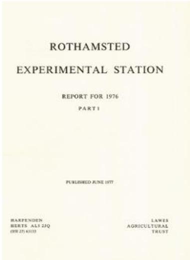
ROTHAMSTED RESEARCH

Report for 1976 - Part 1

Full Table of Content


ROTHAMSTED
EXPERIMENTAL STATION
REPORT FOR 1976
PART 1

Botany Department

C. P. Whittingham

C. P. Whittingham (1977) *Botany Department ;* Report For 1976 - Part 1, pp 31 - 50 **- DOI: https://doi.org/10.23637/ERADOC-1-133**

BOTANY DEPARTMENT

C. P. WHITTINGHAM

Staff

Head of Department C. P. Whittingham, PH.D.

Principal Scientific Officers
A. J. Keys, PH.D.
G. F. J. Milford, B.SC.
Margaret E. Radley, PH.D.
Gillian N. Thorne, PH.D.
Joan M. Thurston, B.SC.
P. J. Welbank, PH.D.

Senior Scientific Officers
I. F. Bird, PH.D.
S. A. W. French
D. W. Lawlor, PH.D.
J. R. Lenton, PH.D.
Mrs. Susan M. Thomas, PH.D.
A. W. Wheeler, PH.D.
E. D. Williams, M.SC.

Higher Scientific Officers
M. J. Cornelius
T. O. Pocock, B.A.
R. W. Soffe
P. J. Taylor, B.SC.
A. T. Young

Scientific Officers
A. C. Kendall, B.SC.
M. A. Parry, M.SC.
I. Pearman, B.SC.

Assistant Scientific Officers
N. E. J. Appleford
Sandra Coxon
S. P. Driscoll
Diana J. French
Hilary Gogay
S. T. Harper
Heather Pellant
K. Plumb
S. J. Rose
Mrs. Janice C. Turner

Temporary Worker
R. Martinez-Carrasco, PH.D.

Secretary
Mrs. Anita J. Webb

Introduction

In the past year work in the Botany Department has concentrated on further studies of the physiology of cereal crops. The unusual weather was unfavourable for cereal yields without irrigation and for studies of later applications of nitrogen fertiliser. Because of the higher summer temperatures photorespiration was higher than in previous years but this year's work confirms previous results that photorespiration under natural conditions in cereal crops is of the order of one-quarter of the rate of real photosynthesis. Unfortunately there are still no promising chemicals which might be used to regulate rates of photorespiration. Studies of the growth of barley in clean air at Woburn were satisfactorily carried through to final yields and evidence is now accumulating that growth in clean air significantly increases grain yield.

Studies on the growth physiology of sugar beet have continued but there is still no growth-regulating chemical which can at present justify extended field trials.

The work on weed biology in the future is to concentrate on studies relating to classical experiments.

A decision is still awaited concerning the rebuilding of the old glasshouse block which is being maintained in use by short-term repair work. This, however, results in far from satisfactory growing conditions.

Cereal crops

Factors limiting yield of winter wheat. There is widespread interest in the maximum yield that could be obtained if cereal crops were grown with the best husbandry and optimal control of all diseases, pests and weeds. Ideally, all the factors that are thought to enhance yields should be tested in a multifactorial experiment, but such a large experiment may be unjustified and impractical.

https://doi.org/10.23637/ERADOC-1-133

In a preliminary experiment, wheat, var. Huntsman, was sown on 23 October 1975 following potatoes at Rothamsted. Three sowing treatments were tested: normal drilling in 17·7 cm (7 in) rows at 120 and 200 kg ha^{-1} and hand planting at 6·3 cm (2·5 in) square spacing corresponding to 120 kg ha^{-1}. Aldicarb was rotavated into the seed bed and the crop was sprayed with fungicides and insecticides. An additional set of plots tested normal drilling at 200 kg ha^{-1} without pest and disease control. All the above treatments were tested at 40, 80 and 120 kg N ha^{-1} and all plots received basal herbicide and chlormequat chloride (CCC).

In the event, seedling establishment was better in the hand-sown than in the drilled plots; average plant numbers were 233 m^{-2} with 200 kg seed ha^{-1}, 125 m^{-2} with 120 kg ha^{-1} both drilled, and 205 m^{-2} hand-planted. The square-spaced plots tillered more than the drilled plots and by 4 May 1976 had 1700 shoots m^{-2} compared to 1050 from 200 kg ha^{-1} drilled, but more of these tillers died before harvest. At final harvest they had 450 ears m^{-2} compared with an average of 420 from 200 kg ha^{-1} and 350 from 120 kg ha^{-1} drilled (Table 1). None of the yields were large because of the exceptionally dry

TABLE 1

Winter wheat yields with each treatment combination

Grain, t ha^{-1} at 85% dry matter

Nitrogen	With pest and disease control: Hand-planted 120 kg ha^{-1}	Drilled at 120 kg ha^{-1}	Drilled at 200 kg ha^{-1}	Without: Drilled at 200 kg ha^{-1}
40 kg ha^{-1}	6·3	5·9	6·1	6·2
80	7·6	5·9	6·3	5·7
120	6·4	6·0	6·7	5·2
Mean	6·8	5·9	6·4	5·7

summer. The highest yield was from hand-planted wheat with 80 kg N ha^{-1} but this may be fortuitous. Mildew was the only foliar disease observed but even so was only slight on unsprayed plots; aphids, which were numerous, were well controlled by the insecticides. Pest and disease control increased the yield more with higher N application. It may be concluded that hand planting at square spacing permitted better yields from a smaller amount of seed, but the evidence is not sufficient to say that square spacing was superior to a similar plant population drilled in rows. It is possible that a wetter summer might have permitted survival of more of the tillers on the hand-planted plots and this could have led to a still higher yield. (Welbank and Taylor, with Widdowson, Chemistry Department and Jenkyn, Plant Pathology Department)

Growth and yield of winter wheat at Rothamsted and Woburn. In a series of experiments in 1971–73 the growth, nutrient uptake and yields of winter-wheat crops at Rothamsted and Broom's Barn were compared (*Rothamsted Report for 1971*, Part 1, 60–61 and 106–107; and *for 1972*, Part 1, 48 and 90–92; and *for 1973*, Part 1, 49–50 and 94–96). The difference in maximum yield between farms was no more than 20%, but it persisted even with N fertiliser dressings as great as 155 kg ha^{-1} with irrigation until early July. The wheat at Broom's Barn took up less N from the soil than at Rothamsted and with small N fertiliser dressings N uptake ceased earlier at Broom's Barn, suggesting that more N was mineralised from the Rothamsted soil and the process continued later in the season.

Duplicate experiments in 1976 at Rothamsted and on the loamy sand of the old Irrigation Experiment site in Butt Close at Woburn were expected to show larger contrasts between sites than in the earlier series. They sought to investigate whether irrigation and N fertiliser would eliminate differences to a greater or lesser extent than before and

https://doi.org/10.23637/ERADOC-1-133

whether the response to N, especially at Woburn, could be enhanced by extending its application over a longer period of time. Wheat, var. Maris Huntsman, was sown following beans at both sites on 31 October 1975 with no autumn N fertiliser, but with a heavy dressing of PK fertiliser combine drilled. Spring N dressings were given at five rates increasing from 22 to 112 kg ha^{-1} at Rothamsted and from 45 to 134 kg ha^{-1} at Woburn and controls receiving no N were included. The N was applied either as a single dressing on 22 April at Rothamsted and 23 April at Woburn or divided so that half was given on the above date and further quarters approximately four weeks and eight weeks later. Half the plots with each N treatment were irrigated. Although slightly more seed was sown at Woburn than at Rothamsted, only 148 plants m^{-2} were counted in January compared with 191. The Woburn crop was never able to overcome this disadvantage. By early April, Woburn wheat had an average of only 213 shoots m^{-2}, and a shoot dry weight of 7·2 g m^{-2}, compared with 387 shoots m^{-2} and a shoot dry weight of 18·2 g m^{-2} at Rothamsted. The numbers of plants and shoots in these experiments were strikingly fewer than in the Factors Limiting Yield study, where a similar sowing rate produced 233 plants m^{-2} and an average of 1050 shoots m^{-2} on 4 May. On 11 May, shoot numbers in the present experiments on plots with comparable N dressings to the Factors Limiting Yield study (50–125 kg ha^{-1}) averaged 513 m^{-2} at Rothamsted, while at Woburn they had actually decreased to 198 m^{-2}. It is now suspected that this poor early growth was caused by residues of simazine applied to the preceding bean crops on both sites, which remained in the surface soil following an unusually dry summer and autumn.

At Rothamsted 43 mm of irrigation water was applied and 108 mm at Woburn before ears emerged about 20 June. A further 19 mm were applied at Rothamsted and 64 mm at Woburn between ear emergence and 10 July, by which time the leaves were senescing and it was judged unwise to apply more. The amounts at Rothamsted were far from sufficient to make good the calculated deficit, but difficulties with equipment, weather and water supply prevented more adequate irrigation.

By 21 June the best plots at Woburn yielded only 392 g shoot dry matter m^{-2}, with irrigation and 75 kg N ha^{-1}. They had 232 ears m^{-2} and a leaf area index (LAI) of 2·5. At the same time the best crop dry weight at Rothamsted was 894 g m^{-2} with irrigation and 25 kg N ha^{-1}, from 324 ears m^{-2} and a LAI of 4·7. Divided N dressings had little effect at either site. Irrigation almost doubled LAI and increased dry weight by over a third at Woburn. Unirrigated plots at Woburn suffered more stress as shown by measurements of plant water potential than at Rothamsted. Decreasing this stress by irrigation did not eliminate the difference between sites. The mean relative growth rates of the best irrigated Woburn plots between 7 April and 21 June were very similar to the best at Rothamsted and their relative leaf growth rates were higher. This implies that the inferior growth of irrigated Woburn crops up to ear emergence was probably a consequence of their poorer establishment and growth during the preceding winter.

By 19 July, shortly before the crop was combined, the best yield of total dry matter at Woburn was 581 g m^{-2}, with irrigation and 75 kg N ha^{-1}, and at Rothamsted it was 1155 g m^{-2} with no irrigation and 125 kg N ha^{-1}. Again, however, the relative growth rate of these crops between 21 June and 19 July was slightly greater for Woburn than for Rothamsted (the advantage perhaps attributable to less interplant competition in the thinner crop).

At harvest the best yields at Woburn were 5·0 t ha^{-1} (at 85% dry matter), with irrigation and 100 kg N ha^{-1}; at Rothamsted 5·5 t ha^{-1} with irrigation and 125 kg N ha^{-1}. Without irrigation Woburn wheat yielded only 2·6 t ha^{-1} with 100 kg N ha^{-1}, so that as far as yield was concerned, water supply was the factor principally responsible for smaller yields in addition to the poorer growth during the winter. (Taylor and Welbank, with Widdowson, Chemistry Department)

https://doi.org/10.23637/ERADOC-1-133

Soil-water deficits, water use and growth of barley. Spring barley, var. Julia, was grown in a small-plot experiment on Little Knott (Rothamsted) under mobile rain shelters (see Day and Legg, Physics Department p. 236). Trickle irrigation was applied weekly to some plots throughout the growing season, or applied to others before, at, or after anthesis or withheld completely. Detailed measurements of water potential, photosynthesis and plant growth were made during the growing season.

Emergence of the crop was uniform after sowing on 31 March 1976, but very small soil-water deficits, corresponding to a water potential of −0·5 bar at the first harvest (10 May 1976), slowed growth of leaves and decreased fresh and dry weight. By the time maximum spikelet number was established, fresh weight was 40% smaller than in the irrigated controls, plant height 50% and leaf area 60% smaller, with deficits of 70 mm compared to 35 mm in controls. Fewer tillers were produced and they grew less well. Crop dry weight was 40% smaller and photosynthesis smaller in the stressed leaves. The effects of early stress persisted even if the crop was watered later. Early watering followed by drought during spikelet formation decreased growth in leaf area and dry weight.

Leaf growth stopped by early June and thereafter further drought caused more rapid death of leaves. Stress slowed development of the apex only slightly and ears emerged at about the same time in all treatments. However, dry soil slowed stem elongation and, as the stressed crop matured earlier, final crop height was less. Reduced growth correlated with a 4–5 bar smaller leaf-water potential in the driest treatments compared to the wettest.

At harvest (2 August 1976) yield of grain and straw was 54%, and grain 50%, smaller in the continuously stressed crop compared to the fully irrigated. Yield of intermediately stressed plots was dependent on time of irrigation and duration and degree of stress and was closely correlated with total dry matter production during the early growth of the crop.

Root density was 2·5 cm cm^{-3} soil in the top 10 cm of the wettest treatment at final harvest and 1·25 cm cm^{-3} in dry treatments. Below 10 cm the density was less than 1 cm cm^{-3} down to a depth of 1 m in all treatments. More complete analysis of the water uptake in relation to water potential gradients will be made and compared with results from controlled environments. (Lawlor, with Day and Legg, Physics Department)

Water flux through the soil and plants. Spring barley, var. Julia, was grown in Kettering loam soil in pots 30 cm diameter and 60 cm deep, to allow adequate root growth. In controlled conditions water flux from the crop was changed by altering atmospheric humidity and irradiance.

Water flux varied from 8×10^{-3} g s^{-1} m^{-2} to 48×10^{-3} g s^{-1} m^{-2} at the start of the experiment and from 1×10^{-2} to 10×10^{-2} g s^{-1} m^{-2} as the plants aged and grew (equivalent to very high rates of evaporation in the field). Plant water potential was high and changed only slightly with increased water flux until soil-water matrix potential decreased to about −1 bar throughout the rooting depth. Thereafter water potential fell, accompanied by stomata closure and restricted photosynthesis. Density of rooting was between 1·0 and 2·5 cm cm^{-3} depending on the horizon. It was concluded that water flux through the plant is not restricted when root density is large and soil-water potential high and further that plant resistance is of minor importance. Only when root growth and density is restricted and evaporation large is control of leaf-water potential lost. (Lawlor and Klar)

Response of three varieties of winter wheat to nitrogen. Observations made in 1975 suggested that increased loss of carbon dioxide by respiration might explain why the grain yield of winter wheat responded to nitrogen less than did leaf area and vegetative

https://doi.org/10.23637/ERADOC-1-133

growth. To examine this further and to investigate the effects of nitrogen on grain size, the three varieties Cappelle-Desprez, Maris Huntsman and Maris Hobbit were grown with eight amounts of nitrogen ranging from 0 to 210 kg ha^{-1}.

Growth and yield. So little rain fell after the nitrogen was applied on 6 May that the nitrogen was not absorbed by the plants in time to prevent the death of tillers in late May. Consequently, ear number was unaffected by nitrogen and averaged only 350 m^{-2} (1·1 per plant), a number characteristic of a nitrogen-deficient site. Grain yields were small; averaged over all varieties, nitrogen increased grain yield from 3·4 t ha^{-1} with 0 kg N ha^{-1} to 5·0 t ha^{-1} with 180 kg N ha^{-1}. Another consequence of the late uptake of nitrogen was that leaf area and vegetative growth were increased by additional nitrogen much less than in previous experiments; the maximum leaf-area index was less than four. Nitrogen did not decrease the efficiency of the leaves in grain production and increased harvest index. The exceptionally hot dry weather caused anthesis to occur early (10 June) and the leaves to senesce fast, thus restricting the grain growth period to only 33 days.

The varieties differed from each other in mean yield and in the components of yield. Mean yields were: Hobbit 4·7, Huntsman 4·3, Cappelle 3·9 t ha^{-1} (SED = 0·1). Hobbit had more grains per spikelet and smaller grains than the other varieties; Huntsman had more grains per spikelet than Cappelle, but of the same size. Nitrogen increased the number of fertile spikelets per ear in all varieties. In addition, it increased the number of grains per spikelet of Hobbit but decreased grain size. (Taylor and Thorne)

Factors determining grain size. To study the importance of the supply of carbohydrate during grain growth and of conditions before anthesis on final grain size, observations were made on developing grains of Hobbit and Huntsman grown on plots receiving different amounts of nitrogen. To improve conditions for ear growth before anthesis, part of each plot was thinned 30 days before anthesis to approximately 180 ear-bearing shoots m^{-2}. This treatment had no effect, presumably because density of ears was already low. On the thinned and unthinned part of each plot the top halves of some ears were removed 5 days after anthesis to increase the supply of photosynthate per grain. Removing the upper half of the ear increased the final dry weight of grains in the lower part of ears of Hobbit but not of Huntsman. The maximum grain volume, which occurred 28 days after anthesis and only 5 days before grain dry weight was maximal, was also increased by halving ears of Hobbit but not Huntsman. This suggests that events occurring before grains reach their maximum volume may determine their maximum dry weight.

When Kleiber spring wheat was grown in pots with a more normal rate of grain development, dry weight per grain at 23 days after anthesis when volume was maximal, was only half the final value reached after a further 47 days of growth. Grains in halved ears grew faster in volume, fresh weight and dry weight than comparable grains in intact ears during the 23 days until volume was maximal. Thereafter, the grains in halved and intact ears increased in dry weight at the same rate even though the supply per grain of photosynthate from the shoot was greater in the halved ears. At least some of the surplus carbohydrate accumulated in chaff and stems, increasing their final dry weight. (Martinez-Carrasco)

Distribution of photosynthate. Measurements of changes in stem dry weight and of respiration rate in Maris Huntsman and Maris Fundin (*Rothamsted Report for 1975*, Part 1, 36) suggested that all the carbohydrate produced after anthesis moved to the grain. Of the ^{14}C remaining in the plant at maturity after supplying $^{14}CO_2$ to the flag leaf, 91% was in the grain when the $^{14}CO_2$ was supplied at 10 days after anthesis and 95%

https://doi.org/10.23637/ERADOC-1-133

when supplied at 24 days. The percentage remaining in the stem was 4 for the 10-day treatment and only 0·5 for the 24-day treatment. When the leaf below the flag leaf was supplied with $^{14}CO_2$ the percentage in the ear at maturity was 85 for the 10-day treatment and 96 for the 24-day treatment. Nitrogen fertiliser had negligible effects on distribution. The semi-dwarf variety Maris Fundin had up to 3% more ^{14}C in its ear at maturity than the taller varieties.

Previous experiments had not examined the movement of pre-anthesis photosynthate. In 1976 the top two leaves were supplied with $^{14}CO_2$ 14 days before anthesis, shortly after the flag leaf was fully expanded. At anthesis about 30% of the ^{14}C recovered in the shoot was in the ear, whichever leaf had been supplied. The remainder was equally divided between the stem above and below the flag leaf node when the flag leaf had been supplied; it was mainly in the lower stem when the leaf below the flag leaf had been supplied. Less than 5% remained in the leaf originally supplied with $^{14}CO_2$. At maturity the ^{14}C content of the ear structures was the same as at anthesis; the content of the stem had decreased to provide the ^{14}C in the grain which amounted to about 20% of the total, irrespective of the leaf supplied. Nitrogen fertiliser tended to increase the proportion of ^{14}C coming from the leaf below the flag leaf that reached the ear at anthesis and the ear structures at maturity. The percentage of the ^{14}C recovered in the ear at anthesis and in ear structures at maturity was greater for Hobbit and least for Cappelle; e.g. after supplying $^{14}CO_2$ to the flag leaf the percentage in the ear at anthesis was 45 for Hobbit, 38 for Huntsman and 29 for Cappelle. There were similar, but smaller, varietal differences in ^{14}C in the grain. The large varietal differences at anthesis suggest that differences in floret development before anthesis were responsible for Hobbit having most and Cappelle least grains per spikelet. Similar observations in other seasons are necessary to show whether these considerable contributions of pre-anthesis photosynthate to grain are general or a peculiarity of a season in which post-anthesis photosynthesis was severely restricted. (Makunga, Pearman and Thorne)

Carbon loss. Measurements made in 1975 of dark respiration rate of shoots and ears of the three varieties and of photorespiration by leaves of Maris Huntsman indicated that the loss of $CO_2\ m^{-2}$ of land by both these processes was increased by nitrogen fertiliser (*Rothamsted Report for 1975*, Part 1, 35 and 36). In the same experiment an attempt was made to estimate the total loss of carbon by respiratory processes from the difference in ^{14}C content of leaves harvested immediately after supplying $^{14}CO_2$ and of comparable shoots left in the crop until maturity. Approximately 20% of the $^{14}CO_2$ supplied to flag leaves 10 days after anthesis had been lost by maturity in the absence of nitrogen fertiliser, and about 40% with 210 kg N ha^{-1}. This increase was only just statistically significant because respiration is estimated rather imprecisely by this method, being a relatively small difference between two large and variable figures.

In 1976 dark respiration of ears and of the rest of the shoot was measured with an infra-red gas analyser (IRGA). Neither shoot nor ear respiration rate per unit dry weight was affected by nitrogen. The rate of ear respiration of Hobbit was only 76% of that of the other varieties although its ears grew fastest. There was no difference in development between the varieties that could account for the slower respiration rate of the ears of the semi-dwarf variety Maris Fundin in 1975. (Pearman, Thomas and Thorne)

Environmental effects on respiratory loss and distribution of ^{14}C-labelled photosynthate. Respiration and distribution of photosynthate may be affected by light intensity and by the time during the photoperiod when the photosynthate was formed. To investigate these effects, two experiments were done in growth rooms which provided light intensities of 400 to 650 $\mu E\ m^{-2}\ s^{-1}$ at 20°C, 75% relative humidity. $^{14}CO_2$ was supplied to the flag

https://doi.org/10.23637/ERADOC-1-133

leaf or the leaf below the flag leaf of the main stems during the first two hours or the last two hours of the 16 h photoperiod. Some leaves were harvested 10 min after the 30 s exposure to $^{14}CO_2$ to estimate the initial content of ^{14}C (leaves sampled sooner contain less ^{14}C because $^{14}CO_2$ is lost from the intercellular spaces during drying). Other shoots were harvested one or three days after supplying $^{14}CO_2$ and the ^{14}C contents of the fed leaf, ear and rest of the shoot determined.

The percentage of the ^{14}C absorbed by the flag leaf that was lost during the next three days averaged 16 in the first experiment but only 9 in the second. The absolute and percentage loss of $^{14}CO_2$ was greater in bright than dim light except in the second experiment for late supply, when the reverse occurred. The light-time interaction was highly significant statistically. In the first experiment most of the loss from the late supply, but not from the early, occurred in the first day; in the second experiment most occurred in the first day with all treatments. Loss of ^{14}C absorbed by the leaf below the flag leaf was greater than of that absorbed by the flag leaf, especially in bright light.

The percentage of the ^{14}C content occurring in the ear after supplying the flag leaf was similar in the two experiments. It ranged from 58 to 86 after one day, increasing to 66 to 90 after three days. It was greater in dim light and greater when the CO_2 was supplied late. Only 36–68% of the ^{14}C supplied to the leaf below the flag leaf was in the ear after three days; the difference from the flag leaf was more obvious for early than for late supply. Anything which increased the proportion of ^{14}C in the ear usually decreased the small proportion remaining in the leaf that had absorbed the $^{14}CO_2$, as well as the proportion in the rest of the shoot.

Most of the these environmental effects and interactions were highly significant statistically although the physiological significance of some of them is not yet clear. The results show that care is needed in interpreting data on ^{14}C distribution and recovery, especially in the variable environment of the field. (Thomas and Thorne)

Photorespiration. Estimates of photorespiration in flag leaves of Maris Huntsman were made in the field in 1976 from simultaneous measurements of $^{14}CO_2$ and $^{12}CO_2$ uptake (*Rothamsted Report for 1975*, Part 1, 33), and from the rate of release of CO_2 from a leaf into a stream of CO_2-free air passing over it. Nitrogen fertiliser had no effect on the gross photosynthesis per unit leaf area ($^{14}CO_2$ uptake), nor on the interception of light by the canopy. The average value from all the measurements at intervals from 14 days before anthesis to 20 days after was $24{\cdot}0 \pm 1{\cdot}1$ mg dm^{-2} h^{-1}, and the intensity of photosynthetically-active radiation at flag leaf level as a percentage of that above the crop was 77. The average rates of photorespiration at similar times were 7·2 and 6·9 mg dm^{-2} h^{-1} estimated by the two techniques respectively, i.e. about 30% of the gross photosynthesis. This percentage was higher than the average in 1975, probably because of the higher summer temperatures. As in 1975 photorespiration as a proportion of gross photosynthesis was increased by nitrogen application. The proportion of photosynthesis lost in photorespiration increased as the leaves senesced. By 28 days after anthesis when the leaves were turning yellow rapidly, $^{14}CO_2$ uptake had fallen to $5{\cdot}6 \pm 3{\cdot}3$ mg dm^{-2} h^{-1}, and photorespiration was about 54% of that value ($2{\cdot}9 \pm 1{\cdot}7$, $3{\cdot}1 \pm 1{\cdot}3$ mg dm^{-2} h^{-1} measured by the two techniques respectively). Nitrogen delayed senescence, so that in crops given 30 to 180 kg N ha^{-1} the rates of gross photosynthesis were 1·8 or 8·6 mg dm^{-2} h^{-1} and the estimates of photorespiration were about 87 and 45% of those values.

Activities of ribulose bisphosphate (RuBP) carboxylase and oxygenase in extracts of flag leaves of Maris Huntsman were measured over the same period as photorespiration. There were no consistent changes in the relative activities with nitrogen (see *Rothamsted Report for 1975*, Part 1, 38). (Thomas)

https://doi.org/10.23637/ERADOC-1-133

RuBP carboxylase protein during wheat flag leaf senescence. Antibodies elicited in rabbit against purified wheat RuBP carboxylase were used to measure RuBP carboxylase protein during senescence of wheat flag leaves. There was a close correlation during senescence between decline in photosynthetic carbon dioxide fixation and in RuBP carboxylase activity. However, there was a greater decline in catalytic activity than in RuBP carboxylase protein suggesting that in senescent leaves a considerable proportion of RuBP carboxylase protein is catalytically inactive.

Treatments designed to delay senescence such as painting fully expanded intact leaves of glasshouse plants at weekly intervals with 1000 ppm chlormequat chloride (CCC) or a mixture of 100 ppm gibberellic acid and 10 ppm kinetin, did not significantly affect photosynthesis but did affect stalk elongation. There was little difference in the RuBP carboxylase protein, RuBP carboxylase activity, chlorophyll or soluble protein in leaves of treated, compared to control, plants and senescence was not retarded. (Hall)

Photosynthesis and photorespiration by wheat at different temperatures. Further studies were made to determine the effect of photorespiration on photosynthesis at 13, 18, 23 and 28°C (*Rothamsted Report for 1975*, Part 1, 32). Wheat, var. Kleiber was grown in a controlled environment with day/night temperatures of 18°/14° and in 16 h days with 500 $\mu E\ m^{-2}\ s^{-1}$ of photosynthetically-active radiation. Measurements were made at temperatures of 13, 18, 23 and 28°C of (a) net photosynthesis in air containing 350 vpm CO_2; (b) net photosynthesis in a gas mixture of 350 vpm CO_2 in 2% oxygen; (c) true photosynthesis estimated by ^{14}C assimilation from air containing $^{14}CO_2$, and (d) CO_2 evolution into CO_2-free air. Values of (b)–(a), (d) and (c)–(a), were used as estimates of photorespiration (Table 2). The third value suggests that the period of exposure to $^{14}CO_2$ was too long and did not give a good measure of true photosynthesis.

TABLE 2

Photorespiration by wheat leaves estimated by three methods: effect of temperature

Temperature (°C)	Method of estimation: Photosynthesis* in 2% O_2 minus photosynthesis in air	Efflux of CO_2* into CO_2-free air	Gross minus net photosynthesis from $^{14}CO_2$ assimilation**
	(% of net photosynthesis)		
13	32	38	10
18	47	53	6
23	48	59	12
28	54	69	17

* Means of estimates before and after anthesis.
** From measurements made when the flag leaves were beginning to senesce.

Photorespiration at 28°C was almost double that at 13°C. The results confirm that if photorespiration could be eliminated this would increase productivity most in hot conditions. (Keys, Sampaio, Cornelius and Bird)

Enzymes of photorespiratory metabolism. Enzymes involved in glycollate metabolism were purified from wheat leaves. The intention was to identify reactions which might result in energy conservation and to examine the action of potential inhibitors of photorespiration on the purified enzymes. Glycollate oxidase and serine-glyoxylate transaminase were only weakly absorbed by a DEAE-cellulose column from dilute buffer at pH 8·5 and were only partly separated; two hydroxypyruvate reductases were absorbed on the column and eluted separately by buffered solutions of sodium chloride. The serine-glyoxylate

https://doi.org/10.23637/ERADOC-1-133

transaminase was not dependent on inorganic orthophosphate for its activity (King & Waygood, *Canadian Journal of Botany* (1958), **46**, 771–779); ammonium ions were inhibitory but there was no evidence of their direct participation in the reaction or in any competing reaction.

RuBP carboxylase was purified from wheat leaves by several methods. The purity was checked by electrophoresis on polyacrylamide gels. Iodoacetamide and 2,3-epoxypropionic acid inhibited equally both the carboxylase and oxygenase activities of the enzyme from wheat leaf contrary to the report by Wildner and Henkel (*Biochemical and Biophysical Research Communications* (1976), **69**, 268–275) that these compounds inhibited the oxygenase activity of the spinach enzyme specifically. The specific activity of the RuBP carboxylase from wheat leaves was 0·25 μmol min^{-1} mg^{-1} protein. This was much lower than might be predicted from the carboxylase activity in crude extracts of wheat leaves. Although stored at 0°C preparations of the enzyme were not always activated by heating (Singh & Wildman, *Plant Cell Physiology* (1974), **15**, 373–379). Preincubation with Mg^{2+} and carbonate were necessary but NADPH was not an activator. Investigation of the low specific activity of the enzyme is continuing; probably some of the enzyme is inactivated during purification without producing a significant change in the physical and chemical properties of the protein. (Cornelius, Sampaio and Keys)

The role of the glycollate pathway in sucrose synthesis. A further study was made to determine whether sucrose is made from intermediates of the glycollate pathway by a route not involving the chloroplast (*Rothamsted Report for 1974*, Part 1, 31). Samples consisting of three segments of the first leaves of wheat plants that were two weeks old were pre-illuminated for 40 min (1200 μE m^{-2} s^{-1} of photosynthetically-active radiation) with their cut bases in water and with air containing 145, 326 or 994 vpm CO_2 flowing over them. Without interrupting the air flow the bases of the leaf segments were transferred to solutions of [3–^{14}C] serine. After illumination for a further 40 min the leaf segments were dropped into boiling ethanol. Water soluble compounds were extracted and the amount of [^{14}C] serine taken up was estimated. Sucrose was separated and glucose obtained from the sucrose by hydrolysis was degraded to determine the distribution of ^{14}C among its carbon atoms (*Rothamsted Report for 1974*, Part 1, 31). The results are shown in Table 3.

TABLE 3

Effect of CO_2 in the atmosphere on the intramolecular labelling of the glucose moiety of sucrose in wheat leaves supplied with [3–^{14}C] serine (0·9μmol; 9μCi) for 40 min in the light

Concentration of CO_2 in the atmosphere (vpm)		145	326	994
^{14}C taken up by the leaf segments (μCi)		5·4	5·6	3·6
^{14}C in sucrose (%)		22	40	46
^{14}C in C atoms of glucose from serine	3 + 4	11·0	5·9	3·8
	2 + 5	24·1	18·0	11·2
	1 + 6	64·9	76·1	85·0

As before (Waidyanatha, *Rothamsted Report for 1971*, Part 1, 108 and *for 1973*, Part 1, 92) increased CO_2 in the atmosphere stimulated rather than decreased sucrose synthesis, although it decreased uptake of [3–^{14}C] serine. As expected, the carbon atoms from the 3-position of serine were mainly incorporated into the 1 and 6-carbon atoms of the glucose. Randomisation leading to ^{14}C in the 2 and 5-carbons of glucose is more extensive than into the 3 and 4-carbons. Increased CO_2 in the atmosphere decreased the extent of the randomisation. The randomisation described cannot be readily explained by conversion of the serine to triose phosphate and rearrangement of the carbon atoms during generation of RuBP; these reactions would not result in randomisation of carbon from the 3-carbon of the triose phosphates (Kandler & Gibbs, *Zeitschrift für Naturforschung* (1959),

https://doi.org/10.23637/ERADOC-1-133

14B, 8–13). It is more easily explained by the recycling of carbon through the glycollate pathway. The amount of carbon recycled through the glycollate pathway is decreased by increased CO_2 in the atmosphere although still significant with 1000 vpm CO_2 (Kumarasinghe, *Rothamsted Report for 1975*, Part 1, 37). Some of the serine supplied must be metabolised to triose phosphate which mixes with triose phosphates in the chloroplast; this pool of triose phosphates provides carbon for glycollate synthesis and for sucrose synthesis. More of the serine carbon may be incorporated into sucrose without metabolism in the chloroplast in the presence of higher concentrations of carbon dioxide. (Bird and Cornelius)

C_4-photosynthesis in a cool temperate plant. The salt marsh grass *Spartina townsendii* is unusual for a species dominant in cool temperate regions because it has many characteristics of the C_4-pathway of photosynthesis usually found in tropical species. It provides an opportunity to study the potential of C_4-photosynthesis in a temperate climate (Long, Incoll & Woolhouse, *Nature, London* (1975), **257**, 622–624). Its rate of photosynthesis at low temperatures (5–10°C) compares favourably with C_3-plants (such as wheat), whereas C_4-plants usually have lower rates of photosynthesis at such temperatures. At higher temperatures *S. townsendii* has higher rates of photosynthesis than C_3-grasses. As a preliminary to the study of its productivity, in collaboration with the University of Essex, photosynthetic carbon metabolism of the leaves of *S. townsendii* was studied. On a cool May morning (10°C, 1000 μE m^{-2} s^{-1} photosynthetically-active radiation) $^{14}CO_2$ in air was supplied to leaves for 5 or 10 s, and the leaves were allowed subsequently to remain in normal air for periods up to 5 min. When the leaves were harvested immediately after the 5 or 10 s pulse of $^{14}CO_2$, over 75% of the radioactivity was found in malate or aspartate, with about 11% in phosphoglyceric acid, 4% in sugar phosphates, 2% in sucrose, and very small amounts in other compounds. When the leaves were left in normal air, the radioactivity moved slowly from the organic acids into phosphoglyceric acid, sugar phosphates and sucrose. After 5 min the percentages in these compounds were 19, 2, 4·5 and 53 respectively. Thus even at relatively low temperatures the pattern of photosynthetic carbon fixation is characteristic of the C_4-pathway. (Thomas, with Dr S. P. Long, University of Essex)

Effect of aerial pollutants on cereal growth. Spring barley, var. Abacus, was grown in four open-top chambers, two closed chambers and on two outside plots. Two of the open tops and one of the closed chambers were ventilated with clean air (i.e. air that has passed through a carbon and absolute filter) and the remainder with ambient field air. The mean ambient field level of sulphur dioxide was 61 μg m^{-3} and was reduced by 70% in the closed, filtered and 50% in the open, filtered chamber. The temperatures and relative humidities within the chambers varied little from those outside. There were no signs of

TABLE 4

Growth of barley in clean air

	O + C	O − C	Out	Cl − C	Cl + C
SO_2 μg m^{-3}	31	54	61	49	25
Grain yield g m^{-2}	316	166	212	301	439
Total plant wt g m^{-2}	816	376	656	694	958
1000 grain wt g	39	33	31	29	42
Sulphur %	0·28	0·33	0·37	0·35	0·33
Fluoride ppm	17	51	46	14	8

O ± C Open chambers with or without filtration.
Cl ± C Closed chambers with or without filtration.
Out Outside control plots.

https://doi.org/10.23637/ERADOC-1-133

visible injury but the plants in filtered air grew better than those in ambient air. By the final harvest the total dry matter, ear weight, grain weight and 1000 grain weight of plants grown in clean air were higher than those grown in ambient field air (Table 4).

Analysis of plant material for sulphur showed the plants from the chambers supplied with clean air to contain least. Higher fluoride contents were observed in plants grown outside and in the unfiltered, open-top chamber. The fluoride content of plants grown in open filtered was slightly higher than those in the closed, filtered chambers. Clearly fluoride pollutants are entering the open but not the closed chambers, indicating a particulate nature for much of the pollutant. (Brough and Parry)

Growth substances in developing wheat grains. The maximum volume of developing wheat grains was reached before maximum dry weight, and was inversely related to temperature so that at lower temperatures larger grain results capable of storing more starch. The expansion stage was associated with a considerable increase in gibberellin content. Abscisic acid content reached a peak shortly before the start of a sharp decrease in water content, and this in turn occurred a few days before dry weight increase ceased.

In a constant temperature of 15°C the third grain of each spikelet increased in dry weight and volume at the same rate as the lower grains, but started later because of later anthesis and ceased at almost the same time. Thus it had a smaller final dry weight than the first two grains. At 25°C the rate of increase of both weight and volume was less. Some ears grown at 15°C had the first and second grains removed, and then the volume and water content of the third grain increased much more rapidly than any grains in intact ears, while the dry weight increased at the same rate as the third grains of intact ears. Hence the difference in volume cannot be due to a greater supply of carbohydrates.

The amount of sucrose per grain remained constant for several weeks and was three times as high at 15° as at 25°C. In intact ears the first two grains and the smaller third grain of the spikelet contained similar amounts per grain. In grains from the partly degrained ears the sucrose content increased with time to a much higher value.

The chloroplasts of the inner pericarp may be one site of biosynthesis of both gibberellin and abscisic acid. The increase in total grain gibberellin ceased at the time when the ability to fix carbon dioxide began to decrease, but the gibberellin content of the outer pericarp continued to increase slowly. The reverse was true of abscisic acid, which decreased sharply in the outer pericarp as the chloroplasts degenerated, but continued to increase in the whole grain. The content of α-amylase in the outer pericarp began to decrease as abscisic acid reached a maximum, but there was no correlation with gibberellin content so that regulation of the enzyme appears to be different from that in germinating grain.

Application of abscisic acid to wheat ears by various techniques (microdrops containing 10 μg applied to the glumes, 10 μg ml^{-1} solution fed to flaps cut in the stems or to the stems of detached ears) reduced uptake of ^3H_2O to both grains and glumes. The amount of [^{14}C]-sucrose translocated to the grains in the xylem of detached ears was also reduced. Radioactive photosynthate moving to the ears through the phloem was not reduced. These effects were presumably due to closure of the glume stomata. The water content of both glumes and grains was generally higher several days after treatment, especially in detached ears, but it is uncertain whether this was entirely due to closure of the glume stomata. Treatment of older ears with abscisic acid decreased water content of glumes and grains relative to controls and in some cases accelerated the yellowing of senescent glumes. The cause of this reversal of response is unknown. Removal of glumes caused a loss of grain water content and a reduction in amount of labelled photosynthate translocated to the grains. (Radley)

https://doi.org/10.23637/ERADOC-1-133

Cytokinins and endosperm cell division. A comparison of primitive and modern wheat varieties shows that the increase in grain weight is possibly related to the increase in number of endosperm cells (Dunstone & Evans, *Australian Journal of Plant Physiology* (1974), **1,** 157–165), which in turn depends on the number and ploidy of the antipodal cells present in the embryo sac. The antipodal cells may function either by supplying the protein requirements of endosperm nuclear development during the coenocytic phase (Bennett *et al., Philosophical Transactions of the Royal Society. Series B* (1975), **272,** 199–227) or by releasing growth-promoting substances during degeneration (Nutman, *Annals of Botany* (1939), **3,** 731–758). The cytokinin content of developing wheat grains is known to be high at the end of the first week after anthesis (Wheeler, *Annals of Applied Biology* (1972), **72,** 327–334) and the present investigation attempted to relate changes in endogenous cytokinins during the first week after anthesis to antipodal and endosperm cell development.

Changes in cytokinins in developing grains were examined in spring wheat, var. Kleiber, grown outdoors. Samples of fifty ears were removed at daily intervals after anthesis and the grains in the two basal florets were dissected from spikelets in the middle third of an ear. The grains were extracted with methanol:water (4:1 v/v) and the basic (pH 8·0) butanol soluble compounds chromatographed on prewashed Whatman 3MM papers using butan-2-ol:3·5N NH_4OH (4:1 v/v) as developing solvent. Two zones of biological activity, at Rf 0·1–0·3 and Rf 0·5–0·8, were detected using the soybean callus and cucumber cotyledon assays. Quantitative estimates of the free base and riboside cytokinins present at Rf 0·5–0·8 were made using the soybean callus assay with zeatin as a standard. The cytokinin content of grains increased from 1·5 ng per grain at anthesis to 10 ng per grain three days after anthesis and declined to 2·5 ng per grain four days after anthesis. These changes have yet to be related to antipodal and endosperm cell development. The compound present at Rf 0·1–0·3 has not been identified or reliably estimated. (Lenton)

Sugar beet

Growth physiology

Effect of light quality and duration on growth. Sugar beet grown in controlled environments with similar daily amounts of visible radiation showed marked responses to changes in daylength. When daylength was extended from 12 to 16 h with photosynthetically-active radiation of three-quarters intensity, leaf area was increased by 18% and plant dry weight increased by 25% after six weeks resulting from an increase in net assimilation rate (NAR). Extending the daylength from 12 to 16 h with low intensity red light (160 $\mu W\ cm^{-2}$, 600 to 700 nm) increased growth to the same extent, again through an increase in NAR.

By contrast, extending daylength for a similar period but with only low intensity incandescent light, rich in energy from the far-red wavelengths, resulted in increases in leaf expansion (50%) and petiole growth (75%) and increased plant dry weight (25%) arising from improved light interception. Differences in the response of laminae and petioles were observed according to the time when the additional 4 h of incandescent light was given during the 12 h of darkness. Leaf area increased more when the additional light was given immediately after the main photoperiod than in the middle of the night and there was no response when it preceded the main light period. By contrast, petiole length increased irrespective of when the additional incandescent light was given during darkness but the response was greatest from the treatment given in the middle of the night. A 15 min exposure to low-intensity far-red light (28 $\mu W\ cm^{-2}$, 700 to 800 nm) at the end of a 12 h photoperiod increased growth of petioles but decreased leaf expansion.

In many plants daylength responses are associated with changes in endogenous growth

https://doi.org/10.23637/ERADOC-1-133

substances. The photomorphogenic reponses of leaves and petioles in sugar beet are similar to those caused by applied gibberellins. Applied gibberellins partially substituted for the photoperiodic stimulus to leaf expansion resulting from extending 8 h natural daylight with 4 h of incandescent light. The concentration of naturally-occurring gibberellins was highest in young leaves at the unrolling stage (which precedes the phase of most rapid expansion) in both natural and extended daylengths and declined as the rate of leaf expansion decreased. It was three times greater in young, faster expanding leaves of plants grown in extended daylengths than in slower expanding leaves of plants grown in 8 h days. These differences in endogenous gibberellins and the positive response to applied gibberellins suggest that gibberellins are involved in photoperiodically-induced leaf expansion in sugar beet. (Lenton and Milford)

Water relations. The effects of sodium chloride fertiliser on leaf-water status and photosynthetic activity were different in field experiments in 1974 and 1975 indicating a possible interaction between the effects of sodium and soil moisture status (*Rothamsted Report for 1974*, Part 1, 62 and *for 1975*, Part 1, 67). This interaction was studied further by examining the effects of sodium at a wide range of soil-water potentials under controlled conditions in growth rooms. Sodium chloride applied to the soil increased the level of sodium in the laminae five-fold and increased the water capacity of the shoot and laminae of the plants by 30% over the range of soil moisture content from 23 to 5% (equivalent to soil-water potentials ranging from $-0{\cdot}01$ to $-15{\cdot}0$ bar). Thus the large increase in sodium in the leaves did not have the expected large effect on the osmotic potential because plants adjusted by increasing the water content of the leaves and the size of the mesophyll cells so that leaf water, osmotic and turgor potentials remained the same as those of plants without sodium. The change in size of the mesophyll cells in plants given sodium produced larger, thicker and more succulent leaves. In the field this larger leaf area results in greater interception of radiation early in the season and greater yield. Also, plants given sodium have a greater water capacity in the shoot because they are buffered against the diurnal and seasonal decreases in leaf-water potential and photosynthesis that occur even in well-irrigated crops and which are substantial when transpiration is high or soil moisture is depleted (*Rothamsted Report for 1974*, Part 1, 34). Hence their leaves function more efficiently except at extreme water stress. (Milford, with Cormack, Broom's Barn Experimental Station)

Ancymidol and the bolting of sugar beet. A marked increase in endogenous gibberellins at the transition from a vegetative to a flowering apex have been observed in sugar beet, but high concentrations of known gibberellin antagonists proved unable to prevent bolting in autumn-sown plants (*Rothamsted Report for 1975*, Part 1, 44). Recent reports suggest that ancymidol is an antagonist of gibberellin which is effective at low concentrations in reducing internode elongation in ornamental crops.

Preliminary experiments with an over-wintered commercial variety and an annual line of sugar beet showed that ancymidol was effective when applied to the shoot apex, although slight damage occurred, and was equally effective as a soil drench but at higher concentrations. Ancymidol reduced the rate of stem elongation, the extent of inflorescence branching and the number of flowers produced.

The possible interaction between ancymidol and gibberellin was examined using a uniform line known to bolt naturally under long days. Ancymidol (as 0·25% solution) was applied as a soil drench at the six-leaf stage as two weekly applications of 50 μg and 300 μg per plant. One week later gibberellic acid (0·25% solution) at 50 μg and 200 μg was applied to the shoot apex. Stem length was measured twice weekly and plants were harvested eight weeks after the start of treatment.

https://doi.org/10.23637/ERADOC-1-133

In the absence of gibberellin, ancymidol delayed the initiation of bolting, whereas gibberellin in the absence of ancymidol hastened it. Moreover, gibberellin overcame the delaying effects of ancymidol. The rate of stem elongation was reduced by the highest rate of ancymidol in the absence of gibberellin, and conversely gibberellin in the absence of ancymidol increased it. Furthermore, it appears that gibberellin can overcome the inhibitory effects of the highest rate of ancymidol on stem elongation.

Growth regulator trials. Four regulators were tested using the screening procedure devised last year (*Rothamsted Report for 1975*, Part 1, 46). An early application of the chemicals was made at the end of May at the eight-leaf stage. Plants were harvested after four and 12 weeks (late June and late August). A late application (early July) at the 30-leaf stage was harvested seven weeks later (end August).

'AC 98203' (***American Cyanamid***) was tested last year as a foliar spray but was re-tested as soil-applied granules. Early application was at rates of 50 mg and 200 mg per plant of the 5% formulation, equivalent to 0·5 and 2·0 kg a.i. ha^{-1}. After four weeks the lower rate reduced petiole weight 15% and increased root dry weight by 15% though the difference was not statistically significant. Conversely the higher rate gave a significant increase in root dry weight of 25%. Sugar concentration as percentage fresh weight rose from 11·4 to 12·4 resulting in a significant increase in sugar yield from 12·4 g to 17·6 g per root. After 12 weeks the root dry weight was 10% above the control though not statistically significant, and at this time both rates of application increased the number of living leaves without affecting total leaf production; the chemical had reduced leaf senescence. The final sugar concentrations were not affected, being 16% fresh weight and 80% dry weight, although total sugar content at the higher rate was increased by 10%.

'AC 94377' (***American Cyanamid***). This and the following two chemicals were applied in solution as microdrops with one-sixth of the total a.i. at any one time applied to the shoot apex and the remainder applied to the soil around the root. 'AC 94377' was applied as 0·1% a.i. solution at the rates of 0·3 mg and 1·2 mg a.i. per plant at the early treatment, and 1·5 mg and 6·0 mg a.i. per plant at the late treatment.

This chemical had by far the greatest effect and both rates produced similar responses. Four weeks after early application dry weight of laminae and petioles were reduced by 10 and 20% respectively and leaf area was decreased by 13% although there was no effect on leaf production or leaf senescence. Specific petiole length (SPL) (cm g^{-1}) was increased by 30% indicating thinner petioles. By 12 weeks the lower concentration increased lamina dry weight by 50%, total leaf area by 30% (reversing the earlier trend) and mean area leaf^{-1} by 40%. The higher concentrations did not affect lamina characteristics after 12 weeks, but reduced petiole dry weight and maintained the increase in SPL. After four weeks the early application had increased root fresh weight by 45% and, although sugar concentrations were reduced by 1% (both as percentage fresh weight and percentage dry weight) the sugar yield was up by 40%. By 12 weeks root dry weight was 22% above the controls but the increase was not statistically significant. The water content of both petiole and root was increased after 12 weeks. Sugar concentrations were not altered significantly.

The late application of this chemical had, after seven weeks, increased total leaf number by 20% to 54 and had increased the proportion of living leaves to 80%, although total leaf area was not affected. Plant dry weight was not significantly affected (although the higher rate tended to produce a larger plant, e.g. root dry weight up by 12%), whereas fresh weights were much higher than the control indicating higher water contents in all parts of the plant. The crown of most plants was swollen and slightly elongated and the

https://doi.org/10.23637/ERADOC-1-133

roots were usually very fibrous. The higher rate reduced sugar concentration to 13% fresh weight and 74% dry weight.

PRB-8 (provisionally known as orthonil) was applied this year to mature plants to extend the effects previously observed in young plants (*Rothamsted Report for 1973*, Part 1, 100). It was applied as a 0·05% a.i. aqueous solution either supplying 150 μg or 600 μg a.i. at the early application and 750 μg or 3 mg a.i. at the late application. After four weeks of the early application only the lower rate showed any response. Lamina dry weight was down 10% and leaf area was reduced by 13%. By 12 weeks, however, both rates showed similar responses. Petiole dry weight was increased and total plant dry weight was up by 15% with, at the higher rate, a small redistribution of dry matter favouring the root. Total leaf area was up by 20% because of larger leaves.

The late application increased total and living leaf number and, although the root dry weight was up by only 8%, the shoot dry weight was unchanged giving a much reduced shoot:root ratio and indicating a change in the distribution of dry matter.

'LS 72 354' (Pepro) is an ethylene-releasing compound with a slow action and was tested because of the possibilities of 'Ethrel' (provisionally known as ethephon) indicated earlier (*Rothamsted Report for 1974*, Part 1, 35). Early treatment of 0·25% a.i. aqueous solution supplying either 750 μg or 3 mg a.i. was phytotoxic. For the late application the same amounts of active ingredient were applied as 0·05% solution.

The higher rate increased the proportion of living leaves and also increased root fresh weight by 18%. However, water content was also increased so that root dry weight was only 7% above the control. (Pocock)

Weed biology

Classical experiments

Broadbalk. Field surveys showed that terbutryne again controlled autumn-germinating blackgrass (*Alopecurus myosuroides*) and corn buttercup (*Ranunculus arvensis*), but the latter was not prevalent on the unsprayed section, presumably because of competition from the dense blackgrass there. Scentless mayweed (*Tripleurospermum maritimum* ssp. *inodorum*), poppies (*Papaver* spp.), Venus' looking-glass (*Legousia hybrida*), wall speedwell (*Veronica arvensis*) and parsley piert (*Aphanes arvensis*) are also controlled by terbutryne in autumn, as well as by herbicides aimed specifically at dicotyledonous weeds in spring, and are declining. Red bartsia (*Odontites verna*) was scarce in 1976, discouraged by drought and night frosts during its germination period.

Field Horsetail (*Equisetum arvense*) was widespread but less dense than usual on account of the summer drought. By late May i.e. soon after its emergence, the soil already showed deep cracks especially on Sections 1 and 5, and *Equisetum* was late and sparse on the most severely cracked plots. Knotgrass (*Polygonum aviculare*) and black bindweed (*Polygonum convolvulus*) suffered from drought and herbicide in winter wheat which was already established when they germinated, but were very vigorous in unsprayed spring-sown beans. The beans failed on account of the drought and were cut early, leaving the soil covered with a welter of *Polygonum* spp. interspersed with numerous ground-keeping potatoes. As soon as the weeds had been surveyed and the soil samples taken for the weed-seed content, the bean stubble was sprayed with diquat to prevent further production of weed seeds.

The wheat was cut in the last week of July. Annual weeds were very scarce in stubble on the sprayed plots but blackgrass was dense between the rows on unsprayed plots. *Papaver* spp. flourished on unsprayed plots especially those receiving FYM, but field

https://doi.org/10.23637/ERADOC-1-133

forget-me-nots (*Myosotis arvensis*) were few and small on account of the drought. Very few of the current season's blackgrass seeds had germinated by 5–6 August when the plots were surveyed.

Perennials were far more serious. Couch grass (*Agropyron repens*) and bent-couch (*Agrostis gigantea*) formed extensive patches in continuous wheat with herbicides, especially on Section 9, despite spraying with glyphosate in autumn 1975. *Equisetum* was prevalent on rotation sections, especially on plots where crop competition was weak and particularly on plot 5 (PKMg), suggesting that the *Equisetum* may benefit from these fertilisers where N-deficiency weakens the crop. Potatoes were the most abundant weeds in rotation wheat. Field bindweed (*Convolvulus arvensis*) again flourished and flowered in large patches in all crops (*Rothamsted Report for 1975*, Part 1, 47). Coltsfoot (*Tussilago farfara*) was scarce.

Two insect-attacks were seen on weeds for the first time on Broadbalk. The moth *Agriphila straminella* oviposited on the severe infestation of *Agrostis* on plot 10·9; after the weed was checked by spraying with glyphosate in the stubble in 1975, the hatching caterpillars attacked the wheat, causing severe crop loss in the area previously occupied by *Agrostis*. Both wheat and *Agrostis* showed some recovery by harvest. The other insect, the fly *Urophora cardui*, caused stem galls on creeping thistles (*Cirsium arvense*) in beans on plots 17 and 18. (Thurston)

Soil samples for weed seed content were taken from the stubble of seven plots of seven sections in 1976 to complete the study begun in 1974 (*Rothamsted Report for 1974*, Part 1, 39). The number of blackgrass seedlings removed to the end of September suggests that the total will probably be similar to that of autumn 1974 (after spraying with terbutryne the previous year) and well below 1975 when spraying with terbutryne was omitted on account of the wet autumn of 1974. So far 11 potato seedlings have been removed from the soil samples taken from wheat stubble in the three-course rotation. These seeds must have been formed in 1971 or 1974, remained dormant until dormancy was broken by the high summer temperatures in 1976 and germinated when the soil was moistened. Only five potato seedlings occurred in the soil from the bean stubble immediately following potatoes on this section in 1975. Potato seedlings were more numerous than some weed species here, and could add to the problem caused by sprouting tubers. On plot 9 (N4PK) the potato seedling population was equivalent to $1{\cdot}0 \times 10^6$ ha^{-1}. Field records do not distinguish between shoots arising from tubers or true seeds.

Over 24 000 seedlings have been removed from the first set of 98 pans, between September 1974 and September 1976. This represents 10 558 seedlings m^{-2} on the field in the course of two years, 43·5% of them during the second year. Germination continues, so this is an underestimate of the total, mainly due to species with long dormancy, e.g. poppies. The ratio of first to second year germination approximates to the 2:1 found by Roberts at Wellesbourne. However, species differ greatly: the three major species, which between them account for 85% of the seedlings, are blackgrass (*Alopecurus myosuroides*), poppies (*Papaver rhoeas* and *P. argemone*) and knotgrass (*Polygonum aviculare*) with 4·5, 60·4 and 37·1% of their two-year germination in the second year. Black bindweed (*Polygonum convolvulus*) had 75·4%.

Both fertiliser and cropping affect the presence and abundance of species.

The differences in number of seedlings of the main species in soil from different sections agree well with field observations on the relative abundance of species. Knotgrass, which was never abundant in winter wheat on Broadbalk before the rotation was introduced, is now the third most abundant species. It proliferates in spring-sown beans where the only weed control is inter-row cultivation. On the sections in the three-course rotation, knotgrass contributed 46 and 33% of the total seedlings, compared with only 1% in the continuous winter wheat. It is controlled by the linuron-paraquat mixture used in potatoes

https://doi.org/10.23637/ERADOC-1-133

and by mixtures containing dicamba in winter wheat, so most of the seeds germinating in soil after rotation-wheat must be the dormant residue of those shed in the previous year in beans. Black bindweed, another spring-germinating species, also proliferates in beans.

Black grass, a predominantly autumn-germinating species, is the most abundant. Of all seedlings to date in the 1974 pans it accounts for 47–64% in continuous winter wheat, 23 and 29% in first and second wheat after fallow, but only 4% in wheat in the three-course rotation. Evidently, the cultural control by two spring-sown crops out of three is more effective than terbutryne applied annually pre-emergence in winter wheat.

The results are subject to confirmation from the results of the 1975 and 1976 pans. (Thurston)

Park Grass. Botanical analyses of samples of herbage taken from the Park Grass plots in 1973 and 1974 (*Rothamsted Report for 1974*, Part 1, 40 and *for 1975*, Part 1, 48) showed, not only large changes in botanical composition of sub-plots which had received lime for the first time or increased rates of lime under the new liming scheme, but also much change since the previous analysis in 1948 and 1949 in sub-plots with unchanged treatment. The analyses were, therefore, extended in 1975 to include plots not yet in the new scheme; samples of herbage were taken from limed (L) and unlimed (U) half-plots of plots 3 (unmanured), 7 (PKNaMg) and 8 (PNaMg) and from the plots receiving nitrogen as sodium nitrate—plots 17 (48 kg N ha^{-1} annually), 16 (as 17 plus PKNaMg) and 14 (96 kg N ha^{-1} annually plus PKNaMg). In 1976, plots 3U, 3L, 7U, 7L, 14U and 14L were again sampled and also sub-plots a, b and c of plot 9 (as 14 but N as ammonium sulphate).

The results showed that, although there had been little change in the number of species on the plots, their relative contribution had changed on most plots. On plot 3U, grasses have tended to increase and legumes decrease; the increase in grasses has resulted mainly from a doubling in percentage of red fescue (*Festuca rubra*) which now makes up a third of the herbage. Salad burnet (*Poterium sanguisorba*), ribwort (*Plantago lanceolata*) and rough hawkbit (*Leontodon hispidus*) remain the main dictoyledonous species on 3U. On 3L red fescue has trebled since 1948 and is now 13% of the herbage. Hairy oat-grass (*Helictotrichon pubescens*) has decreased from 13 to 6%. Despite very different weather conditions preceding the 1975 and 1976 harvests, the botanical compositions of the unmanured plots were very similar. Thus the changes noted represent successional and not seasonal changes. One effect of the drier conditions preceding the 1976 harvest was to increase salad burnet, ribwort and rough hawkbit on 3L and to decrease grasses; this did not occur on 3U, possibly because it is now too acid for any further increase in dicotyledonous species.

On plot 7U, large increase in percentage of common bent-grass (*Agrostis tenuis*) and red fescue has occurred. Common bent-grass now contributes 30% and red fescue 18% of the herbage compared to 4–5% for both species during 1947 and 1948. Yorkshire fog (*Holcus lanatus*) has increased from 2 to 6% but cocksfoot (*Dactylis glomerata*) decreased from 18 to 4%. Legumes, mainly meadow vetchling (*Lathyrus pratensis*) have declined, as also have other broad-leaved species from 30 to 14%, half of which consists of ribwort. On 7L meadow foxtail (*Alopecuris pratensis*), cocksfoot and false oat-grass (*Arrhenatherum elatius*) were equally abundant between the mid 20s and late 40s but by 1975 and 1976 false oat-grass had become the dominant grass species; legumes (meadow vetchling and red clover (*Trifolium pratense*) continued to be plentiful contributing 20% of the yield in 1975 and almost 50% in 1976. The changes that have occurred in the grass composition of 8U and 8L have been similar; sweet-vernal grass (*Anthoxanthum odoratum*) and Yorkshire fog have increased but false oat-grass and cocksfoot have decreased. On plot 17, cocksfoot has also declined but ribwort has increased on both unlimed and limed

https://doi.org/10.23637/ERADOC-1-133

halves. On 16U and 16L false oat-grass has doubled to 40%; on 16U meadow foxtail remains co-dominant but on 16L it contributes only 4%. Meadow buttercup, absent in 1949, now contributes 4% on both half-plots and hogweed (*Heracleum sphondylium*) has increased from 1 to 18% on 16L. On plot 14, which receives the larger amount of sodium nitrate, the vegatation has remained relatively stable with false oat-grass and meadow foxtail co-dominant (each about 37%) on the unlimed half and false oat-grass dominant on the limed half. Cocksfoot has, however, decreased from about 14 to 2% on both half-plots but cow parsley (*Anthriscus sylvestris*) and also meadow buttercup and dandelion (*Taraxacum officinale*) have increased, especially on the limed half. The 1976 samples from plot 9 have not yet been analysed.

During early June 1976 cat's ear (*Hypochaeris radicata*) appeared more prominent than usual on several plots and perennial ryegrass (*Lolium perenne*) and cocksfoot appeared to dominate the permanently-limed sub-plots of plot 18 (N2KNaMg). On sub-plot 4^1c a patch of restharrow (*Ononis repens*) flowered in August; this appeared to consist of a mass of seedlings over a wider area than the smaller number of bush plants previously recorded. (Williams)

Perennial grass weeds

Seed germination and seedling growth of* Agropyron repens *and* Agrostis gigantea *(the couch grasses). The glasshouse experiment on the effect of different frequencies of soil disturbance on the germination of *Agropyron* and *Agrostis* seed in Rothamsted and Woburn soils, started during autumn 1971 (*Rothamsted Report for 1972*, Part 1, 107) was continued during 1975/76. *Agrostis*, but not *Agropyron*, seeds continued to germinate during the fifth year. Over all frequencies of cultivation 4·5% *Agrostis* seeds gave emerged seedlings in Woburn soil but only 1·5% in Rothamsted soil, indicating that seed longevity may be affected by soil type. Total germination was however similar in the two soils (Table 5). The long survival of *Agrostis* seed under enforced dormancy emphasises the

TABLE 5

Percentage germination of Agrostis gigantea *in Woburn and Rothamsted soil (Mean of 3 cultivation frequencies)*

	Year 1	2	3	4	5	Total
Woburn	62·2	4·8	7·1	2·6	4·5	81·2
Rothamsted	63·1	7·3	8·8	2·0	1·5	82·7

fact that once the seeds of this species are incorporated into soil its depletion is likely to be a protracted process. The field experiment, started in autumn 1974, also continued during 1976. This investigated the effect of three different cultivation treatments during the first autumn on the germination and longevity of the weed seeds (*Rothamsted Report for 1975*, Part 1, 49). During 1975/76 about 2·2% of the *Agrostis* and *Agropyron* seeds in plots ploughed early in autumn gave emerged seedlings, but in late-ploughed plots fewer than 1% of the *Agrostis* seeds and fewer than 2% of the *Agropyron* seeds gave emerged seedlings. In plots rotavated in autumn 1974 only about 0·5% *Agropyron* and 0·7% *Agrostis* seeds gave emerged seedlings during the second year. The experiment is being continued.

Experiments in previous seasons had indicated that the growth of weed seedlings in cereal crops showed some interaction between nitrogen supply and the relative time of emergence of crop and weed. In 1975/76 weed seedlings were established in winter wheat, var. Cappelle-Desprez, at the one and at half-leaf stage on 3 and 4 November; third planting intended for the spring was abandoned because of very dry soil. Plots were given 0,

https://doi.org/10.23637/ERADOC-1-133

30 or 80 kg N ha^{-1} on 10 May. The wheat grew moderately vigorously until it was harvested on 29 July but it showed little response to nitrogen, probably because of the dry season. The amount of growth made by the weeds in this experiment greatly exceeded that in any previous year from 1971 to 1975, because they grew for a longer interval in the stubble as a result of early harvest of the crop and because of much rainfall and warm soil temperatures during September. By 22 September both early-planted *Agropyron* and *Agrostis* had mean shoot weights of 47 g m^{-2}; that of *Agropyron* was decreased to 34 g m^{-2} and *Agrostis* to 24 g m^{-2} by delaying 'emergence'. *Agropyron* from the first and second planting had respectively 26 and 20 g rhizomes m^{-2} and *Agrostis* 4 and 2 g m^{-2}. Shoot weight of *Agropyron* was increased by more than 40% from 31 to 44 and rhizomes from 18 to 25 g m^{-2} by the first increment of nitrogen, but there was little further response to the second increment; *Agrostis* growth was not influenced by nitrogen.

The results show that where weed seedlings are allowed to grow undisturbed in cereal stubbles, especially where conditions are conducive to rapid growth, seedlings are capable of initiating new infestations or of prolonging older ones. (Williams)

Staff and visiting workers

S. A. W. French retired on the 31 December 1976 after a period of 47 years continuous service at Rothamsted. Alison Brough left the Department after marrying and moving away from the area. D. C. McIlroy completed his studies for the Ph.D. Degree of London University and after being awarded the degree left the Department to take up an appointment with Dornay Foods Limited at Kings Lynn. N. G. Hall (Bradford University) completed his studies at Rothamsted as part of a CASE Studentship.

Sandwich course students who worked in the Department were A. Davidson, Lisa Gunn, G. Samuel and M. Snow.

Visitors to the Department included Mr O. H. D. Makunga of the University of Fort Hare, Alice, South Africa, who spent six months working on the distribution of photosynthate in wheat and maize sponsored by the British Council. Dr. R. Martinez-Carrasco of the Research Center for Soil Science and Applied Biology, Salamanca, Spain, has spent most of the past year working in the Department studying factors determining grain size in cereals, sponsored by the World Bank through the Spanish Ministry of Agriculture.

C. P. Whittingham attended the '39th Winter Congress of the Institut International de Recherches Betteravieres' in Brussels and also the '9th International Conference on Growth Substances' in Lausanne, Switzerland. In addition, C. P. Whittingham chaired a session on Photorespiration at 'the Gordon Research Conference on Carbon Dioxide Fixation by Green Plants' in New Hampton, New Hampshire, USA. Joan M. Thurston gave a joint paper at the Centenary Celebrations of the French Agricultural College at Grignon in July 1976.

Publications

Thesis

1 McIlroy, D. C. (1976) Biochemical and physiological aspects of bruising in potato tubers. Ph.D. University of London.

General Papers

2 Milford, G. F. J. & Lawlor, D. W. (1976) Water and the physiology of sugar beet. *Proceedings International Institute for Sugar Beet Research 39th Winter Congress February 1976*, 95–108.

https://doi.org/10.23637/ERADOC-1-133

3 THURSTON, J. M. (1976) Weeds in cereals in relation to agricultural practices. In: Symposium on the biology of weeds in relation to their effects on crops. Proceedings of the Association of Applied Biologists. *Annals of Applied Biology* **83**, 338–341.

4 THURSTON, J. M., WILLIAMS, E. D. & JOHNSTON, A. E (1976) Modern developments in an experiment on permanent grassland started in 1856. Effects of fertilisers and lime on botanical composition and crop and soil analysis. *Annales agronomique, A6. hors-serie*, 13–46.

5 WHITTINGHAM, C. P. (1975) Function in photosynthesis. In: *Chemistry and biochemistry of plant pigments*, 2nd edition, T. W. Goodwin, Academic Press, pp. 624–654.

6 WILLIAMS, E. D. (1976) Components of the vegetation of permanent grassland in relation to fertilisers and lime. In: Symposium on the biology of weeds in relation to their effects on crops. Proceedings of the Association of Applied Biologists. *Annals of Applied Biology*, **83**, 342–345.

RESEARCH PAPERS

7 BIRD, I. F., CORNELIUS, M. J., KEYS, A. J., KUMARASINGHE, S. & WHITTINGHAM, C. P. (1975) The rate of metabolism by the glycollate pathway in wheat leaves during photosynthesis. *Proceedings 3rd International Congress on Photosynthesis 1974, Rehovot, Israel* 1291–1301.

8 KEYS, A. J., BIRD, I. F., CORNELIUS, M. J., KUMARASINGHE, S. & WHITTINGHAM, C. P. (1976) Use of isotopes to explore the physiology and biochemistry of photorespiration and its effects on crop yeilds. *International Atomic Energy Agency, Vienna, Technical Report Series 1*, 13–18.

9 LAWLOR, D. W. (1976) Assimilation of carbon into photosynthetic intermediates of water-stressed wheat. *Photosynthetica* **10**, 431–439.

10 LAWLOR, D. W. (1976) Water stress induced changes in photosynthesis, photorespiration, respiration and CO_2 compensation concentration of wheat. *Photosynthetica* **10**, 378–387.

11 LAWLOR, D. W. & FOCK, H. (1977) Photosynthetic assimilation of $^{14}CO_2$ by water-stressed sunflower leaves in large and small oxygen concentration and the specific activity of products. *Journal of Experimental Botany* **28**, 320–328.

12 LAWLOR, D. W. & FOCK, H. (1977) Water-stress induced changes in the amounts of some photosynthetic assimilation products and respiratory metabolites of sunflower leaves. *Journal of Experimental Botany* **28**, 329–337.

13 LAWLOR, D. W. & LAKE, J. V. (1976) Evaporation rate, leaf-water potential and stomatal conductance in *Lolium*, *Trifolium* and *Lysimachia* in drying soil. *Journal of Applied Ecology* **13**, 639–646.

14 MILFORD, G. F. J. (1976) Sugar concentration in sugar beet: varietal differences and the effects of soil type and planting density on the size of the root cells. *Annals of Applied Biology* **83**, 251–257.

15 MILFORD, G. F. J. & LENTON, J. R. (1976) Effect of photoperiod on growth of sugar beet. *Annals of Botany* **40**, 1309–1315.

16 PEARMAN, I., THOMAS, S. M. & THORNE, G. N. (1977) Effects of nitrogen fertiliser on growth and yield of spring wheat. *Annals of Botany* **41** 93–108.

17 RADLEY, M. (1976) The development of wheat grain in relation to the endogenous growth substances. *Journal of Experimental Botany* **27**, 1009–1021.

18 WHEELER, A. W. (1976) Some treatments affecting growth substances in developing wheat ears. *Annals of Applied Biology* **83**, 455–462.

19 WILLIAMS, E. D. (1977) Growth of seedlings of *Agropyron repens* L. Beauv. and *Agrostis gigantea* Roth. in wheat and barley; effects of time of emergence, nitrogen supply and cereal seed rate. *Weed Research* **17**, 69–76.

https://doi.org/10.23637/ERADOC-1-133