ROTHAMSTED RESEARCH

Report for 1954

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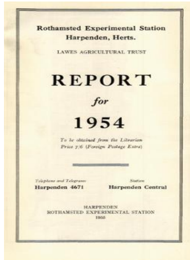

Botany Department

D. J. Watson

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BOTANY DEPARTMENT

D. J. WATSON

D. J. Watson attended the 17th Congress of the Institut International de Recherches Betteravières at Brussels in February, as a representative of the Sugar Beet Research and Education Committee of the Ministry of Agriculture and Fisheries.

J. M. Thurston and D. J. Watson attended the 8th International Botanical Congress in Paris in July, and J. M. Thurston and K. Warington the 2nd British Weed Control Conference at Harrogate in November.

Dr. Elsa B. Kidson, of the Cawthron Institute, New Zealand, came to work in the Department for six months.

PLANT NUTRITION

Interaction between iron and other micronutrient elements (K. Warington)

Solution culture studies on chlorosis caused by iron deficiency, induced directly by low iron supply or indirectly by excess of a micronutrient, have been continued. In previous experiments, the severity of chlorosis caused by excess manganese was increased when sodium molybdate was given, whereas Millikan in Australia found that in some conditions ammonium molybdate had the opposite effect. The two molybdates were therefore compared in a wider range of concentration than previously (0·1–40 p.p.m. Mo) on flax, soybean and peas subjected to direct instead of manganese-induced iron deficiency.

In the early stages of growth, 40 p.p.m. Mo prevented apical chlorosis in flax when the iron supply was low, and deepened the green colour of plants with a high iron supply. The effects were greater, lasted longer and were detectable at a lower concentration (20 p.p.m.) with ammonium than with sodium molybdate. At later stages of growth, 40 p.p.m. Mo produced toxic symptoms, except in high-iron plants, restricting root growth. Similar effects were found in soybean and peas, but the mitigation of chlorosis was not so pronounced or so persistent. The divergent effects of molybdenum on chlorosis were thus shown to depend on the form and concentration of the molybdenum supplied, as well as on the nature and age of the plant, but the conditions in which molybdenum alleviates or intensifies the effects of iron deficiency cannot yet be precisely defined.

In the later stages of growth the high rate of iron supply (30 p.p.m.) was toxic to flax, but its harmful effect was reduced by 40 p.p.m. Mo. This action of molybdenum in offsetting effects of iron excess is similar to those of manganese, copper and zinc described by other workers.

Increased molybdenum supply usually reduced the iron content of the shoot, even when, at the low rate of iron supply, it decreased the severity of chlorosis. It greatly increased the iron content of the roots. High iron supply reduced the molybdenum content of

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both shoot and root, except in the flax plants which showed symptoms of iron excess.

To find out whether the effect of increased iron supply in reducing toxicity due to micronutrient excess occurs inside the plant, or outside it in the nutrient solution, a toxic concentration of vanadium (2·5 p.p.m.) was given to peas and soybeans with high or low iron concentration, in the same solution or separately in successive time intervals. For peas, the reduction in the toxicity of vanadium by the high iron supply was greatest when vanadium and iron were given in the same solution, so that here the interaction occurred, at least in part, outside the plant. But with soybean the highest yields were obtained when iron was given in the initial treatment, either alone or with vanadium.

In an experiment on soybean, iron supplied as the ferric complex of disodium ethylenediamine tetracetate (Fe-EDTA) was found to be more effective in reducing vanadium toxicity than when given as ferric citrate. In the presence of low vanadium (0·1 p.p.m.) 2·5 p.p.m. Fe as Fe-EDTA gave the same dry weight yield as 20 p.p.m. Fe as citrate; plants receiving 2·5 p.p.m. Fe as citrate were chlorotic, and 20 p.p.m. Fe as Fe-EDTA was harmful and reduced the dry weight yield. With the low rate of citrate, 2·5 p.p.m. of vanadium was very injurious, but its toxicity was nearly inhibited by the low rate of Fe-EDTA or the high rate of citrate. The high rate of Fe-EDTA still produced symptoms of iron excess where vanadium was given at the high rate, but they were less severe than at the low vanadium level. Although Fe-EDTA was much more effective than citrate, it caused no greater uptake of iron, but at the lower rates of supply a larger fraction of the iron absorbed was contained in the shoot when iron was given as Fe-EDTA than when it was given as citrate.

Nutrient uptake by excised roots (E. C. Humphries)

Further investigations of factors controlling uptake of ions by excised roots, and especially of the rôle of carbohydrate, has confirmed that the positive correlation between rate of nutrient uptake and sugar content of the roots is attributable to the reducing sugar fraction, and an attempt has been made to find out whether fructose or glucose—the only reducing sugars that have been detected in barley roots—or both, are concerned. The sugar content of roots was varied by change in nitrogen supply to plants from which the roots were taken, by shading the plants or by supplying sucrose to the solution in which the excised roots were held. The effects of these treatments on the rate of potassium uptake by the excised roots, and on their content of glucose, fructose and sucrose were measured. A regression analysis of the results showed that the rate of potassium uptake increased with increase in fructose content, but decreased with increase in glucose or sucrose.

Experiments were also continued on the effect on rate of potassium uptake by low-sugar, low-salt roots of adding different sugars to the 0·01M-KCl solution in which the roots were held. Separate addition of either fructose, glucose or sucrose increased the uptake of potassium and the amounts of all three sugars in the roots. The increase in sugar content continued steadily throughout the absorption period. Statistical analysis of these results is not yet complete.

The effects of sugars other than those normally present in the roots were also tested. Sorbose increased the rate of potassium absorption to about the same extent as fructose or glucose, L- and D-arabinose and L-rhamnose gave slight increases in rate of uptake, L-galactose had practically no effect, and mannose and D-glucosamine had inhibitory effects on the rate of uptake, even in low concentrations (0·1 per cent). It is not yet known whether the sugar applied accumulated as such in the roots or was converted to other forms. The results suggest that the second carbon atom of a hexose sugar is important in determining whether it acts as an inhibitor of potassium uptake.

" Cloud " or " blotchy ripening " of tomato fruits (E. B. Kidson)

The disease of tomato fruits called " cloud " in New Zealand and " blotchy ripening " in this country is thought to be a nutrient disorder, but its cause is not yet understood. Its symptoms are the persistence of green patches on ripening fruits and necrosis of the vascular tissue in the affected parts of the flesh. Its incidence is increased by soil sterilization, and as the plants then also have a high manganese content, manganese toxicity has been suggested as a possible cause. This and a number of other factors were tested in a solution-culture experiment. Though the high-manganese plants showed chlorosis of the leaves typical of manganese excess, the fruits were free from " cloud ". At an early stage of the experiment, vascular necrosis was found in fruits from plants receiving high iron supply, but not where a lower iron supply was given. However, the symptoms were not characteristic of " cloud ", and were not found in fruits that developed subsequently. Typical " cloud " symptoms appeared at a later stage of the experiment when plants were transferred to a more dilute culture solution. These experiments will be continued in New Zealand.

Nutrient uptake from leaf sprays (G. N. Thorne)

Previous attempts to account for low recovery of nutrients supplied in leaf sprays, estimated from the difference in total nutrient content between sprayed and unsprayed plants, showed that, for plants receiving a balanced nutrient supply to the roots, uptake of a nutrient from leaf spray did not reduce uptake of the same nutrient by the roots (Report of Rothamsted Experimental Station for 1953, p. 70). Experiments on swedes have now shown that such a reduction can occur when the supply to the roots of the nutrient concerned is high relative to other nutrients. When sodium phosphate solution labelled with ^{32}P was applied with a paint brush to the leaves of plants grown in a high phosphorus solution, 11 mg. P per plant were absorbed through the leaves, and phosphorus uptake by the roots was reduced by about the same amount, from 31 mg. in unpainted controls to 21 mg. in painted plants.

The results of a series of experiments in which measured volumes of ^{32}P labelled sodium phosphate solutions were carefully applied with a glass rod or paint brush to leaves of swede plants showed that 90 per cent of the phosphorus applied to the leaves was recovered either inside the plant or as an external deposit that could be washed off the leaves. The same recovery was found whether the plants were harvested immediately after treatment or after several days, showing that no continuous loss occurred, and it is therefore concluded that the 10 per cent not recovered represents losses during digestion of the plant material and at other stages of the manipulation. None of the phosphorus absorbed by the leaves was excreted into the nutrient solution surrounding the roots, so it appears that all the phosphorus from the solution retained by the leaves either remained as an external deposit or was absorbed and partially translocated to other parts of the plant.

^{32}P was detected in the roots of small swede plants 4 hours after application of the solution to the leaves. Absorption from the dry deposit continued for 2–3 days, by which time about half the applied phosphorus had entered the plant, but there was no further uptake during the next 10 days. Trebling the concentration of the solution increased the percentage uptake of phosphorus slightly. Absorption was greater through the lower than through the upper surface of the leaf, and was not increased by spraying twice with water at daily intervals after applying the ^{32}P solution.

Some more work was done on application of nitrogen in sprays to winter wheat (Report of Rothamsted Experimental Station for 1953, p. 70). As weed-killers are often applied to wheat at about the same time as a nitrogenous spring top-dressing, one operation could be eliminated if the fertilizer could be applied in the same solution as the weed-killer without detriment to either. To test this, 0·5 cwt. N per acre as ammonium nitrate or urea was applied in mid-April to the soil, or sprayed on the crop in 30 gal. per acre of solution. Half the plots were sprayed with 2-4D, and where the fertilizer was also sprayed, the two were given in the same solution. The weed-killer was supplied, and the spraying done, by the Agricultural Research Council Unit of Experimental Agronomy, Oxford. The wheat was slightly scorched by the nitrogen spray, with or without 2-4D, but soon recovered. Unfortunately, the crop was severely affected by " take-all ", and gave a low yield, with negligible responses to either soil or spray applications of nitrogen, though the nitrogen content of grain and straw was slightly increased. Many of the weeds were of species resistant to selective weed killers, but the amount of mayweed (*Matricaria inodora*) was reduced by the 2-4D spray. The experiment will have to be repeated in conditions that provide greater responses to fertilizer and weed-killer.

Weed Studies

Wild Oats (J. M. Thurston)

In the fourth year of the field experiment testing the effect of different cultivation treatments on the survival of wild oats seeds sown at two depths in October 1950 (Report of Rothamsted Experimental Station for 1953, p. 71) germination fell to a very low level. Less than 1 per cent of the seeds of *Avena fatua* sown in 1950, and less than 0·1 per cent of *A. ludoviciana* seeds germinated. The total germination of *A. fatua* in the four years of the experiment, for the treatment that gave most seedlings, is only 20 per cent, and of *A. ludoviciana* 16 per cent. The cultivation treatments have been discontinued, and the whole area dug with a spade in March and again in September to encourage germination of surviving viable wild oats seeds and to control other weeds. The fate of the 80–90 per cent of seeds that have so far failed to produce seedings is not yet known. When seeds left over after sowing in 1950 and subsequently stored in the laboratory were tested in January 1954, 86 per cent of *A. ludoviciana* seeds and 72 per cent of *A. fatua* were still viable.

The experiment in Hoosfield comparing the effects of winter and spring cereals on the establishment and growth of *A. fatua* (Report of Rothamsted Experimental Station for 1953, p. 71) was continued. This also showed a large reduction in the number of seeds germinating; in winter rye there were 40 per cent of the number found in 1953, and on the other plots only 20 per cent. The inverse correlation found in 1953 between the number of wild oats germinating and weight of the cereal crop at the time was not apparent in the second year, but compared with fallow or spring barley the winter cereals all greatly reduced the growth of wild oats.

A pot experiment was done on competition between wild oats and cereal crops, to study the effect of the size of the crop plant at the time when the wild oats germinate on subsequent growth of the wild oats and the number and dormancy of the seeds they produce. Three sowings of spring barley and spring wheat at two rates were made at weekly intervals, and chitted seeds of *A. fatua* were planted 4 days after the last sowing of the cereal crop, in pots with and without barley or wheat. Competition with the crop reduced seed production by the wild oats; the mean numbers of seeds per plant when 3 wild oat plants were grown in pots with 0, 3 or 9 cereal plants were 748, 181 and 59 respectively. Barley (Herta) was a more effective competitor than wheat (Atle); there were only 62 seeds per plant of wild oats in the barley pots, compared with 178 in the wheat pots. Seed production by the wild oats was reduced by earlier sowing of the cereal crop; when the crop was sown 18 days before the wild oats were planted, there was an average of 71 wild oat seeds per plant, but when the interval was only 4 days there were 192 seeds per plant. This result shows that early sowing and establishment of the crop may have a useful effect in minimizing the multiplication of wild oats in spring cereals. A similar experiment has been started on competition between autumn-sown wheat, barley or rye and *A. ludoviciana*.

Variability in germination of wild oat seeds in the fluctuating temperature of a glasshouse suggested that summer temperatures induce dormancy that can be overcome by cooling and drying the seeds. This was tested in an experiment on both *A. fatua* and *A. ludoviciana* in which imbibed seeds were held in warm (27° C.) or cool (5–10° C.) conditions, or alternated between the two in 2-daily intervals. Half the seeds were pricked to break seed-coat dormancy. After 7–9 weeks, when germination had ceased, the ungerminated seeds were all transferred to cool conditions and allowed to dry. They were then re-moistened and held at 5–10° C. for a further six weeks, until germination stopped again.

The total germination of the pricked seeds up to the end of the final low-temperature exposure was taken as a measure of viability. Exposure to warm conditions reduced the viability of *A. fatua* seeds to 48 per cent, and the alternating temperature to 80 per cent, compared with 93 per cent for those held in cool conditions throughout. The numbers of dormant seeds at the end of the experiment,

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determined from the differences between the total germinations of pricked and unpricked seeds, amounted to 66 per cent of the viable seeds, for those held in cool conditions throughout. Warm conditions, whether continuous or alternating, increased the percentage of viable seeds that were dormant to 90 per cent. No conclusions could be drawn from *A. ludoviciana*, because more unpricked seeds germinated than pricked seeds after exposure to the higher temperature, possibly because pricking led to infection and death of many seeds, but it appears that there was little residual dormancy in *A. ludoviciana* whatever the treatment in the first period. Another experiment showed that the inhibition of germination of *A. ludoviciana* seeds at 27° C. could not be overcome by drying and re-wetting the seeds, but only by cooling them.

Removal of part of the panicles, as might occur if attempts were made to control wild oats by cutting off the inflorescences above the cereal crop before the emergence of the cereal ears (Report of Rothamsted Experimental Station for 1953, p. 72), had no effect on the dormancy of the remaining seeds of *A. fatua*, but increased the percentage of first seeds of *A. ludoviciana* germinating within 10 weeks of sowing. The proportion of second seeds of the spikelets of *A. ludoviciana* that are dormant in the first year after they are produced is normally higher than of first seeds, but when the first seeds were removed at an early stage of their development, it was found that dormancy in the second seeds was reduced to about the same percentage as of first seeds in intact spikelets.

Two experiments on the survival of wild oat seeds under a grazed temporary ley have been started, one in collaboration with the National Agricultural Advisory Service at Boxworth Experimental Husbandry Farm, and the other on a commercial farm.

Other weeds (J. M. Thurston)

In an experiment at Woburn, the effects of autumn-sown and spring-sown cereals on the weed flora were investigated by comparing plots sown in autumn with rye or barley, or in spring with barley or wheat, or fallowed with cultivation as for an autumn-sown or spring-sown crop. Rye was the heaviest crop, and appeared to be almost free from weeds compared with fallow or the much lighter spring cereal crops, which were very weedy. The difference was wholly due to the size of the weed plants, for they were just as numerous on the rye plots as on the others. This illustrates the importance of growing good crops in helping to control weed infestation. *Matricaria inodora*, the most abundant weed species, and *Polygonum aviculare* were almost confined to autumn-cultivated plots. The numbers of plants of these species did not vary with crop or fallow. *Polygonum convolvulus*, on the other hand, was equally frequent on autumn- and spring-cultivated plots, but there were fewer plants in autumn rye than barley, and they were most abundant in spring barley. *Spergula arvensis* also germinated in spring, and was present on plots of all treatments, but was most abundant on spring-cultivated plots. In June there were fewer spurrey seedlings on fallow plots cultivated in spring than in the spring-sown crops, suggesting that the presence of the crop stimulated the germination of spurrey seeds, but later this difference disappeared.

In all, twenty-eight weed species were present and fourteen of these were sufficiently abundant to be recorded separately, but the results for all of them are not yet analysed.

Physiological Effects of Virus Infection

Effect of infection with tobacco mosaic virus on the respiration rate of tobacco leaves (P. C. Owen)

Three weeks after tobacco plants were infected with tobacco mosaic virus, when symptoms of systemic infection had appeared, the respiration rate of older leaves in the 20 hours after they were detached, expressed as CO_2 per g. dry matter, was found to be the same as that of comparable leaves from healthy plants. The respiration rate of younger leaves from infected plants was about 10 per cent less than that of comparable healthy leaves. These effects were independent of seasonal change in light conditions during the growth of the plant. The reduction in respiration rate of the younger leaves by infection persisted throughout the 20-hour period of measurement, though it decreased during the first 5 hours, when the respiration rate of both healthy and infected leaves was rapidly falling. This initial fall is presumably caused by decreasing supply of carbohydrate substrate, and the persistence of the effect of infection into the stage when respiration rate has fallen to nearly steady values suggests that infection reduces the activity of the oxidative mechanism, and not merely the substrate supply.

The initial water content of the older leaves, but not the younger leaves, of infected plants was less than that of comparable healthy leaves, and all the infected leaves absorbed less water than the healthy leaves during the experimental period. The effects of TMV infection on water content were so large that the rate of CO_2 production per g. fresh weight was sometimes significantly increased by infection.

The results of these experiments and some reported previously (Report of Rothamsted Experimental Station for 1953, p. 73) (55, 56) show that the respiration rate of TMV-infected tobacco leaves can be higher or lower than, or identical with, that of healthy leaves, depending upon the time elapsed after inoculation, the environmental conditions during growth, the age of the plants and stage of development of the selected leaves, and the basis of expression of the results. This presumably explains the contradictory statements in the literature on the way TMV affects respiration, and shows the importance of defining these factors in any future work.

So far, the effects of TMV-infection have been measured immediately after inoculation, and after the development of systemic infection. Experiments are now in progress on the intervening period, during which virus is multiplying in the plant.

Growth Analysis

Effect on sugar beet of infection with beet yellows virus (D. J. Watson and P. C. Owen)

The automatic gas-sampling unit used in connection with an infra-red gas analyser to make intermittent measurements of the CO_2 concentration in four gas circuits (Report of Rothamsted

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Experimental Station for 1953, p. 73) was reconstructed to work at higher flow rates. It was used to measure the diurnal CO_2 exchange of whole sugar-beet plants grown in sand culture from the time when they were infected with beet yellows virus until symptoms appeared, and in a subsequent period when infection was well established. Similar measurements were made on healthy plants. At the beginning and end of both periods samples of infected and healthy plants were taken for measurements of total dry weight and leaf area. This will enable net assimilation rates, calculated from dry-weight increments and leaf areas, to be compared with direct measurements of CO_2 uptake during the day and CO_2 loss at night, so that the extent to which the reduction is net assimilation rate caused by infection (Report of Rothamsted Experimental Station for 1952, p. 73) is attributable to decreased photosynthetic gain or increased respiratory loss of dry matter can be determined. The results are not yet all worked out.

Effect of time of application of nitrogenous fertilizer and of mildew infection on the yield of wheat (G. N. Thorne and F. T. Last, Plant Pathology Department)

The primary object of this experiment was to measure the effect of infection with mildew (*Erysiphe graminis*) on the yield of winter wheat. The development of mildew infection is correlated with leaf-growth rate, so it can be varied at different stages of growth by varying the time of application of nitrogenous fertilizer (Report of Rothamsted Exp. Sta. for 1952, p. 92; 1953, p. 93). Many experiments have shown that, apart from short-period weather effects, the response to nitrogenous fertilizer in grain yield of wheat is independent of time of application over a wide range, but the response in straw yield decreases steadily with later application. A second object of the experiment was to investigate the physiological mechanism of this constancy in response of grain yield.

Wheat was grown in soil in pots, and received either no nitrogenous fertilizer or nitrogen applied soon after germination in November, or as a top dressing in April, or at ear emergence in mid-June. Half the pots of each nitrogen treatment were inoculated with mildew spores, and the rest were kept free from mildew by repeated spraying with lime sulphur. At regular intervals pots were sampled for determination of dry weight, leaf area, shoot number, etc., according to the usual growth-analysis procedure, and the intensity of mildew infection was assessed. The dry matter that enters the grain is all produced after ear emergence by photosynthesis, mainly in the flag leaf and its sheath, the stem and the ear. Records were therefore made of the size and longevity of the flag leaves, and the contribution of the ears was measured by shading the ears in half the pots with opaque paper tubes immediately after they emerged so as to prevent them photosynthesizing. The reduction in dry weight caused by the shading gave an estimate of photosynthesis in the unshaded ears. Analysis of the data from this experiment is not yet completed. Contrary to previous experience, the nitrogen application at ear emergence had little effect on grain yield, though the earlier applications caused large increases; the reason for this is not known, and needs further investigation.

Dependence of net assimilation rate on leaf area index (D. J. Watson)

Last year it was reported (Report of Rothamsted Experimental Station for 1953, p. 73) that when leaf-area index (L; ratio of leaf area to land area) of a kale crop was greater than about 2·5, the crowding together of the leaves caused mutual interference in their photosynthesis, and the net assimilation rate (E) was reduced. A more detailed investigation, in which L was varied, as previously, by removing at the beginning of successive 10-daily periods different fractions (usually 0, $\frac{1}{4}$, $\frac{1}{2}$ or $\frac{3}{4}$) of the plant population on different plots, has now shown that E decreased almost linearly with increase of L, so that when L = 5, E was reduced to about a quarter of its value when L = 1. Consequently, the rate of dry-matter production per unit area of land reached a maximum when L was between 3 and 4, and decreased when L was increased to higher values. Close spacing, heavy fertilizer application and frequent rain combined to give a very heavy crop, which, on the unthinned plots, produced a yield of over 6 tons/acre of dry matter at the end of September. The leaf area index of the unthinned crop was greater than 4 from the beginning of July onwards, so that during the most productive part of its growth, the crop had too great a leaf area for maximal dry-matter production. This implies that an even greater total yield of dry matter might have been obtained by repeated thinning of the plants or removal of leaves from each plant, to maintain L at about the optimal value between 3 and 4. The position of the maximum rate of dry-matter production was independent of the seasonal drift in net assimilation rate. It occurred at the same value of L in July, when E (for L = 1 approx.) was over 50 g./m.^{2}/week, as in September, when E was about 30 g./m.^{2}/week.

Measurements made in the same way on sugar beet showed that when L increased from 1 to 5, E was reduced by less than 25 per cent, compared with 75 per cent for kale. Consequently, the rate of dry-matter production per unit area of land increased throughout the whole range of E, and the highest value of L attained by the sugar-beet crop, about 6, was still below the optimum for dry-matter production.

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