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Report for 1952

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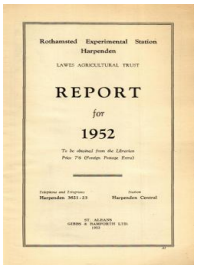
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Botany Department

D. J. Watson

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BOTANY DEPARTMENT

D. J. WATSON

Miss G. N. Thorne was awarded a Ph.D. degree of the University of London.

PLANT NUTRITION

Micronutrients (K. Warington)

Work in the previous year (1951 Report, p. 62) showed that low concentrations of vanadium partially counteract the development of iron deficiency chlorosis induced by excess manganese, though higher concentrations are toxic and eventually cause chlorosis in presence of non-toxic concentrations of manganese. In the early stages of growth, vanadium-treated plants have dark green leaves and stunted shoots suggesting a high-iron, low phosphorus status. Experiments were therefore made with soybean and flax to see (1) whether vanadium increases iron uptake, or reduces phosphorus uptake and (2) whether the effects of vanadium depend on the supply of iron and phosphorus in the culture solution. Injurious effects of vanadium appeared first in the root; when they were slight the only symptom was thickening of the root tips, but high concentrations of vanadium almost suppressed the growth of lateral roots. In the leaves, temporary deepening of the green colour generally occurred, followed by chlorosis and a marked reduction in size. Both 2·5 p.p.m. and 5 p.p.m. V were always toxic, but the symptoms were less severe and developed more slowly with increase in iron supply from 3 to 10 p.p.m.; 0·5 p.p.m. V was harmful when only 3 p.p.m. Fe were given, but not at higher rates of iron supply. Phosphorus supply had less effect on the responses to vanadium, possibly because it was not varied over a wide enough range.

In another experiment on peas a still higher level of iron (20 p.p.m.) was tested, and the low phosphorus supply was reduced from 37 to 11 p.p.m. The toxicity of vanadium was greatly reduced by 20 p.p.m. Fe and there was some indication that it increased at the lower phosphorus level. Chemical and spectrographic analyses will be made on the material from these experiments to determine how the vanadium treatments affected uptake of iron and phosphorus.

An attempt was made to compare the effects of vanadium on iron deficiency induced by excess manganese with that caused by low iron supply in the nutrient solution. As high vanadium supply greatly restricts root growth, the vanadium treatments were withheld until the plants had grown adequate root systems, so as to avoid confusing a direct effect of vanadium on iron uptake with a possible indirect effect due to a reduction in the absorbing surface of the root. Neither 5 nor 0·5 p.p.m. V had any counteracting influence on established symptoms of manganese excess. The results for the low-iron plants were inconclusive, because the chlorosis appeared erratically; the higher rate of vanadium reduced plant dry weight at both high and low levels of iron supply.

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In other experiments, the effects of excess manganese and molybdenum were compared with that of vanadium in similar conditions of varying iron supply, but the results are not yet available.

Nutrient uptake by roots (E. C. Humphries)

It has previously been established (1951 Report, p. 63) that the rates of uptake of nitrogen, phosphorus and potassium by excised barley roots increase with increase in the concentration of sugars present in the roots. Further work has now shown that the rate of uptake depends on the reducing sugar content, and that the sucrose content has little or no effect. Whether glucose and fructose, the main components of the reducing sugar fraction, are both concerned in the absorption process, and the nature of the mechanism involved, are not known. It is unlikely that sugar merely provides energy for accumulation of salts against a concentration gradient, as this would require only very small amounts of sugar.

Experiments by other workers on the bacterium *Escherichia coli* have suggested that uptake of potassium occurs through formation of the potassium salt of a hexose phosphate. If such a mechanism were responsible for potassium absorption by roots, it would be expected that the rate of uptake of potassium would depend on the phosphorus content of the roots, when this is low. Excised roots from barley plants grown with a deficiency of phosphorus were supplied with potassium either as chloride or as phosphate. Phosphorus was absorbed from the K_2HPO_4 solution and the organic phosphorus content of the roots increased, but the rate of uptake of potassium was no greater than that from the KCl solution which did not change the organic phosphorus content. These results do not support the hypothesis that hexose phosphate is concerned in potassium uptake, but it is possible that, although the roots were taken from plants showing severe phosphorus deficiency symptoms, the hexose phosphate content was still not sufficiently low to limit potassium uptake, or else that, although the organic phosphorus content increased when phosphate was supplied to the roots, there was no increase in hexose phosphate.

Uptake of nutrients from solution sprayed on leaves (G. N. Thorne and D. J. Watson)

Chemical analyses of material from the experiment in which leaves of sugar beet grown in soil were sprayed with solutions supplying nitrogen, phosphorus and potassium separately and in all combinations (1951 Report, p. 63) were completed. They showed that uptake of a nutrient from the spray, as measured by the difference in nutrient content between plants that received the nutrient in the spray and those that did not, was the same whether or not other nutrients were present in the spray. However, uptake of a nutrient from the soil was affected by absorption of other nutrients through the leaves; this occurred when the nutrients absorbed by the leaves caused increased growth. Thus, plants sprayed with a solution supplying nitrogen alone grew larger and took up more phosphorus and potassium from the soil than plants

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sprayed with water. Similarly, spraying with solutions supplying potassium but no phosphorus caused increased absorption of phosphorus by the roots.

The increased nutrient content of sprayed plants accounted for about 50 per cent of the nitrogen and potassium and 20 per cent of the phosphorus supplied in the spray solutions. The recoveries of nutrients applied to the soil, determined from the differences in composition between plants with and without a complete fertilizer dressing, were 20 per cent for nitrogen, 10 per cent for phosphorus and 30 per cent for potassium, so that, as in earlier experiments, the apparent recovery in the plant of nutrients applied to the leaves was about twice as great as that of nutrients applied to the soil.

An experiment on sugar beet was made to find out whether nutrient uptake from solutions sprayed on leaves, and its effects on growth, depend on the level of nutrient supply to the roots. The plants were grown without fertilizer, or with N, P and K applied to the soil at sowing, singly and in all combinations. They were sprayed daily with water or with solutions supplying N, P or K separately. The nutrients supplied in the sprays all caused increases in dry weight, and the increases were smaller when the nutrient in the spray was also applied as fertilizer to the soil. Data on the effects on nutrient content of the plants are not yet available. This experiment should provide more reliable comparisons of the efficiency of nutrient uptake from the soil and through the leaves than previous ones, in which recovery from the soil could be calculated only for complete fertilizer dressings.

Tomato plants grown with two levels of fertilizer applied to the soil, and sprayed either with water or a complete nutrient solution, showed no response in yield to the nutrient spray, although the fertilizer application caused a large increase in yield. This confirms a previous experiment (1951 Report, p. 63) which also showed that although spraying with the nutrient solution did not affect yield, it increased the nitrogen and potassium contents of the plants. Whether nutrient uptake from the spray occurred in the 1952 experiment is not yet known.

The possibility of increasing the protein content of sugar beet tops by spraying the leaves with a solution of a nitrogenous fertilizer (1951 Report, p. 65) was further investigated in a field experiment, in collaboration with the Biochemistry Department. Solutions of ammonium nitrate (3 per cent) and urea (2·3 per cent) supplying equal amounts of nitrogen were used and gave similar results. On one series of plots the leaves were sprayed on six occasions in late September and on another series the same volume of solution was applied on the same occasions to the soil between the rows of plants. At harvest in mid-October both treatments had increased the dry weight of leaf lamina and the nitrogen content of all parts of the plant, and the increases from spray applied to the leaves were always greater than from spray applied to the soil. Spraying the leaves doubled their protein yield, and about 30 per cent of the nitrogen applied was converted into protein. Spraying the soil increased the yield of protein in the leaves by 60 per cent, and only 15 per cent of the nitrogen applied was recovered as leaf protein. These results confirmed those of the previous year's experiment

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and also showed that application in solution to the leaves was much more effective than application to the soil. In both experiments, the percentage of sugar in the roots was slightly reduced by the spraying treatments, but there was no significant reduction in yield of sugar per acre.

The leaf area of a wheat crop in the field reaches its maximum towards the end of May, and decreases steadily throughout June and July. This is the time when climatic conditions are most favourable for photosynthesis, so that if the fall could be delayed, yield might be appreciably increased. The senescence of leaves that leads to decline in leaf area is associated with transport of nutrients to the developing ears, so it seemed possible that the life of leaves might be prolonged, and leaf area increased during June and July, by spraying them with nutrient solutions at about the time of maximum leaf area. This was tested in a field experiment in which spraying the leaves with ammonium nitrate on eight occasions in May and June was compared with spraying the same solution on the ground at the same times, and with the same quantity of nitrogen applied as a top-dressing of " Nitro-chalk " in April. In June and July, the leaf area of the sprayed plants was slightly greater than that of the controls without nitrogen, but was no greater than that of plants which received the top-dressing. No significant differences in grain yield between the three methods of nitrogen application were found, but the top-dressing caused a larger increase in straw yield. The recovery of nitrogen from the solution sprayed on the leaves was only slightly higher than that from the application to the soil at the same time. The top-dressing had caused a large increase in leaf area in April and May and it may be, therefore, that spraying in May and June would be more effective if the crops had previously received a top-dressing, and it is intended to test this in 1953.

Potassic fertilizers are said to be ineffective on old stands of lucerne because the plants are so deeply rooted that they are unable to take up potash from the surface layers of the soil, and it has been suggested that better utilization of potassic fertilizers might be secured by spraying them in solution on the leaves. A field experiment was made to test this. On some plots, potassium sulphate at the rate of 120 lb. per acre was applied in a solution sprayed on the leaves on three occasions before each of two cuts; other plots received at the same times the same amount of potash sprayed on the soil between the plants. The treatments had no effect on yield, and information on their effects on potash uptake is not yet available.

Biology of Wild Oats

(J. M. Thurston)

Germination and dormancy

Of the 2,000 seeds of *Avena ludoviciana* fed to a calf (1951 Report, p. 67), three more germinated in the mixed dung and peat bedding kept for a second year in a moist condition in trays in the glasshouse, bringing the total number of seeds that remained viable after passage through the animal to only 10.

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A previous experiment (1951 Report, p. 67) showed that more wild oat seeds germinated in the first season but many fewer in the second season when sown in farmyard manure than when sown in soil. An experiment was started in September on recently harvested seed of *A. fatua* and *A. ludoviciana* to compare the effects on germination of other organic materials, (sewage sludge, straw compost, fresh grass-mowings and peat) with those of farmyard manure. To see whether variation in organic matter content of soil affects germination, seeds were also sown in a range of soils from Barnfield, taken from plots that have received no manure, mineral fertilizers only, rape cake or farmyard manure annually for many years. Barnfield was chosen because it is free of wild oats. Seeds were also sown in sand or in a sandy heath soil for comparison with the heavy loam of Barnfield.

By the end of November, few seeds of *A. fatua* had germinated, presumably because the peak germination period for this species does not occur until Spring. Over 75 per cent of *A. ludoviciana* seeds sown in peat, and 60 per cent of seeds sown in sand had germinated, but for all the other treatments germination was below 50 per cent, ranging from 25 per cent to 45 per cent for the soils, and from 1 per cent to 35 per cent for the organic materials. These results indicate that initially the percentage of dormant seeds was low, but that dormancy was induced by sowing in soil, and to a greater extent by the organic materials (except peat). A similar, though smaller, induction of dormancy by farmyard manure occurred in the first two months of the previous experiment, and it remains to be seen whether, as before, the dormancy will be less persistent in the seeds sown in the organic materials.

Observations were continued on the plots of the field experiment sown with wild oats at different depths in October, 1950, and subsequently receiving varied cultivation treatments (1951 Report, p. 68). More seedlings of *A. fatua*, but fewer of *A. ludoviciana* appeared in the second year than in the first. More seeds of both species germinated on shallow-sown than on deep-sown plots; this repeated the first year's results for *A. fatua*, but was the opposite of that found for *A. ludoviciana*. Shallow-sown plots that were frequently harrowed produced fewer seedlings than those left undisturbed through the summer; this may be partly due to destruction of some of the young seedlings by the harrow before they emerged. Neither autumn nor spring ploughing of the deep-sown plots had any appreciable effect on germination of either species. About 80 per cent of the seeds sown have not yet produced seedlings, even with the treatments that gave the highest germination.

Variability within the species, and the diagnostic value of seed characters.

Avena fatua and *A. ludoviciana* are distinguished primarily by morphological characters of the spikelet, for they differ little in the vegetative stage. In the field at Rothamsted, they germinate at different times, *A. fatua* mainly in spring and *A. ludoviciana* mainly in autumn and winter. Within each species, considerable variation in seed characters has been observed and it is important

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to know whether this is correlated with biological differences that may determine the behaviour of the different types as agricultural weeds, and affect the measures needed to control them.

Germination tests on the produce from the 22 selections of *A. fatua* and 7 of *A. ludoviciana* grown in pots in 1951 (1951 Report, p. 68), showed that the percentage of dormant seeds was higher in *A. fatua* (usually over 90 per cent) than in *A. ludoviciana* (40 to 80 per cent). This difference was mainly due to the low dormancy of the first seeds of the spikelets of *A. ludoviciana*. Of three selections of *A. fatua* with less than 80 per cent of dormant seeds, two resembled each other in some vegetative characters, and were like *A. ludoviciana* in colour of coleoptile and first leaf, number of shoots and early growth habit. Two selections of *A. ludoviciana* with dormancy higher than the rest were unlike in seed and plant characters and differed in dormancy from others which resembled them morphologically. There is, therefore, some evidence of a correlation between seed dormancy and vegetative characters in *A. fatua* but not in *A. ludoviciana*.

Another collection of wild oat seeds from more widely distributed localities in England and Wales and representing a larger number of seed types, was grown in pots in 1952. Representative types from the 1951 collection were included for comparison. Observations on the morphology and growth of the plants were made at intervals and seeds were collected for dormancy investigations.

Most selections of wild oats produced spikelets resembling those of the parents in colour, hairiness and articulation. Two selections of *A. ludoviciana* out of 28 and 2 of *A. fatua* out of 52 produced one or more plants with spikelets different markedly from the parent type. Both the divergent types of *A. ludoviciana* but only one of *A. fatua* were of the same species as the parent as judged by the articulation of the spikelet.

Eleven selections had spikelets differing from those of typical *A. fatua* and *A. ludoviciana* and intermediate in type between wild and cultivated oats; they had a small abscission scar at the base of the first seed only, a few hairs at the base, a slender rachis between the first and second seeds, and a well-developed awn on the first but not the second seed. Three of these produced only plants with spikelets of the same type as the parents, but the other 8 gave rise to varying seed-types, one of them producing 3 variations as well as the parent type. Of 10 aberrant plants, 7 were typical *A. fatua* judged by their spikelet articulation, while the other 3 were intermediate forms like the parents and differed from them only in husk colour and hairiness. None of the intermediate forms gave rise to seeds of the cultivated oat type, though some plants tended towards cultivated oats in width of leaf and sturdiness of culm. One of the aberrant seed-types produced by *A. fatua* was of this intermediate form. The intermediate types therefore appear to be related to *A. fatua*, but there is little evidence of relationship to cultivated oats and none at all to *A. ludoviciana*.

The relationship of spikelet characters to growth habit and morphology has not been fully worked out yet. On the whole vegetative differences within the species were not striking. An exception was the selection of *A. fatua* with grey, very hairy husks,

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and a low percentage of dormant seeds in the 1951 test. The culms had hairy nodes and 3 other selections of similar seed-type also had hairy nodes. Most wild oats have entirely glabrous culms. Another difference associated with spikelet characters was the late-flowering of 3 selections of *A. ludoviciana* with grey, very hairy husks, though a fourth selection of this seed-type flowered at the same time as the other sorts of *A. ludoviciana*. Germination tests of seeds from these plants is not yet complete.

These results show that if spikelet characters are accepted as diagnostic of the two species *A. fatua* and *A. ludoviciana*, there is some overlapping between them in other characters, and that some types of wild oats cannot be included in either species. The status of these is uncertain; some of them may be hybrids. Present methods of study are unlikely to throw much light on the nature of the aberrant types; for this a cytogenetical investigation of the material is required. Meanwhile, plants and ripe seeds of all selections have been sent to Kew Herbarium for taxonomic study.

Physiological Relation of Virus Infection

The following investigations have been made in collaboration with the Plant Pathology Department.

Effect of a dark period before inoculation on susceptibility of leaves to infection. (E. C. Humphries and B. Kassanis)

Bawden and Roberts [1] have shown for several viruses and host plants that susceptibility to infection, measured by counts of necrotic local lesions, is increased if the plants are kept in darkness for a short time before the leaves are inoculated. Work has been started to determine what physiological changes induced in leaves on transfer from light to dark are responsible for this, and changes in the nitrogen fractions of the leaves have been investigated first. When tobacco or French bean plants are kept in darkness, the soluble fraction of the nitrogen in the leaf lamina increases, and nitrate accounts for most of the increase. On return to light after a dark period, the nitrate content falls. The numbers of local lesions produced by leaves of plants kept in light or darkness before inoculation, or in leaves inoculated at successive intervals after the plants were transferred from darkness to light, were usually closely correlated with the nitrate content of the leaves at the time of inoculation, although there were a few exceptions. The nitrate accumulated in the leaf lamina during a dark period was derived from protein, and the large increase in nitrate was accompanied by smaller changes in the contents of amino-N, amide-N and ammonia-N. Nitrate appears to be the end-point of proteolysis in attached leaves in darkness; the stage of nitrate production apparently proceeds rapidly compared with the earlier stages, so that intermediate products do not accumulate. The results suggest that susceptibility to infection may depend on the concentration of simple soluble nitrogen compounds present in the leaf at the time of inoculation, and that the increased susceptibility caused by darkening the leaves before inoculation may be due to an increased concentration of nitrogen compounds suitable for synthesis of virus.

(1) Bawden, F. C. and Roberts, F. M., 1948, Ann. app. Biol., **35**, 418.

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The changes in phosphorus content of attached leaves of darkened plants were also investigated. Total phosphorus content tended to increase, but no consistent relation was found between phosphorus content and lesion counts.

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

Many workers have compared the respiration rate of healthy tobacco leaves with that of leaves infected with tobacco mosaic virus, but their results are inconsistent and sometimes contradictory. A systematic study has therefore been started of the effect of infection on respiration at successive intervals after inoculation. The results show wide variability in response to infection of comparable leaves between plants inoculated at the same time, and between batches of plants grown at different times and used at the same stage of development. The cause of this is not yet understood.

The leaves were inoculated by rubbing with infective sap, and in the earlier experiments the controls were rubbed with water. Some constituent of the sap acted as a spreader, so that less water was retained on the leaf surface after rubbing with sap than with water, and this caused an apparent increase in respiration rate of the leaves rubbed with sap if respiration rate was expressed on the basis of fresh weight after inoculation. In later experiments, therefore, the control leaves were rubbed with healthy sap, and respiration rate was expressed on the basis of final fresh weight or dry weight.

Effect of infection with beet yellows virus of beet mosaic virus on the respiration rate of sugar beet plants. (D. J. Watson)

Previous work (42) has shown that the loss of yield of field crops of sugar beet caused by infection with beet yellows virus (BYV) is partly due to a reduction in net assimilation rate. Though it is reasonable to attribute this mainly to a decrease in the rate of photosynthesis associated with yellowing of the leaves caused by infection, it may be due in part to increased respiratory loss of dry matter. Van Riemsdijk[1] found that the respiration rate of sugar beet leaves infected with BYV was 15 to 25 per cent higher than that of comparable healthy leaves, but there is no published information about the effect of infection on respiration in other parts of the plant. Infection with beet mosaic virus (BMV) also reduces net assimilation rate, but it is not known whether increased respiration is a contributory factor. An investigation has therefore been made of the effect of infection with BYV or BMV on the respiration rates of leaf lamina, petiole and storage root of sugar beet plants, grown in pot culture, at varying intervals after infection. The results are not yet complete, but the general conclusions are as follows:—The respiration rate of the leaf lamina was greatly increased by infection with BYV. The increase was greatest soon after the first appearance of yellowing; the respiration rate of the laminae of yellowed leaves at this time was more than twice that of comparable healthy leaves. The effect was progressively

[1] Van Riemsdijk, J. F. (1935) *Tijdschr. PlZiekt.*, **41**, 317.

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smaller in younger leaves, and also diminished with age in the yellowed leaves. The respiration rate of the petioles was increased by infection, but less than that of the leaf lamina. The respiration rate of the roots was unchanged.

Infection with BMV had similar but smaller effects. The respiration rate of the laminae of infected leaves was never more than 25 per cent greater than that of comparable healthy leaves, and the increase was usually less than this. Increases of up to 50 per cent were found in the petioles. The respiration rate of the roots was unaffected.

In these respiration studies, the rate of CO_2 production was measured with an infra-red gas analyser. An automatic gas-sampling unit was designed for use with the analyser which enables the CO_2 concentration in four gas circuits to be measured and recorded in successive short intervals, so that the respiration rates of four experimental objects can be compared in one experiment and recorded automatically over long periods.