ROTHAMSTED RESEARCH

Report for 1964

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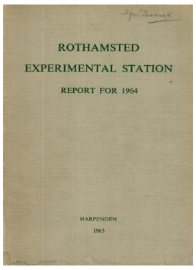

ROTHAMSTED

EXPERIMENTAL STATION

REPORT FOR 1964

HARPENDEN

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Botany Department

D. J. Watson

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BOTANY DEPARTMENT

D. J. WATSON

D. Burnett was appointed to work on growth regulators in the potato plant, supported by a research grant from the Potato Marketing Board. We had two visiting workers from overseas—Mr. J. Nösberger from the Institut für Pflanzenbau, Eidgenössiche Technische Hochschule, Zürich, who came in March for a year, and Dr. J. H. Wilson from the Department of Agriculture, University of Melbourne, who came in July for 8 months. Professor H. N. Barber, F.R.S., of the Department of Botany, University of New South Wales, spent part of his visit to the Station with us.

E. C. Humphries contributed to an international symposium on CCC organised by Cyanamid International at Geneva. Seven members of the department attended the Xth International Botanical Congress in Edinburgh. D. Burnett spent October and November working for UNESCO at the Institute of Biology, Belgrade, and visited other research Institutes in Brussels, Prague, Sarajevo and Szeged.

The general object of our work is to gain more knowledge of how crops grow, particularly of those features of growth that control yield, and of their dependence on internal factors of the plant and on environmental factors. Accordingly, much of our programme consists of field studies in crop physiology, based on the procedure called growth analysis; this relates growth in dry weight to change in leaf area index (L) and net assimilation rate (E), which respectively measure the size and efficiency of the photosynthetic system, and to the morphological changes that control leaf area index. Effects of climate and weather on growth and yield are being measured by growing plants in controlled environments, and also in field experiments by modifying the natural environment, for example, by shading. Work in the laboratory and glasshouses deals with problems arising from the field experiments, and other aspects of the physiology of plant growth that are relevant to crop production, such as the effects of natural and synthetic growth regulators. It also includes studies of the biology of weeds, especially of weed grasses that are still difficult to control by herbicides, and of factors that influence the development and persistence of weed infestations. The ultimate aim of all the work is to distinguish the determinants of crop yield and to suggest how crop plants and crop husbandry should be adjusted to secure maximal production.

Growth Studies on Field Crops

Wheat

Dependence of grain yield on leaf area duration. The material that fills cereal grains is mainly derived from photosynthesis that occurs after flowering, so grain yield depends on the size and persistence of the photosynthetic system, measured by leaf area duration (D) after the ears emerge, or more precisely after anthesis. This system includes not only green leaf laminae but also leaf sheaths, stem and peduncle. When new varieties of winter and spring wheats were compared (Watson, D. J., *et al.* 1963, *Ann. Bot.* N.S., **27**, 1–22), the grain yields were nearly proportional to *D*, so that the grain:leaf ratio (*G*; grain yield divided by *D*) was nearly constant. The same was true when older winter and spring varieties were compared, but *G* was greater for new than for old varieties. A similar difference between old and new varieties of barley was attributed to more photosynthesis by the ears of the newer varieties, but wheat ears photosynthesise too little to explain the variations of *G* (*Rothamsted Report* for 1963, p. 82).

Most of the carbohydrate in the grain comes from photosynthesis by the flag leaf lamina and sheath and the peduncle after ears emerge. Lower parts of the shoot that are still green contribute little, and if these are a larger fraction of the total leaf area in older varieties they could make the photosynthetic system, as measured by *D*, seem less efficient than in newer varieties. If this is so, grain yield should be more closely correlated with leaf area duration calculated from green area above the flag leaf node than from total leaf area, and *G* calculated on the basis of flag leaf *D* should be nearly constant for old and new varieties. This was tested in a wheat variety trial at Rothamsted in 1963, the results of which have now been analysed. The old variety Squarehead's Master and the newer Cappelle-Desprez and Prestige sown in autumn, and Jufy I and Prestige sown in spring, were compared each with 0·5 or 1·0 cwt/acre N applied as "Nitro-chalk 21" in spring.

The differences in grain yield between the newer varieties, sown either in autumn or spring, were closely related to total *D* after ear emergence, and *G* calculated on this basis was nearly constant, but again Squarehead's Master had a value of *G* about two-thirds of those for the others. The effects of different amounts of N on grain yield were also generally correlated with its effects on *D*.

Leaf area duration from ear emergence calculated for the green parts above the flag leaf node gave a slightly wider range of *G* among the newer varieties, i.e., it did not account for the differences in grain yield between these varieties any better than total *D*. However, Squarehead's Master with 0·5 cwt/acre N now fitted the general relationship between yield and *D* shown by the newer varieties, with a *G* value close to the mean, but with 1·0 cwt/acre N its *G* value was still less than for other varieties. Calculating *G* from flag leaf *D* after anthesis instead of ear emergence diminished its range among newer varieties, but did not alter the position of Squarehead's Master with either nitrogen rate. The reason why Squarehead's Master given 1 cwt/acre N failed to yield commensurately with its post-anthesis *D* is not clear; possibly an inherent restriction to the size of its ears limits grain yield as *D* increases.

Thus, although *D* calculated from anthesis for green parts above the flag-leaf node defined the size and persistence of the photosynthetic system responsible for filling the grain better than when calculated from total leaf area index after ear emergence, the improvement was small and did not wholly explain the small *G* of Squarehead's Master. (Welbank, French and Witts)

Dependence of grain : leaf ratio on radiation. In 1963, when small plots in a spring wheat crop were grown from ear emergence to maturity unshaded or under shades of different densities, the grain : leaf ratio decreased with decrease in mean daily radiation. However, the slope of this regression was much less steep than that calculated by Thorne between *G* and mean daily radiation in the period between ear emergence and harvest for unshaded cereal crops grown in different years (*Rothamsted Report* for 1963, p. 82). The value of *G* for the unshaded plots in 1963 fitted Thorne's regression line very well, but mean daily radiation was much below the average of the previous years, partly because ears emerged late, ripening was slow and harvest was delayed until the short days of September.

The experiment was repeated in 1964, using winter wheat, var. Cappelle-Desprez, because there was no suitable crop of spring wheat. Shades made of Tygan screencloth that transmitted 64, 45 or 24% of solar radiation were placed over small plots on 25 June, when 50% of ears had emerged; other plots were left unshaded. The ripe crop was harvested on 24–25 August. The dry weight of grain per acre was decreased from 35 cwt to 32, 19 and 10 cwt by shades of increasing density. Straw yield and number of ears per plot were unaffected. So shading affected grain yield by decreasing the weight of grain per ear, mainly by giving smaller grains, but the two denser shades also gave fewer grains per ear; apparently some grains failed to grow to maturity. Shading slightly delayed senescence of leaves, but had no significant effect on *D*.

The mean daily radiation and *G* for the unshaded plots were near the middle of the range covered by Thorne's regression line relating *G* to mean daily radiation in different years, and fitted closely to the line. The slope of the line relating *G* to mean daily radiation in the 1964 shading experiment was again much less than that derived from different years, so that *G* was greater on shaded plots than on unshaded plots in years of corresponding small mean radiation. The relation of *G* to mean daily radiation in the shading experiment appears to be curved, and the results were consistent with a linear relation of *G* to log daily radiation, as found by Blackman and Wilson (1951, *Ann. Bot.* N.S., **15**, 63–94) between net assimilation rate and light intensity varied by shading.

The difference between the relation of *G* to mean daily radiation in different years and its relation to radiation changes produced by shading in any one year is probably explicable by the fact that, in comparisons between years but not between shading treatments, change in daily radiation is associated with change in temperature. Partial regressions of *G* in different years on daily mean temperature or on mean daily maximum temperature were positive and significant, but a partial regression on mean daily minimum temperature was negative and accounted for very little of the variance of *G*. When the values of *G* for different years were corrected for differences in mean daily temperature from the value found in 1964 they fell very close to the regression line obtained from the results of the shading experiment.

The general conclusion is that cereal grain yield depends on leaf area duration, especially of the flag leaf, between anthesis and maturity, on the amount of sunlight received by the crop and on temperature during this period. (Welbank and Witts)

Effects of CCC on growth and yield of spring wheat. The growth regulator CCC (2-chloroethyltrimethyl-ammonium chloride) inhibits stem growth of wheat, and when applied to young wheat has been reported to increase yield by shortening the straw and so preventing lodging. There is also some evidence that it increases yield in crops that do not lodge. An experiment was done with spring wheat to measure effects of CCC on yield and on growth at earlier stages. To increase the likelihood of lodging, the variety Phoebus was sown at 4½ bu/acre (1½ × normal rate), and supplied liberally with nitrogen (0·25, 0·75 or 1·25 cwt/acre N as "Nitro-chalk 21"). The crop was sown on 13 March, and nitrogen applied on 31 March. Some plots were sprayed with CCC solution (2·5 or 5 lb in 67 gall/acre) on 13 May, when plants had about six leaves. Plants were sampled and measured on 14 May, 3 June and 24 June (about the time of ear emergence), and the ripe crop was harvested on 24 August.

On 3 June, three weeks after spraying, CCC at either rate decreased shoot height by about one-third. At ear emergence spraying with CCC approximately halved shoot height on plots that received the two smaller amounts of N, but with the largest amounts the sprayed plants were 60% as tall as unsprayed plants; nitrogen increased shoot height more in plants sprayed with CCC than in unsprayed plants. CCC shortened all internodes and delayed ear emergence by about 6 days. It increased ear number per plot at harvest, because more tillers survived to bear ears; it decreased mean 1,000 grain weight, possibly because the extra ears were small and produced small grain. Although there was no lodging, both rates of CCC increased grain yield with all rates of N supply. Averaging all rates of N and both rates of CCC, grain was increased from 39·7 to 41·9 cwt/acre (85% dry matter). 1 cwt/acre N increased yield by four times the mean increase by CCC.

CCC decreased leaf area index to between 70 and 80% of that of unsprayed plots; the decrease was least with the most N. Although most of the decrease was probably in leaf sheath area, more light penetrated the canopy of crops sprayed with CCC than of unsprayed crops, and this may account for the increased survival of shoots. CCC apparently increased net assimilation rate slightly, probably a consequence of the decrease in leaf area index rather than a direct effect on photosynthesis.

A treatment that shortens straw would be more useful with barley, which is more susceptible to lodging than spring wheat, but unfortunately CCC has little or no effect on shoot length of barley. In tests with six varieties grown in pots, CCC decreased the shoot length of the old long-strawed variety Plumage-Archer, but not of Proctor, Maris Badger, Europa, Cambrinus or Impala. (Humphries, Welbank and Witts)

Potato

Effects of mineral nutrient supply on growth and yield. The effects of variation in nitrogen and potassium supplies on growth and yield of the potato crop in 1963 were described in *Rothamsted Report* for 1963, p. 84.

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The nitrogen contents of stems, leaves and tubers have since been determined. Soon after tubers formed, their N content per cent of dry matter increased with increase in the amount of N supplied as fertiliser, and this relation was maintained until they were mature, implying that the nitrogen content of the material translocated to the tubers throughout their growth continued to be increased by increase in N supply. The smallest application of N fertiliser (0·5 cwt/acre N) increased leaf area, and hence the growth rate of tubers, relatively more than it increased N uptake, so that the tops became deficient in N and died sooner than the tops of plants without N fertiliser. To prolong the life of the tops and substantially increase leaf area in September required 2 cwt/acre of N. Increasing N had no effect on net assimilation rate before tuber formation, but decreased it during the 6 weeks afterwards, when increasing N retarded tuber growth but increased the growth of leaves and stems.

The most N given in 1963 was not enough to produce maximum tuber yield, so in 1964 N was increased by a half to 0, 0·75, 1·5 and 3·0 cwt/acre, given in all combinations with 0 or 1·5 cwt/acre P_2O_5, and 0 or 1·5 cwt/acre K_2O. A site where the soil was deficient in P and K was chosen to ensure that P and K fertilisers would affect yield. Plants were sampled at intervals of two weeks for growth measurement. Despite the drought, the maximum tuber yield reached 15 tons/acre. The tubers had exceptionally large dry-matter contents—more than 27% at the final harvest. Yield continued to increase over the whole range of N; the mean yields with increasing N were 9·8, 12·7, 14·4 and 15·2 tons/acre. The mean increases by P and K were 1·5 and 1 ton/acre respectively.

Maximal leaf area indices were small, increasing from 1 to 2·5 with increase in N supply. Phosphorus increased *L*, especially during the first 10 weeks, when potash had little effect. All fertiliser applications hastened senescence of lower main stem leaves; N increased the leaf area of lateral shoots, and the size of the 7th–19th main stem leaves; P increased the size of leaves 4–12 and K of leaves 5–19.

Tubers began to form on 11 June, independently of nutrient supply. Nitrogen and potash retarded tuber growth during the next 10 days, but phosphorus hastened it throughout. This difference may depend on nutrient supply affecting competition for carbohydrate between shoots and tubers, as phosphorus affected leaf growth mainly before tuber formation, whereas nitrogen and potash increased leaf growth while tubers were growing.

Between late June and the end of August the rate dry weight of tubers increased was nearly constant. It was slightly increased by N, but N also increased tuber yield by extending the growth period. Phosphorus increased tuber yield mainly by increasing growth rate soon after tuber formation, and potash wholly by lengthening the growth period. (Dyson)

Sugar beet

Relation between net assimilation rate and leaf area index. The dependence of *E* on *L* of sugar beet was investigated in 1954 (Watson, D. J. (1958) *Ann. Bot.* N.S., **22**, 37–54) by measuring the rate dry weight increased in a late-sown, closely spaced crop differentially thinned to produce different values of L. E decreased very slowly with increase of L within the range from 1–6, and seemed independent of L in the range from 1–3, implying that the leaves are so arranged that photosynthesis is only little affected by leaves shading one another as L increases.

Field experiments with sugar beet in 1960–63 suggested that the situation has changed: the crop is now sown earlier, maximal L is seldom greater than 3·5, and E decreases slightly with increase of L within this range. The present dependence of E on L was therefore investigated in 1964, by the same technique as in 1954, using crops sown on 2 or 27 April or 25 May, with 0 or 1·6 cwt/acre N applied at sowing. Four experiments were done in the period July–September. At the start of each experiment 0, $\frac{1}{4}$, $\frac{1}{2}$, or $\frac{3}{4}$ of the plants on different plots were removed, and the thinnings used to estimate the initial dry weight and leaf area index of the crop. After two weeks the remaining plants were harvested and their dry weights and leaf areas measured.

In the two experiments of 1964 done on similar dates to those in 1954 with the same variety Kleinwanzleben E, the leaf area index was only half that in 1954, but the dry weights of plants were similar in the two years. L decreased in August because of drought, whereas in August 1954 it increased from 4 to 5·5. The crop was therefore irrigated before the two later experiments and L increased slightly during September. During August and September dry weight increased as much as in 1954, in spite of the smaller L. The experiments confirmed that current crops have smaller L and larger E than those of ten years ago, which suggests that E depends more on L than in 1954, but the critical data relating E to L in 1964 are not yet analysed. (Goodman)

Effect of drought on growth of sugar beet. In his analysis of results from the Woburn Irrigation Experiment, Penman (1962, *J. agric. Sci.*, **58**, 343–379) assumed that crop growth ceases at a critical soil-water deficit. An experiment to measure how growth rate depends on soil-water deficit was done in the Dutch-light glasshouse equipped with automatically metered spray lines. Sugar-beet plants raised in soil blocks were transplanted to the glasshouse on 20 May, 3 weeks after sowing. All plots received 3 in. of water in the following 6 days. Thereafter half the plots were watered freely, and the other half received no water. Samples were taken weekly to measure growth.

Relative leaf growth rate (R_L) was significantly decreased by the increasing water deficit on the unirrigated plots after 2 weeks, and total dry weight after 5 weeks, but from late June onwards, when the soil-water deficit was 2 in., R_L of unwatered and watered plants became similar and remained so until the end of the experiment, when the deficit was 5 in. At the final harvest on 3 September the total dry weight of plants on unwatered plots was 70% of plants on watered plots. The difference was determined by drought slowing R_L during June, which continued to decrease leaf area later. Net assimilation rate was unaffected by drought. After late June the plants on the dry plots evidently obtained adequate water from deeper soil layers. The soil-water deficit was never large enough to stop growth. (Orchard)

Growth in Controlled Environments

Effects of variation in temperature at different stages of growth. The results of an experiment on the effects of deviations of temperature from the natural climatic trend on the growth and yield of sugar beet and barley (*Rothamsted Report* for 1963, p. 79) were analysed. Plants growing in the natural outdoor environment, except that they were not allowed to suffer water stress, were transferred for periods of 4 weeks to three growth rooms, where the photoperiod, atmospheric water vapour pressure and, in one room, temperatures during the daily light and dark periods were the same as the outdoor means; in the other two rooms the temperatures were 3° C above or below the outdoor means, respectively. The light intensity in the rooms was the maximum possible (3·6 cal/cm^2/h). After 4 weeks the plants were returned outdoors for the rest of the growth period, and fresh batches of plants were put in the rooms. The experiment with sugar beet included 5 successive 4-week periods, and with barley 4 periods, from sowing on 23 April.

Sugar beet grown continually outdoors had similar dry weights to those transferred to the growth room with the mean outdoor temperature, except at the end of the first period when they were similar to those of plants from the colder room. Plants from the growth rooms had darker green, smaller leaves with shorter petioles than those grown outdoors. Net assimilation rate outdoors was less than in the room with similar mean temperature, although in the first 8 weeks the outdoor plants had much more light. At the final harvest on 23 October the total dry weight of plants that had been in the room with intermediate temperature for any period was similar to that of plants always outdoors.

Comparison of plants in the three growth rooms showed that at the end of each 4-week period leaf area, leaf number and total dry weight per plant increased with increasing temperature, particularly in the first period. For the first three periods the increase in leaf area by temperatures 3° above the means were approximately 200, 100 and 35% respectively, and the decreases by temperatures 3° below the means were 60, 30 and 20%. In the 5th period, which ended 6 weeks before the final harvest, temperature had no effect. These effects of temperature deviations on leaf growth persisted for up to 10 weeks after the plants were returned outdoors. The effects on dry weight of differences in temperature during periods 2, 3 and 4, but not the larger effects produced in the 1st period, persisted until the final harvest. Plants from the warm room in periods 2, 3 or 4 had about 13% more total dry weight, and those from the cold room 6% less, than plants from the room with the mean outdoor temperature. The corresponding increase and decrease in dry weight of the storage root were 16% and 9% respectively.

Barley plants grown continually outdoors had dry weights and leaf areas similar to those of plants from the cold growth room at the end of periods 1 and 2, and from the intermediate room at the end of periods 3 and 4. But at the final harvest on 16 September plants grown continuously outdoors had slightly more ear dry weight and less shoot dry weight, fewer green ears and more ripe grain than plants that had been in any growth room in any period. Difference in light quality between the rooms and outdoors probably affected the rate ears developed, and hence the distribution of dry matter between ear and shoot. Transferring plants to any growth room for period 2, during which ears were initiated, or to the cold or intermediate rooms, but not the warm room, for period 3, during which the ears emerged, delayed ear emergence.

Dry weight and leaf area of barley plants removed from the growth rooms at the end of period 1 increased greatly with temperature during the period, but the differences had disappeared by the final harvest. Increasing temperature during period 2 also increased leaf area and dry weight at the end of the period, but it decreased them in periods 3 and 4, during and after ear emergence, presumably by hastening senescence of leaves, and increased ear dry weight by hastening ear emergence. At the final harvest plants that had been in the cold room for periods 2, 3 or 4 had about 14% more ear dry weight, and usually more total dry weight than those from the intermediate room. Plants that had been in the warm room during periods 3 or 4 had 12% less ear dry weight than those from the intermediate room. However, the fraction of ears still green at harvest decreased with increasing room temperature, so the yield of ripe grain was greatest from plants that had been in a warm room and least from those that had been in a cold one. (Thorne, Ford and Watson)

Effect of humidity and temperature on growth. Variation in atmospheric humidity at 20° C affected the dry weight and leaf area of several species considerably (*Rothamsted Report* for 1963, p. 79), so the effect of change of temperature may depend on whether or not the water-vapour pressure remains constant or is allowed to change. This was tested with kale and wheat by comparing growth at 15° C and 25° C, with constant water-vapour pressure (VP) or constant vapour-pressure deficit (VPD). The three growth rooms were arranged to maintain the following conditions: (1) day temperature 15° C, VP 11·6 mb, VPD 5·4 mb. (2) day temperature 25° C, VP 11·6 mb, VPD 20·1 mb.; (3) day temperature 25° C, VP 26·3 mb, VPD 5·4 mb.

All the rooms had 15° C and 68% RH at night and a 16-h day with fluorescent and tungsten light of 1,900 f.c. intensity (6·6 cal/cm^2/h visible radiation). Kale and wheat plants were grown in soil in pots, transferred to the growth rooms 4 weeks after sowing, and harvested 2 and 4 weeks later. The pots were watered frequently to keep the soil as moist as possible without drainage.

Water loss per unit leaf area was similar in rooms (1) and (3) with the same VPD, but was almost twice as great in the warm, dry room (2) as in the others. Increasing the humidity at 25° C increased the leaf area and dry weight of both species; at the second harvest the increase in leaf area was 42% for kale and 20% for wheat, and the increase in dry weight was 24% for both species. Consequently, increasing temperature from 15° to 25° C had no effect when the water-vapour pressure was unchanged, but increased leaf area of both species by about 28%, and dry weight slightly less, when the water-vapour pressure was increased to keep the vapour-pressure deficit constant. Net assimilation rate was independent of humidity at 25° C, and was greater at 15° than at 25° in the second interval only. (Thorne and Ford)

Effect of CO_2 concentration on growth. Increasing the CO_2 concentration of the air in glasshouses in winter is said to increase the growth of some horticultural crops, in spite of the low light intensity. To test this more critically than is possible in commercial glasshouses, the CO_2 concentration of the air in the growth rooms was varied by injecting pure CO_2 into the fresh-air supply; CO_2 concentrations of 300 ppm (normal air), 1,000 ppm and 3,300 ppm were maintained in different rooms. Other conditions were identical in all rooms, viz., 16 hours per day of fluorescent and tungsten light of 2,000 f.c. intensity (7·1 cal/cm^2/h visible radiation), 20° C and 72% RH in the light, and 15° C and 92% RH in the dark. Kale, sugar beet, barley and maize plants growing in pots of soil were transferred from the glasshouse to the growth rooms 5 weeks after sowing, and harvested 3 or 6 weeks later.

The dry weights of kale, sugar-beet and barley plants were increased nearly equally by increasing the atmospheric CO_2 concentration to 1,000 or 3,300 ppm, and all parts of the plant were affected; at the second harvest the increase in total dry weight was about 30%. Leaf area was increased only by 1,000 ppm; with 3,300 ppm it was similar to or less than with normal air. Net assimilation rate increased by about 35% and 65% of the rate in normal air with increase to 1,000 and 3,300 ppm respectively.

The maize plants were more variable than the others and showed few significant effects; their dry weights and leaf areas were apparently increased at the second harvest, but not at the first.

Thus, with light intensity and daily visible radiation much less than those outdoors in mid-summer, but greater than in a glasshouse in winter, enriching the atmospheric CO_2 content had large effects on dry weight and also affected the form of the plants. The work needs to be repeated with still less light. (Thorne, Orchard, Goodman and Ford)

Growth of spring wheat in artificial climates. Growth, development and yield of field crops presumably depend on the sequences of change in external conditions that constitute different climates. The nature and magnitude of this dependence cannot be determined by growing plants in natural environments, because different climates occur in widely separated places, and the smooth seasonal climatic change is confused by short-period weather fluctuations, but they can be studied by growing plants in artificial climates. An investigation of this sort was attempted with spring wheat, grown from sowing to maturity in controlled-environment rooms. The three rooms were arranged to provide three different environments: (*a*) long day (18 hours of fluorescent and tungsten light) with warm day temperature (20° C); (*b*) short day (14 hours) with warm day temperature; (*c*) long day with cold day temperature (15° C). All rooms had 5·6 cal/cm^2/h of visible radiation, 15° night temperature, and relative humidity of 72% in the light and 92% in the dark. Comparisons of (*a*) with (*b*) and of (*a*) with (*c*) provide measures of the effects of difference in daylength (photoperiod) and of difference in day temperature, respectively. Seeds of spring wheat were sown in pots of soil in the rooms, and were watered frequently to avoid water stress.

The growth of wheat includes three phases: (1) vegetative growth, from germination to initiation of ears; (2) from ear initiation to anthesis, when ears are developing; (3) from anthesis to maturity, when the grains are filling. At the time of ear initiation, and again at anthesis, plants were moved between rooms so that different groups of plants experienced all possible combinations of the 3 environments in the 3 growth periods, i.e., 27 different climatic sequences between sowing and harvest were compared.

The dry weight of grain at the final harvest depended on conditions in all three periods; it varied with treatment from 16 to 38 g/pot. Shorter days in period 1 increased grain yield by 6%, but in periods 2 and 3 decreased grain yield by 23% and 14% respectively. Colder day temperature increased grain yield, by 6, 21 and 15% respectively for periods 1, 2 and 3. Conditions during the last period affected the yields of main stems and tillers nearly equally, but in periods 1 and 2 temperature chiefly affected the tillers and daylength the main stems. There were interactions between conditions in different periods that have not yet been fully investigated.

Cold in the first period delayed ear initiation by 1 day, and short days delayed it by 9 days. Dry weight, leaf area and shoot number at the time of ear initiation were increased by short days, and unaffected by cold. Both short days and cold in period 2 lengthened the interval between ear initiation and anthesis by 20 days, and in period 1 they lengthened it by 4 days. Total dry weight, shoot dry weight and leaf area at anthesis were increased by short days or cold before and especially after initiation. The number of shoots was increased by cold before initiation and by short days before or after initiation. The dry weight of ears at anthesis was unaffected by conditions before initiation, but was increased by cold and short days afterwards. The number of spikelets per ear of main stems was increased by cold or short days before initiation, but was independent of conditions afterwards. The interval between anthesis and maturity was 10 days longer with the shorter daylength and 30 days longer at the colder temperature than with long, warm days. It also depended on conditions before anthesis; cold between ear initiation and anthesis shortened it by 15 days, and both cold and short days before ear initiation shortened it by 8 days.

These complex effects of climate on growth and development evidently greatly influenced the size and persistence of the photosynthetic system. Whether the differences in leaf area duration account for the differences in dry matter production and grain yield, or whether net assimilation rate and grain:leaf ratio also varied, remains to be investigated. (Thorne, Ford and Watson)

Laboratory and Glasshouse Studies

Effect of drought on leaf growth. Growth analysis of field crops shows that drought decreases yield mainly by decreasing leaf growth, and has only small effects on net assimilation rate. Field experiments are too slow and cumbersome for detailed studies of how water stress influences the processes involved in leaf growth, so a simple and rapid laboratory method was developed to measure effects of a wide range of factors on leaf growth in defined states of water stress.

Kale seedlings are grown in small pots of a standard compost in a controlled environment. When pots are watered daily to constant weight and leaf area is measured on alternate days, the relative leaf growth rate (R_L) is almost constant for about 4 weeks. When watering is interrupted on the 15th day the soil moisture content falls to the wilting point in 8–10 days. Daily weighings measure the rate of water loss and the magnitude of soil-water deficit during this period, so that R_L of the unwatered plants can be compared at any required deficit with the constant R_L of watered plants. The procedure attempts to ensure that the soil is well explored by the root system but is sufficient for unrestricted growth. Results so obtained in a single period of increasing drought are easier to interpret than those of prolonged experiments that include a succession of cycles of drying and rewetting the soil.

Drought affects leaf growth in these conditions in two ways: it slows leaf expansion, and causes older leaves to die prematurely. These effects are separated by calculating leaf expansion on the assumption that no leaf died or decreased in area, and the difference between this R_L and R_L calculated from the surviving leaf area measures senescence rate. The method gives no information on effects of drought on cell division because before the experiment starts cell division has stopped in all leaves that become measurable during the experiment. With the compost used, leaf expansion rate is linearly related to soil moisture content, so an analysis of covariance can be used to increase the precision of means of several replicates and to permit treatment comparisons at the same soil-water deficit.

Preliminary studies, mainly to test the method, showed that varying the age, and hence the size, of plants at the start of the drought period had little effect on the relation of leaf expansion rate to soil-water deficit. Increasing the atmospheric CO_2 concentration also had no effect, confirming that drought interferes with use, not production, of assimilate. Contrary to reports by other workers, CCC did not diminish the effect of drought on leaf growth. A phyto-kinin, N benzyl adenine, delayed senescence induced by drought, but did not increase leaf expansion rate. Increased nitrogen supply also delayed drought-induced senescence, but had no effect on leaf expansion. (Orchard)

Dependence of photosynthesis on growth and utilisation of photosynthate. The rate of photosynthesis in detached rooted leaves of dwarf French bean or runner bean increases with increase in the growth rate of the roots (5·4), presumably because when photosynthetic products are used slowly for root growth they accumulate in the laminae and inhibit photosynthesis. To test this, changes in composition of laminae of rooted bean leaves were measured when the roots of some were in culture solution at 12° and of others at 20° C, which accelerated root growth. The total sugar content of the laminae at first decreased faster with roots at 20° than at 12° C, but later it increased steadily, and with roots at 12°, but not at 20° C, eventually exceeded the initial value. It was increased when roots were transferred from 20° to 12° C, but was unchanged by transfer of roots from 12° to 20° C. After repeated transfers the sugar content of laminae increased above the initial value whether the final temperature was 12° or 20° C, but this was probably a symptom of senescence. The sugar content of the roots was not affected by growing them at different temperatures.

Starch content of the laminae changed more than sugar content. With roots at 12° C it increased more than five-fold, but with faster-growing roots at 20° C it decreased to about half the initial value. Transferring roots from 20° to 12° C increased starch in the laminae, and transfer from 12° to 20° C decreased it.

The changes with time in sugar and starch content were relatively small compared with those in other components. An unidentified fraction of lamina dry weight increased more when roots were growing at 20° C than at 12°, and transfers between temperatures had little effect on its accumulation, presumably because it is not a labile reserve but structural material. It may be a mixture of substances, probably including protein and cell-wall constituents, because palisade cells of excised leaves continued to increase in length after the laminae attained their maximal area. The results suggest that accumulation of sugar and starch in the leaf when root growth is slow inhibits photosynthesis, and that their loss when root growth rate is increased permits faster photosynthesis.

The protein content of the lamina of leaves with roots at 20° C approximately doubled in 5 weeks, but accounted for only a small fraction of the increase in dry matter. (Humphries)

Previous work (5·4, 5·6) established that the rate of photosynthesis or net assimilation rate of plants may depend on their capacity to use photosynthetic products in growth or to accumulate them in storage organs. Workers at Nottingham University concluded that this effect controls the rate potato plants photosynthesise when the tubers are growing, and similarly, growing cereal grains have been said to control photosynthesis after the ears emerge. To test these conclusions the relative sizes of sources and sinks for photosynthate must be varied experimentally, and the effects on photosynthesis measured. This is difficult with field crops, but was attempted with plants in pots.

Potato plants (var. Epicure) were grown from single-eyed sets in pots so arranged that tubers produced in a covered, dark space above the soil surface could easily be excised without disturbing the roots. From some plants all tubers were removed as soon as they appeared; other plants were allowed to form tubers normally. When tubers started to form and at intervals afterwards until the plants were mature, dry weight and leaf area were measured on sample plants. In each interval between samplings half of the plants to be sampled on the next occasion were grown under shades that transmitted 40% of daylight, and the other half in full day-light.

Removing tubers more than doubled the number produced per plant. It caused swellings on lateral branches of the stem and increased the dry matter in main stem and leaves. It greatly decreased net assimilation rate.

Shading also decreased *E*, but removing tubers equally affected *E* of shaded and unshaded plants.

In a second experiment seed pieces of Majestic were planted in pots with or without extra nitrogen fertiliser. Removing all tubers as they appeared again greatly decreased *E*. The nitrogen increased leaf area relatively more than it increased tuber number and weight, and perhaps because of this, slightly decreased *E* of intact plants. Removing tubers had less effect on *E* of plants given N. The results show unequivocally that removing the tubers, the main sinks for photosynthate, slows photosynthesis even though other tissues partially replace the tubers as sites where dry matter accumulates. (Nösberger and Humphries)

Florets at the base and tip of ears of Maris Badger barley growing in pots were removed to give 24 or 12 grains per ear. At the same time the ears of some plants were covered with opaque shades, other plants had their leaves, stems and peduncles shaded and others were left unshaded. Plants were harvested when treatments began, and 10, 17, 31 and 42 days later. Photosynthesis of attached flag-leaf laminae, measured with an infra-red gas analyser 2 weeks after the experiment began, was greater with 24 grains per ear than with 12 grains per ear and was unaffected by shading the ear.

The dry weight per grain from ears with 12 grains was only slightly greater than from ears with 24 grains, so ears with 24 grains yielded nearly twice as much as ears with 12 grains. However, little of the extra dry matter in the ears with more grains was derived from the extra photosynthesis shown by the measurements of CO_2 uptake; most came from increased translocation from the stem. At the 2nd and 3rd harvest the extra dry matter in ears of plants with 24 grains per ear almost equalled the extra dry matter in the stems of plants with 12 grains per ear. This was true even of plants with shaded stems, which presumably had less translocatable carbohydrate than unshaded plants. At the end of the experiment, when the plants were ripe, the weight of stems of plants with 24 or 12 grains per ear was the same, presumably because all labile carbohydrate was respired. For unknown reasons, shading the ears affected grain yield much less than in previous experiments.

In this experiment the main effect of changing the capacity of the ears to use photosynthate was to alter the distribution of photosynthate within the plant rather than to change its rate of production. (Nösberger and Thorne)

Betaines. Betaines are quaternary ammonium compounds that occur in many plant species. They are chemically related to choline, and to the synthetic growth regulator CCC. Glycine betaine, which occurs in sugar-beet plants and seed balls, is active as a growth regulator when assayed with bean-leaf discs, wheat coleoptile sections or cress hypocotyls. The presence of betaines in dwarf French bean leaves was established by chromatography (*Rothamsted Report* for 1963, p. 88). Colorimetric estimation of these betaines by eluting the red-brown spots given by iodine vapour on paper chromatograms gave larger values than by assay with discs cut from etiolated bean leaves, suggesting that they contained a mixture of substances, including some that have little effect on growth of bean-leaf discs. Further chromatographic separation showed that the aqueous extract contains four substances that travel at different rates, viz., glycine betaine, trigonelline (N-methyl nicotinic acid betaine), which runs more slowly than glycine betaine, and a faster-running spot that probably consists of choline and tryptophane. Choline chloride, trypophane and trigonelline, at concentrations of 10^{-4} to 3×10^{-3} M, all failed to affect growth of bean-leaf discs in light; these concentrations of glycine betaine slowed growth.

Growth-regulating properties of betaines from other plants were also tested. An indole derivative, probably hypaphorine (tryptophane betaine) extracted from seeds of *Erythrina* sp. (Coral tree), and a betaine extracted from leaves of *Stachys sylvatica* (hedge woundwort), possibly turicine (4-hydroxyproline betaine), both retarded growth of bean-leaf discs in light.

Glycine betaine applied to whole dwarf bean plants via the roots inhibited growth of internodes and primary leaves less than did CCC, but retarded elongation of wheat or barley coleoptile sections more. Glycine betaine may act directly on growth, whereas CCC may act by decreasing the effectiveness of endogenous growth regulators present in whole plants but not in the coleoptile sections. Previous work showed that CCC retarded growth of leaf discs only when they were supplied with gibberellic acid, or when the discs were illuminated and so produced endogenous gibberellin (*Rothamsted Report* for 1961, p. 93). Neither trigonelline nor nicotinic acid applied via the roots affected the growth of dwarf bean plants; nicotinic acid, but not trigonelline, retarded growth of bean-leaf discs in light. Possibly trigonelline is an inactive store of nicotinic acid in plants.

The function of betaines in plants is not known. Differences in cell number per leaf of dwarf bean plants grown at different temperatures were accompanied by comparable differences in betaine content. If, as has been suggested, betaines are waste nitrogenous products rendered innocuous by methylation they may be waste products of cell division. (Wheeler)

Sugar accumulation in virus-infected plants. The effects of virus infection on the sugar and fructosan contents of plants were studied by circular paper chromatography. Fructose and glucose in sugar-beet leaves were greatly increased, and sucrose slightly increased, by infection with beet yellows virus (BYV): sugar content was increased more by an avirulent than by a virulent strain. Yellow-net virus decreased the sugar concentration, whereas yellow-net mild yellows virus increased it. Sugar accumulated in magnesium-deficient plants, which also show symptoms resembling virus yellows.

Carrot motley dwarf virus increased fructose, glucose and sucrose concentrations in carrot leaves, but in petioles and roots sucrose increased while fructose and glucose decreased: more sugar accumulated in plants infected late than early. Applying menazon to the seed to control aphids increased the sucrose concentration of the roots.

Cereal yellow dwarf virus (CYDV) increased fructose, glucose, sucrose and four fructosans in leaves of oats, an avirulent strain more than a virulent one. Virulent strains of BYV and CYDV apparently decrease photosynthesis more than avirulent ones. (Goodman with M. A. Watson, Plant Pathology Department)

Weed Studies

Wild oats (*Avena fatua* and *Avena ludoviciana*)

Geographical variation within species. When 4 species of wild oats from different countries were grown in uniform conditions in pots at Rothamsted plants from seeds collected in lower latitudes flowered sooner than those from seeds of the same type from higher latitudes (*Rothamsted Report* for 1963, p. 90), and some selections differed from the others in dormancy and periodicity of germination. Seeds of *Avena fatua*, type fA, and *A. ludoviciana*, type 1A, collected from the plants grown here were sown in pots in 1964 to find whether the progeny of the original plants inherited the differences in flowering and germination behaviour and showed them under different weather conditions. The length of the interval between sowing and flowering, and the rate ears emerged, were as with the original seed, with two exceptions: *A. fatua* from Pakistan and *A. ludoviciana* from Iraq, that previously flowered very quickly, took 17 and 13 days longer in 1964. Of the other types, those originally grown in 1960 or 1961 flowered more quickly in 1964, and those originally grown in 1963 more slowly, probably because the date of sowing in 1964 was later than in 1960 and 1961 and earlier than in 1963. Tests on seed collected from the 1964 experiment showed differences in early germination similar to those of the original seeds. They are being continued to determine the proportion of dormant seeds. In the germination tests set up in 1961 on seeds from different countries many pans still had more than 10% ungerminated seeds after 3 years. Abundant germination in November showed that many of these seeds were still viable but dormant. (Thurston)

Effect of light on germination. In previous experiments a 16-hour photoperiod of dim light inhibited germination of imbibed seeds of *A. fatua* or *A. ludoviciana* held at 15° C, but nearly all *A. ludoviciana* seeds and half the *A. fatua* seeds germinated in an 8-hour photoperiod. (*Rothamsted Report* for 1963, p. 90.) In 1964 seeds of *A. fatua* and *A. ludoviciana* were kept moist at 12–13° C either in continuous dim light or in darkness. Unpricked seeds of *A. fatua* did not germinate, but pricked seeds germinated equally well in light and dark. The 1st and 2nd seeds of *A. ludoviciana* spikelets were separated; none germinated unpricked. All pricked first seeds germinated in 13 days in darkness, but only 55% in light. Germination continued slowly in light, but 21% of pricked first seeds were still dormant after 40 days. The pricked second seeds were slower starting to germinate than first seeds and were less sensitive to light; by the 40th day 98% germinated in darkness and 91% in light. When the unpricked seeds that remained ungerminated after 40 days were pricked, all 1st and 2nd seeds germinated within 13 days, whether in light or dark.

The reasons for the difference in sensitivity to light between species and between 1st and 2nd seeds of *A. ludoviciana*, and for the loss of sensitivity to light when *A. ludoviciana* is stored moist, are unknown. (Thurston)

Black Grass (*Alopecurus myosuroides*)

Germination of seeds of different ages. Seeds collected at Rothamsted in 1961, 1962 and 1964 and at Cambridge in 1964, and stored in tins in the laboratory, were sown in pans of sterilised soil on 9 September 1964. Germination started sooner in the old samples; in the first 2 weeks it was 48% and 34% for the 1961 and 1962 seeds, and only 5% for the 1964 seeds. However, in the 5th week germination greatly increased, and more 1964 seeds than of those from earlier years then germinated. When the main autumn germination period ended in mid-November Rothamsted 1961 had germinated 77%, Cambridge (ripe) 70%, Rothamsted 1962 and 1964 56% and Cambridge (unripe) 30%. Germination peaks occurred 2 weeks after the soil was disturbed in this as in other experiments with *Alopecurus*. (Thurston)

Effect of fertilisers and crop competition. *Alopecurus* plants were collected on 25 June 1964 from selected plots on section 5a (1st crop after fallow) and 5b (6th crop after fallow) of Broadbalk to find how their growth and seed production were affected by fertiliser treatment and competition with wheat. Plants were taken from plots 2 (farmyard manure), 3 (unmanured), 7 (minerals and sulphate of ammonia) and 9 (minerals and nitrate of soda). There were fewer *Alopecurus* plants on section 5a than 5b except on plot 7, but the plants on 5a were larger; the mean number of ears per plant was 5·5 and dry weight per plant 2·0 g compared with 4 ears and 1·1 g on 5b. This was presumably because of the increased nitrogen supply after fallow, and the decreased competition caused by some wheat plants being killed by wheat bulb fly.

Alopecurus plants from the farmyard manure plot were only slightly larger than those from the unmanured plot, probably because more competition from the wheat offset the increased nutrient supply; the mean number of ears per plant was 3·5 on both plots and the dry weight per plant 1·3 g on plot 2 and 0·8 on plot 3. The largest plants were on plot 7, with 6·5 ears per plant and 2·5 g dry weight. (Thurston)

Effect of herbicides on Broadbalk. For the first time all Broadbalk field except sections 5a (first year after fallow) and 4 (fallow) was sprayed with herbicide. This year "Banlene" (methoxychlorobenzoic acid and MCPA) was used. Because of this spraying and the very dry summer there were far fewer annual weeds than usual, especially in the stubble. The unsprayed plots of section 5a were heavily infected with *Vicia sativa* (common vetch); *Tripleurospermum maritimum* (scentless mayweed) was also abundant, especially where the wheat crop was thinned by wheat bulb fly. Perennials were little affected by the herbicide, and there were dense patches of *Cirsium arvense* (creeping thistle), *Tussilago farfara* (coltsfoot), *Convolvulus arvensis* (bindweed) and perennial grasses. *Equisetum arvense* (common horsetail) was more abundant than ever before, occurring in large, dense patches on all plots except 2, 7 and 8. Its absence from these plots suggests that competition with wheat prevents it spreading. Soil samples were again taken from five plots in sections 1a, 1b, 5a and 5b, to continue the study of changes in the weed-seed population of the soil since the introduction of herbicide spraying. (Thurston)

The Park Grass Plots. The common spotted orchis (*Dactylorchis fuchsii*), found on Park Grass for the first time in 1963, occurred again on plots 2L and 8L. A single plant of another orchid new to Park Grass, the twayblade (*Listera ovata*), was found in 1964 on plot 2L. Two other species recorded on the plots for the first time were groundsel (*Senecio vulgaris*) on plot 10L and rayless mayweed (*Matricaria matricarioides*) on plot 11^2L. Carnation sedge (*Carex flacca*), first found in 1963, was present in 1964 on both limed and unlimed parts of plots 2 and 3. Tufted vetch (*Vicia cracca*), which reappeared in 1963 on plot 19LH after being absent since the early years of the experiment, was again found in 1964, but did not appear to be increasing. (Witts)

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