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Rothamsted Report for 1963

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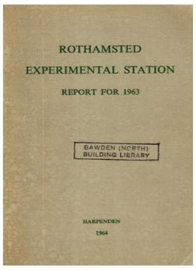

Botany Department

D. J. Watson

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BOTANY DEPARTMENT

D. J. WATSON

Visiting workers from overseas were Mr. J. C. S. Allison from the University College of Rhodesia and Nyasaland, Mr. Ken-ichi Hayashi, of the National Institute of Agricultural Sciences, Japan, Dr. G. L. Wilson, of the Department of Botany, University of Queensland, and Dr. P. Odgaard, of the Statens Unkrudtforsøg, Denmark. E. C. Humphries and A. W. Wheeler were invited by the Centre National de la Récherche Scientifique to contribute to the Fifth International Conference on Natural Plant Growth Regulators at the Phytotron, Gif-sur-Yvette, in July.

Physiology of Crop Growth and Yield

Studies in controlled environments. The three controlled-environment rooms in the West Building were used for experiments on plant growth during 47 weeks of the year.

Effect of temperature on leaf growth. In the first test of the newly completed growth rooms, kale, spring beans and spring wheat plants were grown in day temperatures of 25°, 20° or 15° C and a constant night temperature of 15° C and illuminated for 16 hours per day with fluorescent and tungsten light of 1,400 or 1,200 f.c. intensity (4·2 or 3·2 cal/cm^2/h visible radiation). Leaf area was measured by rating 2, 3, 4 and 5 weeks after sowing, and after 6 weeks the plants were harvested.

Numbers of leaves or shoots, final dry weight, leaf area, but not relative leaf growth rate (R_L), of kale and wheat were greater with the larger light intensity, but beans were unaffected.

Leaf area of kale throughout the growth period and final dry weight were slightly greater at 25° C than at 20° C and least at 15° C. Leaf area and dry weight of beans also were least at 15° C. The number of living leaves of both crops was also greatest at 25° C and least at 15° C. Leaf area and shoot number of wheat were greatest at 20° C; they were greater at 25° C than at 15° C for 3 weeks after sowing and smaller for the next 3 weeks. Final dry weight was greatest at 20°C and greater at 15°C than at 25° C.

Although leaf area per plant tended to increase with increasing temperature, R_L of kale and wheat between 3 and 6 weeks after sowing was greatest at 15° C and least at 25° C; R_L of beans was apparently unaffected by temperature. These results imply that the larger leaf areas produced by increasing temperature resulted from more rapid expansion of leaf initials in the first 2 or 3 weeks after sowing before the areas were large enough to measure by rating. (Thorne and Ford)

Effects of humidity on growth. It is commonly assumed that atmospheric humidity has little effect on plant growth. An experiment was done to test

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this and to determine suitable humidities for studies on the effects of other environmental factors. Kale, sugar beet and spring wheat were grown in pots of soil and sampled 4, 6 and 8 weeks after sowing. Day temperature was 20° C and night temperature 15° C. The plants were illuminated at 1,700 f.c. for 16 hours per day and watered generously. The relative humidity in the wet room was 92% during the day and about 98% at night, in the intermediate room it was 64% and 86% and in the dry room 44% and 43%. Water consumption per pot in the dry room was 20% more than in the wet one for sugar beet, 70% more for kale and 80% more for wheat. Water loss per unit leaf area in the dry room was more than twice that in the wet one.

Total dry weight of wheat was unaffected by atmospheric humidity. Leaf area was smaller and net assimilation rate (E) was greater in the dry room than in the others. Initially, there were most shoots in the wet room, but later most in the dry one. At the last sampling, ears had emerged in only the intermediate room. This anomalous result needs confirmation to ensure that some difference between rooms other than humidity was not the cause. Leaf area of kale and sugar beet increased with increasing humidity. The number of living leaves was unaffected; rates of production and death were increased slightly by higher humidities. Dry weight of kale increased with increasing humidity and of sugar beet it was greater in the wet than in the intermediate and dry rooms. E of both species was greater in the dry room than in the others. Thus all species showed some response to humidity, though they differed in sensitivity. The dry weight and leaf area of kale was increased by about 30% by each step in increasing humidity, and there were similar increases between dry and intermediate rooms in leaf area of wheat and between intermediate and wet rooms in dry weight of sugar beet. (Thorne, Orchard and Ford)

Effects of variation in temperature at different stages of growth. One way of studying effects of weather on crop growth is to transfer plants for short intervals, at various times during the growth period, from the natural variable outdoor environment to constant-environment rooms providing different intensities of an environmental factor. After treatment some plants can be sampled to show the immediate effects and others returned to the natural environment, where their subsequent growth can be measured to study the persistence of the treatment effects. The effect of variation in temperature deviations from the seasonal trend on growth of sugar beet and barley was investigated in this way.

The growth period was divided into 4-week intervals, for each of which the growth rooms provided three temperature régimes with day and night temperatures similar to, and 3° C above or below, the long-term mean outdoors. All three rooms had the same daylength and atmospheric water-vapour pressure as the outdoor means and the maximum possible light intensity. Plants were grown in pots, kept in the open air under a transparent roof of polythene sheet to avoid leaching by rain and frequently watered to avoid moisture stress. At the beginning of each interval some were put into each growth room, and at the end of the interval plants from outdoors and half of those from each room were harvested. The

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remainder were returned outdoors, their leaf areas were measured regularly for the rest of the growth period and they were harvested when mature.

The constant environments differed from each other only in day and night temperature, but all three differed from the natural outdoor environment in other ways, especially in light quality and intensity, and this complicates the interpretation of the results. At some samplings plants from the growth rooms looked different from those outdoors, e.g., sugar beet in the growth rooms tended to have darker green leaves with shorter petioles than outdoors, but usually the dry weights and leaf areas of the plants from outdoors fell within the range of those from the three controlled-environment rooms.

The results of this experiment, which involved nearly 600 pots, are not yet fully analysed. (Thorne, Ford and Watson)

Photosynthetic and respiratory components of net assimilation rate. The net assimilation rate (E) of a plant—the mean rate of increase in dry weight per unit leaf area, usually measured over a period of one or two weeks—represents the excess of the rate of photosynthesis of the leaves (P) over the rate of respiration of the whole plant (R), both expressed per unit leaf area, i.e., $E = P - R$. Differences in E are usually assumed to reflect changes in P, but changes in R could also contribute, so a method is required for determining these two components of E.

The photosynthetic component P is made up of photosynthesis during the light periods of each day in the interval over which E is measured, and the daily contribution (p) can be estimated by keeping plants in the dark on one or more days to prevent photosynthesis and determining the change in E. If E is the mean net assimilation rate of plants illuminated every day during a period of N days, and E' that of plants illuminated on only n days and shaded on the others, $E = Np - R$ and $E' = np - R$. From these equations p and hence $P(= Np)$ and $R(= E–P)$ can be estimated provided that R is unaffected by shading and that mean p is the same for plants illuminated every day or on only some days. To achieve uniform p, plants were grown in a controlled environment, so that external conditions were identical on every day, and shading was done on days distributed systematically throughout the experimental period to avoid effects of change with age in photosynthetic rate. With these precautions, a close linear relation was found between E' and n, when n was varied within the range from 0 to 7 in a 14- or 15-day period. This implies that the contribution of one day's photosynthesis to E, measured by the regression coefficient of E' on n, and the value of R, were both unaffected by shading on some days.

The method was used to compare the photosynthetic and respiratory components of E of sugar beet and barley; previous work has consistently shown that E of sugar beet is much greater than that of barley. Five experiments were done on plants, initially with 4–6 leaves, held in different controlled environments. There were no significant differences between species in R, and the mean values of R were identical, so the difference in E between sugar beet and barley was wholly attributable to a difference in the

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rate of photosynthesis. The means for all experiments in g/m²/week were:

	E		*P*		*R*	
Sugar beet	71	±0·8	81	±2·9	10	±2·6
Barley	43		53		10	

The estimate of *R* obtained in this way represents the respiration rate of the whole plant including that of the leaves in the light period and the roots, and *P* therefore measures the rate of true photosynthesis. (Hayashi and Watson)

Growth studies on cereals

Interaction of row spacing, seed rate and nitrogen on the growth and yield of spring wheat. Previous work (*Rothamsted Report* for 1962, pp. 85–86) suggested that grain yield of cereal crops may be increased by producing more ear-bearing shoots per unit area of land, perhaps by closer spacing of the drill rows, provided that a compensating decrease in leaf area per shoot by increased competition between shoots for nutrients can be avoided.

An experiment was done with Jufy I spring wheat to test these possibilities by measuring the effects of varied row spacing, and its interactions with seed rate and nitrogen supply, on attributes of growth that control grain yield. The crop was drilled in rows at the normal 7 in. spacing or at 3·5 in. at two seed rates, 174 and 348 lb/acre (i.e., the normal rate of 2¾ bushels/acre and twice the normal rate). Seed was also sown broadcast at the same rates, but germination was late and plant establishment poor, so the results obtained probably reflect difference in plant population rather than in spatial distribution. Three rates of nitrogen supply—0·3, 0·6 and 1·2 cwt N/acre as "Nitro-Chalk" applied at sowing—were compared in all combinations with the spacings and seed rates. Samples of the crops were taken at intervals of two weeks from shortly before ear emergence (10 June) until the grain was ripe (20 September), and the dry weights and leaf areas, including leaf sheaths and green parts of peduncles, were estimated on each occasion. Some lodging and severe mildew attack occurred on plots with large seed rate and much nitrogen.

On the average of all seed rate and nitrogen treatments, closer spacing did not significantly increase grain yield compared with normal spacing. The largest increase was from 30·9 to 33·1 ± 0·7 cwt/acre with the larger seed rate and 0·6 cwt N/acre; with other treatments the increase from closer row spacing did not exceed 1 cwt/acre. The mean difference between seed rates was not significant where the wheat was drilled in rows, but on broadcast plots the larger seed rate increased yield, presumably by counteracting the poor seedling establishment. Grain yield was increased by increasing nitrogen application from 0·3 to 0·6 cwt/acre, but 1·2 cwt N/acre gave less grain than 0·3 cwt, possibly because of mildew.

The greater yield from closer row spacing, as well as the effects of nitrogen, were mainly attributable to differences in number of ears per unit area of land. Ear number was also increased by increasing seed rate, but on the drilled plots this was offset by decreases in grain size (1,000 grain weight) and number of grains per ear, so that yield was not increased. On broadcast plots the larger seed rate decreased only grains per ear. The number of grains per ear was increased by nitrogen at the larger seed rate, but not at

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the smaller one, suggesting that it may have been restricted by competition between shoots for nitrogen before ear emergence on the densely sown plots. The usually smaller grain weight per ear associated with the greater number of ears per unit area of land on plots drilled at the larger seed rates suggests that there was also competition between shoots after ear emergence. The effects on leaf-area index and duration associated with these differences in grain yield have not yet been fully examined. (Welbank, French, Hayashi and Witts)

Photosynthesis of ears of cereals. The rates of apparent photosynthesis of ears of wheat, measured in 1962, were much less than of barley, measured in 1961 (*Rothamsted Report* for 1962, p. 90). To see whether this is a real difference between species and not merely between experiments, photosynthesis of intact ears and shoots (i.e., flag-leaf lamina and sheath, and peduncle) of Proctor and Plumage Archer barley and of Jufy I and Atle spring wheat was measured with an infra-red CO_2 analyser. Ears and shoots were selected at random *in situ* on small plots near the laboratory. As before, wheat ears absorbed small amounts of CO_2 compared with the shoots, but barley ears and shoots absorbed similar amounts. For the first 3 weeks after ear emergence ears of wheat absorbed less than 0·5 mg/h, wheat shoots about 3 mg/h and both ears and shoots of barley about 1 mg/h. Later, ears of wheat evolved CO_2 in daylight, i.e., their apparent photosynthesis was negative, and the other rates of uptake decreased to zero as the shoots ripened.

This experiment confirms that differences in ear photosynthesis cannot account for differences in grain yield between the wheat varieties, although they can for the barley varieties, and other explanations of the difference in grain yield between Jufy I and Atle must be sought. (Thorne)

Dependence of grain : leaf ratio on radiation. The grain yield of cereal crops in experiments at Rothamsted in different seasons was found to be correlated with leaf-area duration (integrated leaf-area index) after ear emergence, but the grain : leaf ratio (G; ratio of grain dry weight to leaf-area duration after ear emergence) differed between years. G is a measure of the photosynthetic efficiency of leaves, analogous to net assimilation rate, that is applicable to the period when the grains are growing. Values calculated for seven wheat or barley experiments between 1955 and 1961 showed that G increased with increase in mean daily radiation during the period between ear emergence and harvest. Thus differences in cereal grain yield between years were determined by differences in both the size of the photosynthetic system and in its efficiency, which depended on the energy income. (Thorne)

To test experimentally whether G is affected by mean daily radiation, shades of different densities made of "Tygan" or white cotton cloth were placed over small plots in a field of Jufy I spring wheat at the time of 50% ear emergence on 11 July, and other plots were left unshaded. The green area of shoots was estimated periodically between ear emergence and final harvest, when the grain was ripe on 25 September.

The mean yields of dry grain in light intensities of 100, 80, 50 and 40%

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of full daylight were 25·1, 24·0, 14·4 and 13·7 ± 0·58 cwt/acre respectively. As might be expected, the shading had no effect on straw yield or ear number, and the decrease in grain yield was caused by decreases in number of grains per ear and weight per grain. There was an increase in 1,000-grain weight between 50 and 40% daylight, accompanied by a disproportionately large decrease in grains per ear. It was associated with a difference between open-mesh "Tygan" screen and close-woven cotton cloth, but the significance of this is not clear.

Leaf-area duration after ear emergence was not affected by shading, so *G* decreased with decrease in mean daily radiation, but the regression coefficient of *G* on radiation per day was only about a third of that found by Thorne. Unfortunately, the mean daily radiation without shade was less than in any of Thorne's experiments, partly because of cloudy sunless weather and because late sowing delayed ear emergence, and ripening continued into the short days of September. (Welbank, Witts and Hayashi)

Effect of water supply on growth and yield of wheat. An experiment was done in a Dutch-light glasshouse, equipped with automatically metered overhead spray lines, to measure effects of soil moisture stress and irrigation at different times on the growth and yield of Jufy I spring wheat and Proctor barley. Although fertilisers were not given, barley was badly lodged, and wheat was slightly lodged but was supported by strings. Only the results for wheat will therefore be discussed.

The experiment consisted of a 6 × 6 Latin square sown on 19 April. In the 7 days between sowing and germination all plots received 1·8 in. of water, sufficient to bring the moisture deficit to zero. The following six treatments were applied to whole plots in the interval between germination and 50% ear emergence on 22 June: A held near field capacity by frequent irrigation, B water at twice A, C water at half A, D no water, E no water for 48 days, then as A for 17 days, F as A for 48 days, then no water for 17 days. At the time of the change-over in treatments E and F the main shoots of wheat had 6 or 7 leaves.

The total amounts of water supplied in inches, were: A, 3·4; B, 6·8; C, 1·6; D, 0; E, 3·0; F, 2·0.

After ear emergence these treatments were stopped, and water was then withheld from half the plots. Enough water was given to the other half to continue the wet régime previously maintained on the A and E plots. The soil of plots previously receiving treatments C, D and F was therefore drier than this.

No difference between treatments was detectable 18 days after germination (4-leaf stage), but 14 days later (5-leaf stage), shoot height, leaf area, water content and total dry weight of wheat on the plots with restricted water supply (C, D and E) was less than on the A plots, and these effects persisted until harvest. The extra water on the B plots slightly increased leaf area and dry weight. Net assimilation rate was slightly but not significantly decreased by restricted water supply.

When the E plots were watered after the initial drought the plants resumed growth in dry weight at the same rate as those of treatment A, and did not overtake them, so that the effects of the drought period persisted

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in the final yield. Treatment F had no effect on growth except a slight hastening of leaf senescence and a decrease in moisture content.

Continued irrigation after ear emergence delayed senescence of the leaves. All plots were harvested on 26 July because of the risk of damage by birds, and at this time the plots without water since ear emergence had more grain than the watered ones, but the watered plots were still green and might have yielded more had harvesting been delayed until they were ripe.

Treatment D decreased grain yield by 30% of that of the fully watered A plots. Treatment B gave a 10% increase, C a 15% decrease and E a 10% decrease. The late drought of treatment F did not affect yield.

The results confirm that loss of dry matter from water shortage is caused mainly by decreased leaf area and much less by decrease in net assimilation rate. There was no evidence of a greatly increased growth rate on watering wheat after drought, such as occurred with sugar beet (*Rothamsted Report* for 1962, p. 88). (Orchard)

Effects of mineral nutrient supply on growth and yield of potato. Effects of nitrogen and potassium and their interaction on the growth and yield of the potato crop were studied by growth analysis in a field experiment comparing all combinations of 0, 50, 100 and 200 lb N/acre as "Nitro-Chalk" (N_0, N_1, N_2, N_3) with 0, 150 and 300 lb K_2O/acre as potassium sulphate (K_0, K_1, K_2). All plots received 100 lb P_2O_5/acre as superphosphate. Unfavourable weather and soil conditions delayed planting of chitted seed tubers of King Edward until 5 May and hindered subsequent cultivations for weed control. The crop was sprayed repeatedly to control blight, and in August to control aphids. Samples were taken by hand digging on eight occasions at 2-week intervals from 12 June, 14 days after 90% emergence of shoots, and more frequently during the period of tuber initiation in June, until 2 October when the haulms were dead.

The results are still being analysed, and few conclusions can yet be drawn, but nitrogen increased leaf area very early and maintained a larger leaf area, despite faster senescence, by producing more leaves. This increase in area persisted to the end of the season; plants receiving the most N were the last to die completely. Potash also increased leaf area, particularly when combined with the larger N dressings. The growth of tubers was at first retarded by increasing N supply, but later it was hastened. Because of their slower initial growth rate, N_3 plants had a smaller tuber yield than N_2 plants until 4 September, but eventually gave 1·7 tons/acre more than N_2. The final mean yields of tubers for treatments N_0, N_1, N_2 and N_3 were 7·7, 9·8, 11·8 and 13·5 tons/acre respectively, and for K_0, K_1 and K_2 they were 9·7, 10·5 and 11·5 tons/acre.

The date when tuber formation started was independent of nutrient supply, but the initial rate of tuber growth was decreased by N and increased by K. Tuber number was increased by N_1 and N_2, partly because more stolons were formed, but N_3 decreased it. These effects were reflected in the size of tubers at the final harvest; N_1 increased yield by increasing the number of small tubers, N_2 by increasing the number of all tuber sizes and N_3 by increasing the number of large tubers and decreasing the number of small ones.

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Optimal rates of application for the potato crop are usually about 100 lb N and 150 lb K_2O/acre, but in this experiment increases continued beyond these rates. A possible explanation is that the common practice of burning off the haulms in mid-September restricts the effects of large doses of N and K, particularly with the late-maturing Majestic. (Dyson)

Growth of the sugar-beet crop

Interaction of spacing and variety. The study of growth on different soils (*Rothamsted Report* for 1962, p. 86) showed that large yield of the sugar-beet crop is a consequence of large leaf area index (L), partly offset by decrease in photosynthetic efficiency, yet the largest values of L (between 3 and 4) in these experiments were much less than the maximum (over 5) found at Rothamsted for crops sown in May, which in turn was apparently below the optimum for dry matter production (Watson, D. J. (1958), *Ann. Bot., Lond.* N.S., **22**, 37–54). The early sowing now practised has increased yield by bringing maximal L nearer to mid-summer when climatic conditions most favour photosynthesis and give maximal net assimilation rate, but decreases maximal L. If L in July could be increased by closer spacing of plants, yields might be still further increased. Closer spacing might also produce smaller, more uniform beet, more suitable for mechanical harvesting. The increased payment in 1963 for sugar contents above 16%, and larger penalties for those below, have revived interest in the Z strains of sugar beet, bred for large sugar content. They usually have smaller roots and tops than E strains, and may therefore be more suitable for closer spacing.

Three experiments were done in 1963 to compare Sharpe's Klein E and Klein Z, grown at different spacing and nitrogen supply. At Rothamsted, plants were sown in rows spaced at 15, 12 or 10 in. and singled to approximately square spacings, giving populations of 34, 51 and 68 thousands/acre, and nitrogen was supplied at 0·8, 1·4 and 2·0 cwt/acre. At Broom's Barn the plants were in rows 20 in. apart and singled to 10 in., or in rows 10 in. apart and singled to 12 or 8 in., giving populations of 32, 54 and 79 thousands/acre; they received 1·0 or 1·6 cwt N/acre. At Ely, on black fen soil, plants sown with a uniform row spacing of 19 in. were singled to 12, 9 or 6 in. apart in the rows to give 33, 40 or 44 thousands/acre, and received 0·4, 0·8 or 1·2 cwt N/acre. Basal dressings of potash, phosphate and salt (except at Ely) were given to all plots. Total dry weight and leaf area were measured at intervals throughout the growth period, and samples were taken for sugar analyses, not yet completed. Effects of the treatments on root shape were also assessed.

Total dry weight was not consistently different between varieties throughout the growth period. Differences in plant population had little effect on dry matter yield at Ely. At Broom's Barn and Rothamsted until September, but not later, yield was greater with the larger populations. Nitrogenous fertiliser increased dry matter yield at Broom's Barn, but not significantly at Rothamsted or Ely. The dry matter yields showed interactions between varieties with spacing and nitrogen. Final yield of Klein E was greatest at the medium spacing (about 50 thousands/acre), both at Broom's Barn and Rothamsted, but yield of Klein Z was not significantly

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affected by spacing. At Ely Klein E produced most dry matter at the middle nitrogen rate, but Klein Z was not affected by nitrogen.

There was no consistent difference in leaf area index between varieties at any site. *L* increased with increase in plant population at Rothamsted, but smaller increases at Broom's Barn and Ely were not significant. Nitrogenous fertiliser increased *L* at Rothamsted and Broom's Barn, especially after September, but not at Ely. No interaction was found between spacing, varieties and nitrogen treatments in their effects on *L*.

These experiments indicate that only small increases in *L* and dry matter yield of E strains can be expected from spacings closer than in current practice and increasing N supply; the effects on Z strains were still smaller, but whether there were beneficial effects on sugar yield is not yet known. (Goodman)

Dependence of photosynthesis on growth. CCC (2-chloroethyltrimethylammonium chloride) applied to mustard plants increased their leaf area, but greatly decreased stem growth and total dry weight (5.4). The suggested explanation was that the net assimilation rate (*E*) was decreased because inhibition of stem growth decreased the demand for photosynthate. If this is correct, other treatments that decrease stem extension should have a similar effect on *E*. This was tested by growing mustard plants in controlled environments with 8 or 16 hours photoperiod, but with the same total radiation per day. Although plants grown in the long days had stems longer (20%) and heavier (35%) than those of short-day plants, there was no difference in *E*. However, the effects of photoperiod on stem growth were much less than those of CCC in the previous experiments.

The rate of photosynthesis of rooted detached leaves of dwarf French bean increases with increase in size of the root system (*Rothamsted Report* for 1962, p. 89). Similar results were found with rooted leaves of runner bean, when the growth rate of the root systems was varied by differences in nitrogen supply or in temperature of the culture solution, but the effect of root temperature on *E* was less for runner bean than dwarf bean. Runner-bean leaves produced larger root systems than dwarf beans at all temperatures and had correspondingly larger *E*, in accordance with the hypothesis that in these systems with very restricted capacity for growth the rate of photosynthesis depends on the size of the only sink for photosynthetic products, i.e., the root system. (Humphries)

Estimation of leaf area by rating. A rapid and convenient method of estimating the total leaf area of plants is by rating individual leaves on a scale determined by a graded series of standard leaf patterns. The accuracy of this method was investigated (5.6). Hitherto, facsimiles of leaves of the species being studied have been used, but standard areas of circular, elliptical or square shape have now been tested. They can be used with nearly the same accuracy as leaf shapes, but for reasons not yet known, ellipses gave larger errors than circles or squares when used to rate potato or sugar-beet leaves. Usually, a set of standards forming a geometric series that increases in the ratio of $\sqrt[3]{2}$ at each successive step has been used,

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but this appears to have no advantage over an arithmetic series with equal intervals of 20 cm^2. (Humphries and French)

Growth Regulators

Relation of growth of bean leaves to gibberellin and IAA. The cells in primary leaves of dwarf French bean were counted at intervals from germination until the leaves were fully expanded, by disintegrating the tissues after incubation with pectinase and EDTA (Humphries, E. C. & Wheeler, A. W. (1960) *J. exp. Bot.* **11**, 81–85). The areas of the leaves were also measured. Similar leaves were immersed in boiling water to ensure that IAA (3-indolylacetic acid) was not liberated from a bound form or inactivated; they were then extracted with ethyl acetate, and the extracts assayed for IAA and gibberellin. Comparison of the changes in leaf area and in cell number showed three phases in leaf expansion. In the first, area increased faster than cell number, because leaf growth was mainly from absorption of water by cells already existing in the embryonic leaf. In the second phase area increased proportionately to cell number, i.e., growth was mainly by cell division. In the third phase area increased faster than cell number, because growth was again predominantly by cell enlargement. Free IAA was detected only in the second phase, between the 3rd and 7th days at 25° C, when cells were dividing most rapidly. Gibberellins were present in maximum amount in the third phase, after 7 days, shortly after cell enlargement began. Subsequent increase in cell size, estimated indirectly as the reciprocal of cell number per unit leaf area, was correlated with decrease in gibberellin concentration. The results suggest that the reason why cell division in leaves stops is disappearance of IAA. (Humphries and Wheeler)

During expansion of primary leaves of dwarf French bean the content of free extractable gibberellin increases to a maximum corresponding with their maximum growth rate, possibly by liberation from a protein-bound form. To test this, leaves were macerated and incubated at 37° C for 24 hours with or without ficin, a protease that increases five-fold the gibberellin extractable from mature bean seeds (McComb, A. J. (1961), *Nature, Lond.*, **192**, 575–576). Incubation with ficin did not release any more extractable gibberellin, indicating that protein-bound gibberellin was absent from the leaves. However, the auxin content of the extracts was increased three-fold by incubation alone, and eleven-fold with ficin, but the sample of ficin itself contained auxin. (Wheeler)

Primary leaves of dwarf French bean grew faster initially when sprayed with dilute aqueous gibberellic acid (GA), but their ultimate size was unaffected (Humphries, E. C. (1958), *Nature, Lond.*, **181**, 1081). In these experiments some of the GA spray undoubtedly fell on the stem. When GA was applied only to the young primary leaves with a micrometer syringe, the increased growth rate of the leaves continued longer, and the mature leaves were larger and heavier than untreated leaves. GA applied only to the epicotyl increased the initial growth rate of leaves, but not their final size; it also increased stem extension twice as much as GA applied to the leaves. This preferential growth of treated leaves

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or stems indicates that little GA moves between them. (Wheeler and Humphries)

Effect of soaking bean seeds. Prolonged soaking of dwarf French bean seeds in water before sowing decreases germination and growth of the seedlings (*Rothamsted Report* for 1960, p. 100). Water in which beans were soaked at 25° C for 1–24 hours was shown by chromatographic separation to contain a gibberellin that promotes growth of bean leaf discs, but no auxin when assayed with wheat coleoptile sections. The water also contained a substance identified as a betaine by its *Rf*, colour reaction with iodine vapour, and inhibition of growth of bean leaf discs in light. After longer soaking the seedlings were smaller and the cotyledons contained less gibberellin, but the water contained more. Longer soaking also decreased the auxin content of the cotyledons, and increased the betaine content of the water. Auxin activity was found in the water when the soaking was done at 5° C instead of 25° C, suggesting that it was extracted but inactivated at the higher temperature. When soaked seeds were treated with solutions of GA or betaine for half an hour before sowing, germination was little affected, but GA increased stem elongation, and betaine slightly increased growth of the primary leaves. The results support the hypothesis that soaking affects the behaviour of the seeds by eluting growth substances. (Wheeler)

Betaine in bean leaves. The presence of betaine in dwarf French bean leaves has been established by chromatography, and the amounts present estimated on chromatograms of aqueous extracts by the colour produced with iodine vapour and by assay with leaf discs (5.11). The betaine content per leaf increased fifty-fold during leaf expansion, but the amount per g fresh or dry weight decreased with age. Colorimetry gave larger values than bio-assay, suggesting that the substances giving similar colour reaction have less effect on leaf expansion than betaine. By chromatography with wetter solvents, the aqueous fraction was separated into three parts; one had the same *Rf* as betaine, one ran a little faster and the third a little slower than betaine. All three promoted leaf expansion. The sensitivity to betaine of discs cut from primary leaves of dwarf French bean grown in light changes with age of the leaf. Betaine had most effect on discs from leaves 5–6 days old; it had less on discs from young leaves, because they contain more betaine, and from older leaves, because the tissues were nearly mature and had little capacity for further expansion. (Wheeler)

Effect of CCC on nitrogen and protein content of leaves. Application of CCC to the soil in which sunflower plants were grown increased the dry matter, total nitrogen and protein content of leaves (*Rothamsted Report* for 1962, p. 91). Further experiments on sunflower confirmed this, and showed that the effect of CCC occurred whether the nitrogen supply from the soil was large or small. When N supply is deficient the increase of leaf N content by CCC can be partly ascribed to the N contained in the CCC. However, CCC also increased the N content of leaves when 126 mg N were given per pot compared with 16 mg N supplied by the CCC, and

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when increase of N supply without CCC had no effect on N content of the leaves. Experiments in which the soluble protein in the leaves was estimated by precipitation with trichloracetic acid or 80% ethanol showed that CCC increased the protein content concomitantly with the increase in total N content. CCC increased leaf size, so it also increased nitrogen and protein per leaf as well as per unit dry matter or leaf area. (Humphries)

Effects of gibberellic acid and CCC on growth of potato. Treating potato tubers with gibberellic acid (GA) hastens sprouting, but produces spindly plants with small leaves. Treatment with CCC produces compact plants with short internodes. It may therefore be possible to secure early emergence with GA and prevent undesirable effects of GA by subsequent CCC treatment. A pot experiment was done to study the action of these growth substances applied separately or in combination. Shoots of GA-treated tubers (immersed in 50 ppm solution for 1 hour) emerged above the soil 10 days before those of untreated controls. A single application of 50 ml of 5×10^{-3} M or 2×10^{-2} M CCC solution per pot was given to the soil at the time when the controls emerged.

GA accelerated stem growth and depressed leaf growth at first, but later increased the size of leaves. It also produced longer, thinner stolons and delayed tuber formation. The larger dose of CCC decreased leaf area and stem length; the stolons were shorter and thicker, and tubers formed earlier and increased in dry matter more rapidly than on untreated plants. The leaves of CCC-treated plants were darker green, contained more nitrogen and survived longer. Tubers were fewer because lateral stolon branches were suppressed, but they were more uniform in size.

The undesirable effects of GA were not prevented by CCC, possibly because it was applied too late. The effect of CCC lasted only 30 days; in future work an attempt will be made to prolong it by repeated applications. (Dyson and Humphries)

Weed Studies

Broadbalk weeds. Broadbalk was under snow until the beginning of March, and this retarded growth of weeds as well as of the wheat crop. Seedlings of *Ranunculus arvensis* (corn buttercup) and *Alopecurus myosuroides* (black grass), which normally germinate in autumn and winter, were scarce in April but increased in numbers later. In June the plants were small and about 3 weeks later than usual in development. No weed species was eliminated by the severe winter.

Wheat-bulb fly killed many plants on Section 2 after fallow, and *Tripleurospermum maritimum* (mayweed) and *Polygonum aviculare* (knot grass) flourished vigorously in the gaps. Four of the most affected plots on this section were cut green, and the crop and weeds removed to avoid a heavy reinfestation with weed seeds.

Counts of viable weed seeds in soil samples taken from Sections Ia and Ib in 1960 showed that Ia, where herbicides have been used since 1957, had 15% fewer seeds than Ib, which remains in the fallow cycle without herbicides. The herbicide sprays halved the numbers of seeds of *Arenaria*

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serpyllifolia, *Capsella bursa-pastoris*, *Medicago lupulina*, *Polygonum aviculare*, *Ranunculus arvensis*, *Stellaria media*, *Valerianella locusta*, *Vicia sativa* and *Lithospermum arvense* in the soil, but this was offset by substantial increases in *Aphanes arvensis*, *Legousia hybrida*, *Veronica arvensis*, *Euphorbia exigua* and various grasses; the numbers of seeds of eight other major species and the totals of 18 minor species differed little between the sections.

The quarterly totals of seedlings from the soil samples showed no change in seasonal periodicity of germination after four successive May applications of herbicide, although seeds of susceptible species on the sprayed plots must have come mainly from late-germinating individuals. However, spraying with herbicides increased the proportion of all weed seeds germinating in the first of the three years of the test period by about 10%, i.e., it tended to break dormancy. Many species responded in this way; the largest effect was with *Vicia sativa* (49% more in the first year), and increases between 10 and 30% occurred in *Ranunculus arvensis*, *Papaver* spp. *Odontites verna*, *Legousia hybrida* and *Veronica hederifolia*. (Thurston)

***Germination of seeds of* Alopecurus myosuroides.** Seeds of *Alopecurus myosuroides* (black grass) were collected on Broadbalk in 1962 just before they shed, from plots 3 (unmanured) and 8 (complete fertiliser with 600 lb sulphate of ammonia/acre) on sections Ia (sprayed with herbicide) and Ib (no herbicide), and sown in pans of sterilised Rothamsted soil in the glasshouse. Germination in the first year was decreased by about 5% by the herbicide spray, but fertiliser had a greater effect; the total germination of plot 3 seeds was 76% and of plot 8 seeds 57%. Whether the difference is in viability or dormancy is not known yet, but it is probably in viability, because nearly all viable seeds of black grass germinate in the first year. The effect of fertilisers may be a direct one, or a consequence of increased competition from wheat with high nutrient supply. (Thurston)

Wild Oats

Geographical variation within species. Thirty samples of wild oats seeds from Australia and seven from other countries, received since the previous experiments (*Rothamsted Report* for 1962, p. 241), were grown in pots in comparison with previously studied sorts, mainly British ones. Seeds produced by the plants were tested for dormancy and periodicity of germination.

Because of the severe winter, this experiment was started 16 days later in the year than the previous two, but the British wild oats reached the flowering stage (50% panicle emergence) on the same date as before, and the Australian ones only 8 days later. However, *Avena sterilis* from Israel took 12 days longer than previously. A new sample of *Avena fatua* from Pakistan took 94 days from sowing to flowering, and three from Yugoslavia 113 days, compared with 129 days for samples from Western Europe in previous experiments. These results agree with the conclusion that wild oats from lower latitudes flower sooner (*Rothamsted Report* for 1961, p. 81). A sample from the Philippine Islands took 111 days, longer than expected from the latitude, but this stock may have come recently

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from the U.S.A., like a sample separated from durra (*Sorghum*) imported into Norway from the U.S.A., which took 112 days. Another sample found growing in a Norwegian field took only 109 days to flower, but this also may be a recent arrival in imported feed grain.

Plants raised from seeds of the same sort but from different countries sometimes differed greatly in agriculturally important characters. For example, full-grown Australian *A. fatua* plants were 1–1½ ft shorter than British ones grown in the same conditions, had 50% more culms per plant, but only half or two-thirds as many seeds. Type fA from Pakistan was only 3½ ft tall, had 10–12 culms and less than 500 seeds per plant, compared with over 6 ft maximum height, 5 culms and 800 seeds per plant for British fA. *A. fatua* from Yugoslavia, the U.S.A. and the Philippine Islands were more like British specimens. The dormancy tests are not complete, but some type fA from abroad had a much smaller proportion of dormant seeds than British ones, and may be useful material for studying the causes of dormancy. (Thurston)

Effect of photoperiod on germination. Dormancy and germination of seeds of *A. fatua* and *A. ludoviciana* are affected by daylength. When moistened intact seeds of both species were put in a growth-cabinet at 15° C with dim light (<50 f.c.) from mixed fluorescent and tungsten lamps for 33 days no seed of *A. ludoviciana* and only 18% of seeds of *A. fatua* germinated in 16 hour photoperiod, but in 8 hour photoperiod 92% of 1st seeds and 84% of 2nd seeds of *A. ludoviciana* and 53% of *A. fatua* seeds germinated. When the ungerminated seeds were de-husked, pricked and returned to the same conditions an inhibitory effect of long days still persisted; 1·5% of 1st seeds and 16% of 2nd seeds of *A. ludoviciana* and 5% of seeds of *A. fatua* failed to germinate in the long days, but all except one *A. fatua* seed germinated in short days. (Thurston)

Park Grass Plots

The severe winter killed up to three-quarters of the *Holcus lanatus* (Yorkshire fog) on the unlimed halves of plots 10, 11–1 and 11–2, but by the summer the species had re-established itself from seeds in the soil. In the early years of the experiment *Vicia cracca* (tufted vetch) was present in small quantities on one plot, but soon disappeared completely. In 1963 it was found again on the heavily limed part of plot 19. *Carex flacca* (carnation grass) was found for the first time on plot 3 (limed); it may previously have been confused with *C. caryophyllea* (spring sedge), which was recorded in earlier years on this plot.

Single specimens of *Dactylorchis fuchsii* (common spotted orchis) were found in June flowering on the limed ends of plot 2 and plot 8—the first record of this orchid on the Park Grass plots. (Witts)