate temperatures, 15 and 20°C, NAR was similar for the two species. The maximal RGR was at 15°C for *L. perenne* and at 25°C for *S. townsendii*. The short exposure to low temperature did not produce subsequent significant depression of growth in either species. Previous work suggests that a significant depression would have been expected in other C_4 grasses, e.g. *Zea mays* and *Sorghum bicolor*. These results indicate that the C_4 species *S. townsendii* is not as well adapted to a temperate climate as the C_3 grass *L. perenne*. Growth of *S. townsendii* is very much poorer at 10°C and better only at temperatures above 20°C under the light and water conditions studied. However, we have demonstrated that growth rates of *S. townsendii* are similar to *L. perenne* at 15°C and still significant at 10°C, temperatures at which growth in other C_4 species is poor or non-existent. (Dunn, Thomas and Keys)

Growth substances in cereals

Gibberellins in germinating grain. There has been some confusion concerning the occurrence of GA_1 and GA_3 in germinating cereal seeds. Moreover, whilst the effects of applied GA_3 on the release of hydrolytic enzymes from the aleurone layer have been frequently investigated, most biosynthetic studies have examined the metabolic fate of GA_1. Relatively large amounts of biologically-active gibberellins accumulate in the endosperm of wheat seeds during the first week of germination (*Rothamsted Report for 1975*, Part 1, 40) and this material has been used to attempt an unambiguous identification of the gibberellins by combined gas chromatography-mass spectrometry (GC-MS).

Extracts from one-week-old germinated seed (var. Maris Huntsman) were purified by column and thin-layer chromatography (TLC) prior to derivitisation and analysis by gas-layer chromatography (GLC). A large mass of interfering material eluted together

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with the suspected gibberellins from columns of OV-101 was sufficiently resolved on columns of OV-210. No mass peaks of the suspected gibberellins could be detected by analytical GLC (OV-210) so for combined GC-MS analysis computer controlled continuous repetitive scanning was used to generate and process the mass spectral data. The results indicated a good full mass spectrum of MeTMS GA_1 and a much weaker full mass spectrum of MeTMS GA_3. We now hope to obtain reliable quantitative estimates of these compounds in germinating grain using suitable deuterated internal standards and selected ion current monitoring. (Lenton, with Mr. P. Gaskin and Prof. J. MacMillan, University of Bristol)

Gibberellins in developing wheat grain. The content of biologically-active gibberellins in developing wheat grain is optimal at maximum grain fresh weight and at the time of most rapid grain filling (Wheeler, *Annals of Applied Biology* (1972), **72**, 327–334). Attempts to modify the relationship between gibberellin content and dry matter accumulation in intact plants by altering the environment have proved relatively unsuccessful (Radley, *Annals of Applied Biology* (1976), **82**, 335–340). Evidence from short-term feeding of the precursor, *ent*-kaurene, or from applications of the inhibitor, chlormequat chloride (CCC), to detached ears in solution culture suggested that they had only a limited capacity for *de novo* gibberellin synthesis but that the enzymes for the later steps to the gibberellins were present. A more detailed understanding of the chemical nature and metabolism of the gibberellins in various tissues of the developing grain is required before their functional significance can be assessed.

Initial attempts to isolate and identify the gibberellins in developing seeds by combined GC-MS have proved difficult because of large amounts of impurities present in extracts. Nevertheless, several novel gibberellins have been tentatively identified in extracts of field-grown grains (var. Maris Huntsman) harvested in 1976 and 1977. Confirmation of the proposed structures will have to await partial synthesis from known compounds. Briefly, two known gibberellins, GA_{19} and GA_{44}, have been conclusively identified. Among the novel compounds are two trihydroxy- and one dihydroxy-derivatives of GA_9, a monohydroxy derivative of GA_6 and a compound closely related to GA_{16}. The extent to which these new compounds contribute to the biological activity remains to be assessed. Undoubtedly, the sequence of events occurring in the developing grain will prove far more complex than those of the germinating grain. (Radley and Lenton, with Mr. P. Gaskin and Prof. J. MacMillan, University of Bristol)

Gibberellin from developing wheat embryos. It is known that the embryos of germinating wheat grains synthesise gibberellin which readily moves out of the tissue. The synthesising ability of the embryos of developing grains which were incubated 24 h on agar have now been studied using greenhouse-grown plants of wheat var. Sicco. Considerably more gibberellin was found with incubated embryos taken 21, 28 or 35 days after anthesis, although hardly any gibberellin moved into the agar at 42 days after anthesis. This indicates that the biosynthetic system for gibberellin is present in the developing embryo. It is proposed to use this technique to obtain gibberellin samples free from many of the impurities which interfere with mass spectrometry. (Radley)

Grain enlargement in wheat. The factors regulating grain growth were studied by comparing the large grains developed after most of the grains were removed from the ear soon after anthesis with grains from intact ears. When grain removal took place 10 days after anthesis the effects on grain volume and weight and aleurone cell number were less than the effects due to early degraining (*Rothamsted Report for 1977*, Part 1, 41), but the endosperm cavity was similar in size indicating that the endosperm cells in both

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groups had not enlarged to fill the space available. The starch grains in caryopses from the late degrained ears were fewer and heavier than in those from early degrained ears or intact ears. The percentage of dry matter that was not starch was greatest in caryopses from early degrained ears, presumably due to the structural part of the increased number of cells or to increased protein. The endogenous growth substance content of the caryopses during the early stage of development is being examined. (Radley)

Sugar beet

Temperature and leaf development. The previous study using varieties commercially grown in Britain of early leaf growth in controlled environments with temperatures between 7 and 20°C (*Rothamsted Report for 1977*, Part 1, 41), has been extended to a further 14 European genotypes. Mathematical analyses of the expansion of individual leaves and leaf area per plant have been based on generalised logistic curves fitted to the data by the maximum likelihood programme. The analysis has shown that faster rates of leaf growth of certain varieties are initiated early in leaf development, between primordial formation and leaf unfolding. (Milford, with Janet Riley, Statistics Department)

Temperature is probably the major climatic factor affecting leaf growth in the field. One of the objectives of the controlled-environment work is to help interpret leaf area development in the field. Therefore, during 1978, parallel studies began on the development of leaf canopies in the field within the wider context of a collaborative crop productivity investigation at Broom's Barn (pp. 64–65). (Milford, with Broom's Bar staff)

Effect of light quality and duration of growth. The effect of extending day length with light of different spectral quality on vegetative growth of sugar beet has been described previously (*Rothamsted Report for 1976*, Part 1, 42). Plant dry matter was increased 25% after 6 weeks at 15°C through an increase in NAR with less effect on leaf area when day length was extended from 12 to 16 h with either photosynthetically-active radiation or low intensity red light. By contrast, extending the day length with a mixture of red and far-red light of low intensity from incandescent lamps also increased plant growth by 25% but did so by markedly increasing leaf expansion and petiole growth thus modifying the leaf canopy so as to increase light interception. It appears probable that the far-red component of incandescent light is responsible for the photomorphogenetic stimulation of leaf growth. This hypothesis was tested directly by growing young plants under a standard 12 h day (400 μE m^{-2} s^{-1}, 400–700 nm) with 4 h extensions of low energy non-photosynthetically-active incandescent light (17 μE m^{-2} s^{-1}, 600–760 nm), red light (6 μE m^{-2} s^{-1}, 600–700 nm) or far-red light (4 μE m^{-2}, s^{-1}, 700–760 nm).

Day length extensions with pure red light increased plant dry weight by 10% after 5 weeks and there was some indication of an increase in dry matter partition in favour of storage root growth. Day length extension with incandescent light increased plant dry weight (25%), leaf expansion (32%) and petiole growth (42%); far-red light alone increased growth even more and increased dry weight (34%), leaf area (45%) and petiole length (56%). Thus the far-red wavelengths are the photomorphogenetically-active components of incandescent light.

These observations may have important implications for field-grown crops. Green leaves transmit far-red light more than other wavelengths. Thus the crop canopy shifts the balance in incident light towards the photomorphogenetically-active wavelengths and in certain situations this could have effects on shoot growth and dry matter distribution. The known changes in spectral energy distribution of sunlight towards the far-red wavelengths at sunrise and sunset are probably used by plants as a timing mechanism for

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various physiological events but the growth responses to far-red light reported here are difficult to reconcile in terms of current concepts of phytochrome action in green plants. (Milford and Lenton)

Endogenous gibberellins in sugar-beet leaves. Preliminary attempts to isolate and identify the gibberellins of young sugar-beet leaves suggested the possible presence of gibberellic acid (GA_3). A purified extract of young apices gave a peak on analytical GLC (OV-101) with a retention time corresponding to MeTMS GA_3 which on GC-MS analysis gave a mass spectrum with significant ions at m/e 504 (M^+ of MeTMS GA_3, MeTMS GA_{30} or MeTMS GA_{22}) and m/e 474 (unidentified) (*Rothamsted Report for 1977*, Part 1, 43). In order to exclude the possibility that GA_3 may have been a laboratory contaminant the experiment was repeated with all glassware washed in chromic acid before use. This time no mass peak of the suspected gibberellin was detected by analytical GLC (OV-210) so the repetitive scanning technique was used for GC-MS analysis. Identifiable mass spectra of MeTMS GA_{19}, MeTMS GA_{44}, MeTMS GA_{20}, MeTMS GA_1, MeABA and MePA were obtained. There was no evidence of GA_3 in this extract. The amount of useful information that can be generated from relatively impure plant extracts using sophisticated data acquisition facilities for GC-MS analysis is far superior to that obtained from manual scanning of mass peaks which was employed in the initial attempt. The importance of using ultraclean glassware to avoid possible cross-contamination is also apparent. (Lenton, with Mr P. Gaskin and Prof. J. MacMillan, University of Bristol)

Root growth and sugar accumulation. The potential capacity of different varieties of sugar beet to store sugar is related to root structure. Root size is determined by the number of cambial rings produced and the extents of cell division and expansion in each ring, whereas sugar concentration is determined largely by the ultimate sizes of the cells (Milford, *Annals of Applied Biology* (1973), **75**, 425–438). It is therefore important to understand the developmental anatomy of the storage root, and examine how it varies with genotype and is modified by cultural or environmental conditions.

The anatomical development of the storage root of widely different genotypes of *Beta vulgaris* has been analysed with reference to ring numbers and their relative contributions to final root volume. Two commercial beet varieties were compared with a small root/high sugar breeding line and with mangold. Few plants of the breeding line were available but the data suggest that it develops in a similar way to the commercial beet varieties without reaching the same size. Ring number at maturity ranged from seven in mangold to eight to ten in the breeding line and 11 to 15 in the two commercial varieties. When roots were 10 mm in diameter the inner three rings contributed 60–70% of the cross-sectional area in all types. During subsequent development significant differences occurred. In mangold at maturity the first four rings contributed 60% of the total area (accounting for 80% of the diameter) whereas in commercial varieties the contribution of later-formed rings increased so that at maturity each ring contributed more or less equally to total area. Morever, the width of the first four rings in mangold continued to increase late into the season, long after such activity had ceased in comparable rings in the commercial varieties.

This work will continue with detailed studies of the sizes and sugar contents of cells within each ring. (Pocock)

Growth regulator trials. The short-term trials described last year (*Rothamsted Report for 1977*, Part 1, 43) have been used to determine the effects of the chemical triacontanol on sugar beet. Triacontanol is a naturally occurring straight chain primary alcohol

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($CH_3(CH_2)_{28}.CH_2OH$) reported to have exceptional growth stimulatory properties (e.g. Ries *et al.*, *Science* (1977), **195**, 1339–1341; Ries & Wert, *Planta* (1977), **135**, 177–182).

Sugar-beet seedlings grown in a greenhouse were sprayed to run-off with an aqueous solution of triacontanol containing 1, 0·1, 0·01, 0·001 and 0 mg a.i. litre^{-1} after the first two leaves were expanded. After 1 week plant dry weight was reduced by 10% at all but the highest concentration although fresh weight was not affected. After a further week, plant dry weight was increased by 12% at 0·01 mg litre^{-1} and by 20% at 0·001 mg litre^{-1}. Three weeks after treatment, when the plants had six leaves, plant dry weight at 0·001 mg litre^{-1} was 30% greater than the control.

The trial was repeated using younger plants (sprayed when the first two leaves were just appearing) which are more comparable to the material used by Ries *et al.* However, after 2 weeks there was a reduction in plant dry weight by 10% at all concentrations.

The results justified incorporating triacontanol in a large-scale pot trial during the summer. Triacontanol at 2 mg and 0·02 mg a.i. litre^{-1}, was sprayed on plants at the four to six leaf stage at 60 ml m^{-2}, and samples taken throughout the season (*Rothamsted Report for 1975*, Part 1, 46).

One week after treatment leaf area and petiole weight of treated plants were increased by 15%, reflecting an increase in total leaf number from 8·0 to 8·5. However, this effect was lost and 4 weeks after treatment plants treated with the lower rate of triacontanol had a lower total leaf number, although total leaf area was not reduced.

After 9 weeks, low and high rates of triacontanol reduced petiole length by 15 and 30% respectively, although neither number nor weight of petioles was affected. Twelve weeks after treatment root weight was increased by 15% by triacontanol at 2 mg litre^{-1} with no effect on total plant weight.

At the end of the season in late September there was a significant increase of 18% in root fresh weight by triacontanol at 2 mg litre^{-1}. The low rate increased root weight by 12% although this was not significant. Again, total plant dry weights were not affected. Since sugar concentrations at final harvest were not affected sugar yield per root paralleled root weight.

Triacontanol appears to increase total dry weight of young plants of sugar beet depending on the time of application, whereas in older plants it increases root weight without altering total plant weight. (Pocock)

Potatoes

Leaf canopy structure and crop growth. Tuber yields are related to the amount of light intercepted by the crop (Scott & Wilcockson, In: *The potato crop* (1978), Ed. P. M. Harris. Chapman & Hall, pp. 679–704). Varying haulm structure affected the proportion of radiation intercepted, but in 1977 the effects on growth and yield were small (*Rothamsted Report for 1977*, Part 1, 44). The growth, radiation interception, photosynthetic rates and yield of Pentland Crown crops with varying haulm structure were examined further in 1978. Either the apex from all above-ground stems, or all axillary branches were removed from initiation onwards; alternatively morphactin (chlorflurecol methyl, an anti-auxin which promotes branching) was sprayed as a 10 ppm aqueous solution at 830 litre ha^{-1}.

The crop grew rapidly after emergence, but soon after initiation in mid-June haulm growth slowed and leaf areas declined from mid-July with complete senescence in mid-September. Removal of the apex produced a short bushy plant with many small leaves and the stems lodged slightly later than in the untreated crop. Removal of the axillary branches gave longer stems with fewer, larger leaves. Despite these differences in structure haulm weight, leaf areas and leaf area duration (LAD) were unaffected. Yields were

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unchanged: 45·6, 43·9 and 45·3 ($\pm$ 1·64) t ha^{-1} for control, apex and axillary branch removal. The results suggest that the branching structure of the haulm is of less importance than the production of sufficient well-orientated leaves to give maximal radiation interception and maintaining this for as long as possible.

As in 1977, morphactin caused stunting, malformation of new leaves, decreased leaf size and total leaf area and final yields were lower (39·2 t ha^{-1}). Throughout the growing season total plant and tuber dry weights were greater for a given LAD than in the control. In 1978 in the 4 weeks after treatment with morphactin LAI was less than three and ground cover incomplete. Over this period LAD was 25% less than in the control, but radiation interception was decreased by only 8–9%, indicating that the leaves were orientated in such a way that the light was more effectively intercepted. NAR was 20% greater than in the control. Although there was no clear indication of a greater photosynthetic capacity of individual upper leaves, the overall net photosynthetic rate of the crop was greater. Thus at low LAI leaf orientation within the canopy is important in determining radiation interception and crop growth. This advantage in crop growth was soon lost and yields were restricted by earlier haulm senescence.

Morphactin treatment shortly after initiation restricted haulm growth rather than tuber bulking, and although there was partial recovery of haulm growth the plants senesced earlier. Other factors, such as low temperature, low light intensity, or shortage of water, can have a similar effect. (Wood, Antoniw and Taylor)

Investigation of potato source/sink relationships using grafting techniques. The rate of tuber bulking is often regarded as being limited by internal factors within the plant. Moorby (*Annals of Botany* (1970), **34**, 297–308) and others have suggested that this is because the rate of photosynthesis is regulated by tuber activity. Evidence to support this has come from experiments where NAR was increased by reduction of source size and decreased by reduction of sink size (Dyson, *Ph.D. Thesis, University of London* (1965); Nösberger & Humphries, *Annals of Botany* (1965), **29**, 579–588). However, these experiments often involved complete tuber removal, and were often continued only over a short period. In the experiments to be described here, the ratio of haulm to tuber was doubled or halved, leaving an entire range of leaf or tuber ages and sizes.

Plants from two single-eye pieces of the potato var. Pentland Crown were planted one either side of a central polythene division in a 30 cm pot. The stems of each pair of plants were grafted together so that the graft had taken before tuber initiation occurred. Eight or 27 days after initiation the stem of one of the paired plants was cut below the graft—thus removing one entire root and stolon system plus tubers. A third treatment was to cut one of the paired stems above the graft 27 days after initiation, thus removing one entire haulm. The control plants were grafted but not cut. This was a preliminary experiment using only three paired plants per treatment. Plants were harvested 13 weeks after initiation, when haulm senescence had begun.

Doubling the haulm:tuber ratio increased tuber yield on the remaining stolon system by 52% when stolons and tubers were removed shortly after initiation or 62% when stolons and tubers were removed at the beginning of the linear bulking phase. This suggests that tuber bulking rate was controlled by assimilate availability. The yield of plants cut at 8 days was similar to that of plants cut on day 27 but tuber number was increased in the former and the mean size of existing tubers increased in the latter.

Halving the haulm:tuber ratio at the beginning of the linear bulking phase resulted in a tuber yield greater than 50% of the control. This suggests some control of tuber bulking by sink size, but removal of one haulm may have increased light availability to the remaining leaves. This work will be continued. (Antoniw, Wood and Soffe)

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Examination of leaf stolon and tuber growth using observation pots. There is evidence for the directional transport of assimilates in potatoes, from a leaf to stolons and tubers on the same side of the stem (Gray & Smith, *Potato Research* (1973), **16**, 293–295; Frier, *Ph.D. Thesis, University of London* (1975)).

The use of observation pots provides an opportunity to study the pattern of stolon growth, tuberisation and growth of individual tubers. The results of such studies have sometimes been contradictory (Gray, *Potato Research* (1973), **16**, 80–84; Wurr, *Potato Research* (1977), **20**, 63–65) and further detail, especially in terms of growth of lateral stolon and of haulm is required.

The observation pots used were two-thirds filled with soil which was covered with nylon mesh on which the tuber piece was placed. The roots grew down through the mesh and stolons and tubers grew in the upper, vermiculite-filled chamber. The chamber was darkened by a black-backed white polythene pot cover. Development of individual leaves, stolons and tubers were measured weekly.

The data are still being analysed, but there is some evidence of a relationship between leaf area on one-third of the stem circumference and tuber yield in the corresponding third. (Antoniw, Wood and Soffe)

Weed biology

Broadbalk

Weeds in the field. The spring was very late in 1978. Hence in addition to routine herbicide-spraying, paraquat was used on the fallow to control large weeds, especially blackgrass (*Alopecurus myosuroides*). This departure from the normal weed-control on the fallow (cultivation only) seemed justified because soil conditions had delayed spring cultivations. Fine weather for a month before harvest enabled both crop and weeds to catch up.

Wheat sections were surveyed on 9–10 May, after spraying to control dicotyledons but before the seedlings became unrecognisable. The rotation sections had very few weeds, especially after beans and after fallow. The lower ends of many plots on Section 9 (continuous wheat), at the bottom of the field, were unpleasantly muddy and annual meadow-grass (*Poa annua*) was present on the wet areas, especially on plot 9 (N_4PKMg). Section 8 (no herbicides) had outstandingly more weeds than any other, and the black-grass plants were more advanced than where the autumn-germinators had been removed by spraying with terbutryne. Creeping thistle (*Cirsium arvense*) was prevalent on the unsprayed section and present elsewhere, but coltsfoot (*Tussilago farfara*) was rare. Field horsetail (*Equisetum arvense*) vegetative shoots were only just emerging but a sporophore was seen for the first time on Broadbalk, on plot 10 section 8 (N_2 no herbicides). Of the species now almost confined to the no-herbicide section, shepherd's needle (*Scandix pecten*) was unusually abundant on plots 3 and 9, at opposite ends of the soil-fertility range (unmanured and N_4PKMg); lamb's lettuce (*Valerianella dentata*) was more abundant than usual on the unmanured plot where it always occurs and corn gromwell (*Lithiospermum arvense*) occurred on plots 16 and 17 (N_2PKMg and $N_2\,\frac{1}{2}P\,\frac{1}{2}K\,\frac{1}{2}Mg$); only one red bartsia (*Odontites verna*) plant was seen on each of plots 22 (farmyard manure, FYM) and 8 (N_3PKMg).

Grass weeds were surveyed in the standing wheat crop on 10–14 July, when most of them were flowering. Wild oats (*Avena* spp.) were almost minor species because of thorough hand-pulling over many years; *A. fatua* occurred on only 15 plot-sections out of 131, nine of which had only one to three plants and only three averaged one or more plants per m^2. *A. ludoviciana* was slightly more widespread, occurring on 23 plot-sections,

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nine of which had only one or two plants and the rest less than 1 m^{-2}. As usual in a wet season, rough-stalked meadow-grass (*Poa trivialis*) was flowering above the wheat; it occurred on 13 plot-sections compared to only five for couch grass (*Agropyron repens*). Bent-couch (*Agrostis gigantea*) was not flowering in July. The major grass-weed was blackgrass, present on 121 plot-sections out of 131. On the no-herbicide section it was very plentiful or completely covered the ground on all except the no-nitrogen plots 3 (unmanured) and 5 (P K Mg). On the continuous wheat sections 0 and 9, only five plot-sections had less than 1 m^{-2}, but infestations were less in the second wheat crop after fallow and least directly after fallow or following beans after potatoes.

The stubble survey on 5 and 6 September, after the straw was baled, showed the extent of infestation with bent-couch, which occurred in large patches on section 8 (no herbicide) and 9 (continuous wheat) and as isolated clumps and young plants elsewhere. Field bindweed (*Convolvulus arvensis*) maintained its increase (*Rothamsted Report for 1975*, Part 1, 47; *Rothamsted Report for 1976*, Part 1, 46). Coltsfoot seemed to have increased during the year and now several patches were dense, with leaves 20–25 cm across. Creeping thistle formed large patches on 16 plot-sections with herbicide and 14 without. Annual broad-leaved weeds were not a problem, although fool's parsley (*Aethusa cynapium*) and dwarf spurge (*Euphorbia exigua*) were more abundant than usual. Fool's parsley was distributed on eight plot-sections, four no-herbicide and four rotation, with six different fertiliser combinations all supplying some nitrogen. Dwarf spurge was distributed on four plot-sections and even more abundant on five, all without added nitrogen, some in continuous wheat and others in rotations; on plot 5 section 0 (P K Mg, continuous wheat with herbicides since 1956) it reached 1 m^{-2}. Red bartsia was scarce as in spring, even on the no-herbicide section, presumably because of cold nights and wet soil in March when its small seeds should have germinated. In 1976 (*Rothamsted Report for 1976*, Part 1, 45) night frosts and spring drought were blamed for absence of this interesting semi-parasite on Broadbalk; night frosts at germination are the common factor, combined with adverse soil conditions at opposite extremes of moisture-content.

Section 2 in beans was surveyed on 10 May, when crop-rows were visible but the bean plants were too young to show differences due to soil-fertility. Weeds were very numerous, but most annuals were only at the cotyledon stage. Knotgrass (*Polygonum aviculare*) was abundant as usual, black bindweed (*P. convolvulus*) occurred in dense patches, but orache (*Atriplex patula*) was unusually abundant, equalling or exceeding one or both of the *Polygonum* spp. possibly because it germinated after them and in somewhat milder weather. Wild oats were not seen in beans in July, but spring-germinated blackgrass occurred on all plots varying from two to three plants per plot to the same number per m^{-2}. By 5 September, in the standing crop but after the bean leaves had begun to wither, plots varied from weedy to very weedy indeed. Knotgrass predominated but scentless mayweed (*Tripleurospermum maritimum*) was a close second, with black bindweed climbing up the beans and forming tangled patches on top of them. Orache, being prostrate, was partly hidden by the taller species.

The potatoes (***section 4***) were planted the day before the spring survey of the wheat sections, so were weed-free on 9 May. By 9 June annual weeds were small and scarcely a problem but perennials, field horsetail on no-nitrogen plots, creeping thistle on six plots covering a range of fertiliser treatments and coltsfoot on plot 16 (N_2 P K Mg), were emerging. Grass-weeds were too few to justify a special survey in July. By 4 September, before both tops and weeds were removed by flail, patches of the perennial weeds field

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horsetail and creeping thistle had become dense and there was a large patch of coltsfoot on plot 16 (N_2 P K Mg). Clumps of field bindweed were climbing over the potato haulms on parts of six plots (*Rothamsted Report for 1977*, Part 1, 46) but annual weeds remained unimportant.

Weed seedlings in pans. The 3-year period for the soil samples taken in 1975 ended in September 1978 so the results can be compared with the 1974 set completed in 1977 (*Rothamsted Report for 1977*, Part 1, 46). The 1975 set produced approximately 46 000 seedlings in all compared to only 26 000 for the previous set, because terbutryne was not applied in 1975 (*Rothamsted Report for 1975*, Part 1, 47) and consequently blackgrass proliferated, accounting for 70% of the total seedlings in that year, compared to 38% in 1974. Inevitably, the percentage of all species germinating in each of the 3 years of the 1975 set closely resembles that of blackgrass alone; only 3% of the total germinated in the third year, compared to 8% in the third year of the 1974 set. The behaviour of the blackgrass seeds was similar in both years, although the numbers were so different; 92·6%, 6·7% and 0·7% germinated in the 3 years of the 1975 set and 95·2%, 4·5% and 0·3% in the corresponding years of the 1974 set. The third set, taken in 1976, will not finish until September 1979.

The 18 pans from 1974, kept for a fourth year (*Rothamsted Report for 1977*, Part 1, 46) showed that knotgrass under these conditions germinates mainly in 3 years. It only appeared in one of the six pans in which it had been seen previously, and in that only 2% of the total came in the fourth year. Fumitory (*Fumaria officinalis*) showed an unusual pattern of germination. Out of 44 seedlings in 4 years, 64% came in the third year and 9% in the fourth. Moreover, germination is continuing into the fifth year, one seedling appearing in November 1978, so this pan will be retained. The well-known longevity of seeds of poppies (*Papaver rhoeas* and *P. argemone*), red bartsia, parsley piert (*Aphanes arvensis*), scentless mayweed, common vetch (*Vicia sativa*) and corn buttercup (*Ranunculus arvensis*) was confirmed. Annual meadow grass and red bartsia both recurred after lapses of 2 years without seedlings, and occasional seedlings of wall speedwell (*Veronica arvensis*), fumitory, parsley piert, scentless mayweed and even one blackgrass seedling reappeared at some time during the four years after a 1-year absence. One seedling of greater plantain (*Plantago major*) occurred in the fourth year without the species showing up in that pan during the previous three, although there was no likely source of contamination with seeds of this species. (Thurston)

Park grass. Specimen dandelions (*Taraxacum* spp.) were collected in May by Dr. R. Pankhurst and Mr. A. Chater for identification and classification at the Herbarium of the British Museum (Natural History). Dr. J. Richards (Botany Department, University of Oxford) recognised eleven species on Park Grass plots in April 1969 and some of the less common ones were found again on the same plots in May 1978. Our own dandelion survey could not be done until 17 May, when many of the dandelion capitula were fruiting and showed up less well than the yellow flowers. This may have accounted in part for the lower scores than in recent years. Dandelion distribution was uneven on some plots, but plots 6a and 6b showed stripes of yellow in the green background according to previous micro-plot treatments, probably potash levels. The re-inclusion of this plot in the Classical experiment is therefore not justified until residual treatment-differences have diminished.

Cowslips (*Primula veris*) flowered well on the unmanured plots and there was one plant on plot 4^1c (P only, pH 5·4). Fritillaries (*Fritillaria meleagris*) also flowered well on their usual site on plot 17 (N_1 as sodium nitrate only, pH 5·7) and four flowers were

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also seen on plot 14 at the limed end (N_2 P K Na Mg, N as sodium nitrate, pH 6·7 to 7·0). During sampling for dandelions, three plants of lady's mantle (*Alchemilla vulgaris*) were seen close together somewhere on plots 2 or 3 (unmanured) but a week later, when the surrounding vegetation had grown taller, they could not be found for detailed recording and photographing. This may explain why lady's mantle is not recorded in the routine spring and autumn surveys.

The survey before the first cut was done a little early this year (31 May to 2 June) as only one person was available to score, enter and check the 81 sub-plots before cutting began. It was difficult to distinguish between downy oat grass (*Helictotrichon pubescens*) and false oat (*Arrhenatherum elatius*) which were only just coming into flower, and may have led to underestimation of these species and also of Yorkshire fog (*Holcus lanatus*). The vegetation on all plots tended to be shorter than usual, probably because of the cold spring. A 3½-h thunderstorm with heavy rain on 1 June caused lodging of 30 to 90% of the area of 16 of the taller sub-plots, and on many, cow parsley (*Anthriscus sylvestris*) was standing while the surrounding grasses were laid flat.

The autumn survey at the end of August showed the field as a whole lush and green, with clovers, mainly *Trifolium pratense*, flowering freely on those plots where they occurred. There were no dried-out patches, and the bare areas of peat around the grass-clumps on the very acid plots were small. A few fresh mole-hills were seen, but by the beginning of November they had spread from plot 13 to plot 7, the moles appearing to travel along the close-mown paths, re-entering the soil where rabbits had scraped away the grass. Plots 13a and 13b (FYM and fish meal, limed), 12a (unmanured) and 8a (P Na Mg, limed) seemed to be the most seriously affected and no acid plots had been entered. It is intended to survey the damage during the winter. Mole-hills break up the dense sward, allowing air-borne weed seeds to give rise to seedlings; they may also bring dormant seeds to the surface where they can germinate.

No hay analysis was made this year. (Thurston)

Staff and Visiting Workers

C. P. Whittingham was elected Special Professor of Plant Physiology in the Department of Physiology and Environmental Studies at the University of Nottingham from 1 October 1978. Joan M. Thurston was elected to the Council of the European Weed Research Society.

J. N. Gallagher joined the Department in February to undertake studies on the factors influencing grain size in barley; this work has been made possible by a grant from the Home-Grown Cereals Authority.

Dr. Felix Mächler arrived on 1 April to spend a year in the Department sponsored by The Royal Society; he has been primarily concerned with studies on photorespiration and in particular on the enzyme ribulose 1,5-biphosphate carboxylase/oxygenase.

Dr. Godwin Roberts completed his visit to the Department in June and returned to the Tea Research Institute in Sri Lanka. He was able to demonstrate the existence of photorespiration in tea plants during his period here and hopes to continue this work back in Sri Lanka. Rodney Dunn spent a period of 4 months at Rothamsted whilst holding a CASE award in which the academic partner is the University of Essex; he has been studying the growth potential of C_4 plants.

C. P. Whittingham attended a seminar sponsored by the EEC on the Future of Publishing by Scientific and Technical Societies in Luxembourg on 3/4 April 1978. Susan M. Thomas and J. N. Gallagher attended the EUCARPIA Workshop on Crop Physiology and Cereal Breeding held in Wageningen from 13 to 16 November 1978 and gave papers concerned with the physiology of the cereal crop.

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