Rothamsted Report for 1951
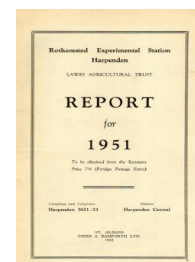
Botany Department

D. J. Watson

BOTANY DEPARTMENT

By D. J. Watson

There were only two changes in the scientific staff during the year: Miss J. M. Patterson resigned, and Mr. S. A. W. French, who had served for more than 20 years on the assistant staff, was appointed Experimental Officer.

P. C. Owen and J. H. Wilson were awarded the Ph.D. degree of the University of London. Dr. Wilson returned to his post in the Department of Agriculture, Tasmania, in June.

PLANT NUTRITION

Micro-nutrients

Dr. K. Warington continued her investigations in solution culture on interactions between micronutrient elements (32). The chief objects were to determine (1) if iron-deficiency chlorosis induced by manganese excess can be offset by the addition of either molybdenum or vanadium and (2) if addition of molybdenum affects the sensitivity of oats to varying manganese supply. In the first series, molybdenum was provided at rates ranging from 0·1—20 p.p.m., but the upper limit of the range for vanadium was a rate equivalent to 10 p.p.m. Mo, because of the greater toxicity of this element. Molybdenum at 20 p.p.m., and to a less extent at 10 p.p.m., intensified chlorosis induced in soybean and flax by manganese excess (10-25 p.p.m.), though these concentrations were harmless in the presence of 1 p.p.m. Mn. Vanadium ($\equiv$1·0, 5 and 10 p.p.m. Mo) counteracted some of the symptoms of manganese toxicity, but the two higher rates were themselves harmful to growth irrespective of the level of the manganese supply. These toxic concentrations of vanadium at first deepened the green colour of the shoot, suggesting some alleviation of the iron deficiency, but apical chlorosis generally followed later. Low molybdenum (0·1 p.p.m.) or equivalent vanadium had no influence on growth or iron nutrition at either level of manganese. Visual differences were corroborated by changes in the nitrogen, phosphorus and iron contents of the plants. There was no evidence of replaceability of molybdenum by vanadium.

In the second series, oats were grown in nutrient solutions containing various combinations of manganese (nil — 400 p.p.m.) and molybdenum (nil — 20 p.p.m.). The appearance of manganese deficiency symptoms was not affected by the quantity of molybdenum provided, and the manganese and molybdenum contents of the leaves were mutually independent of the quantity of each element supplied.

Physiology of nutrient uptake by roots.

The results of work by Dr. E. C. Humphries on nutrient uptake by excised root systems of barley and peas, summarized in previous Annual Reports, have now been published (27, 28) and discussed in the light of current theories of ion absorption. The roots were taken from plants grown in solution culture with a range of conditions of nutrient supply, and nutrient absorption was measured in a subsequent period when the root systems were held in constant

conditions in the laboratory. It was shown that the rate of uptake of a particular element depends on the concentration of that element already present in the root, and on the total carbohydrate content of the root, but appears to be independent of the concentration of other elements. It is concluded that the results are best explained on the assumption that absorbed ions combine with special substances in the root cells. Sugar is probably a precursor of these ion-binding substances.

Subsequent experiments have confirmed the importance of carbohydrate supply by showing that addition of sucrose to the nutrient solution in which the excised root systems are held increases the rate of uptake of nitrate, phosphate and potassium.

Investigations have also been started on the absorption of ions by roots of intact plants. By a special device for sealing intact roots into a vessel containing culture solution, it has been possible to follow ion-uptake and respiration by the root simultaneously. One of the objects of these experiments is to see if there is an increase in respiration rate when active ion absorption is occurring; this should be so, according to the " salt respiration " theory of ion absorption, but has not been confirmed in experiments with excised roots. An interesting fact which has emerged from these experiments is that, in spite of maintaining the intact roots at a constant temperature, the respiration rate exhibited a diurnal rhythm, and was higher during the day than at night. This is probably connected with variation in the carbohydrate supply from the shoot, but so far this point has not been specifically investigated.

The installation of a compressed-air supply in the glasshouses has enabled experiments on the effect of aeration on the growth and uptake of ions by barley plants to be begun. The analytical results of these experiments are not yet complete.

Uptake of nutrients from solutions sprayed on leaves

Miss G. N. Thorne has completed the chemical analyses of plant material from her 1950 pot experiments. In one of these, the leaves of sugar beet plants were sprayed daily with a nutrient solution supplying nitrogen, phosphorus and potassium either for eight weeks in the early part of the growth period, or for the subsequent nine weeks. Early spraying caused a greater increase in final dry weight and in total nutrient uptake than late spraying, but did not appreciably affect nutrient content per cent of dry matter, while later spraying increased the per cent content of N and P.

It was noted in the 1950 Report that spraying with a nutrient solution had no effect on the growth or yield of tomato plants, although these were grown in poor soil and showed symptoms of nitrogen and potassium deficiencies. Chemical analyses have now established that the nitrogen and potassium contents of the plants were increased by spraying. The reason why tomato plants, unlike other species tested, failed to show growth responses to nutrients taken up through the leaves is not known.

In all the 1950 experiments the spray solution supplied nitrogen, phosphorus and potassium together. To find out whether the presence of one nutrient in a solution sprayed on the leaves affects the uptake of other nutrients, either from the spray solution or

through the roots, an experiment was made on sugar beet in 1951 in which nitrogen, phosphorus and potassium were applied in spray solutions separately and in factorial combination. Harvests were made after spraying daily for 4, 8 and 11 weeks. Nitrogen caused a marked increase in leaf area and in the dry weights of all parts of the plants at all harvests, and at the last harvest potassium also increased dry weight.

A second experiment was done to compare the uptake of Na, K, Ca and Mg from solutions containing equivalent concentrations of the chlorides. None of the spray treatments gave increased yields, presumably because the soil supplied adequate amounts of these elements.

A third experiment compared uptake of nitrogen from solutions of ammonium sulphate, calcium nitrate and urea of equivalent nitrogen content. Sugar beet plants sprayed with these solutions had darker green leaves than plants sprayed with water, and the leaf weight was also increased. Calcium nitrate and urea increased root weight, but ammonium sulphate had a much smaller effect, possibly because it caused some scorching of the leaves in the later part of the experimental period. The total nitrogen uptake was nearly identical for all three nitrogen compounds.

It is not known whether uptake of nutrients from the spray solutions is limited to the period when the leaves are still wet, or whether it can take place from the dry deposit of solute after the solutions have evaporated. If the former is true, increasing the length of the wet period by spraying with water should increase nutrient uptake. This was tested in an experiment where plants were sprayed with nutrient solution on two days each week, half of them receiving additional sprayings with water on the other days.

An experiment planned in 1950 to measure the effect of nutrient sprays on the growth of barley failed through mildew infection, and was repeated in 1951 on a mildew-resistant variety. Spraying with a complete nutrient solution increased the number of tillers, and the yield of grain and straw. When the plants were ripening, the foliage of the sprayed plants remained green longer than that of the unsprayed.

Much of the information on nutrient uptake that these experiments will give is not yet available, because the chemical analyses are incomplete. Measurements of leaf area made at regular intervals will enable the efficiency of absorption per unit leaf area of different substances and at different periods of growth to be compared.

The glasshouse experiments so far described were intended to establish the possibility of nutrient uptake through leaves and measure its extent and its effects on growth, and frequent sprayings were used to ensure maximal effects. Such frequent sprayings over long periods of time would obviously be impracticable in the field. It is possible, however, that useful results may be produced in field crops by a few sprayings at an appropriate stage of growth. As the quantities of nutrients taken up depend on leaf area, such sprayings are likely to be effective only at times when the crop has developed a large leaf area. One possible application of this method of nutrient supply is to increase the nutritional value, particularly the protein content, of green forage crops. In collaboration with the Biochemis-

try Department, a field experiment was made to test whether the protein content of sugar beet leaves can be increased by spraying with a solution of a nitrogenous fertilizer at a stage close to harvest, without serious adverse effects on the sugar content of the roots. If successful, this might provide a valuable method for rapidly converting inorganic nitrogen into protein. Apart from increasing the feeding value of the beet tops, it would improve their value as material for extraction of leaf protein by the methods developed in the Biochemistry Department.

Field plots of sugar beet were sprayed with a 3 per cent solution of ammonium nitrate on six occasions in two periods of three weeks at the end of August and in September; the total amount of ammonium nitrate so applied was 180 lb. per acre. At harvest in mid-October, spraying had increased the dry weight of leaf lamina by 20 per cent. The nitrogen and protein contents per cent of dry matter were both raised, and the yield of protein in the leaf lamina was increased by 30-50 per cent depending on the time of spraying. The total recovery of nitrogen in the whole plant was 80 per cent of that applied in the spray solution. The nitrogen content of the roots was increased by some 16 per cent, but data on the effects on sugar content are not yet available.

Work has been started to develop a method of measuring nutrient uptake by leaves over short periods of time by the use of radio-isotopes.

Potassium deficiency in sugar beet

Previous work has shown that sugar beet are not very sensitive to variation in potassium supply, provided the level of sodium supply is kept high, suggesting that sodium can fulfil some of the functions of potassium in the plant. However, when potassium salts were omitted from nutrient solutions used in sand culture so that the only potassium available was that present in the seed or as impurities in the other salts or in the sand or water, and ample sodium salts were given, growth, especially of the storage root, was greatly reduced though the plants survived for long periods. In these conditions the rate of carbon assimilation was very low, and the plants were very depleted in carbohydrate. It therefore seemed possible that the effect of lack of K on growth in these conditions might be due to carbohydrate deficiency resulting from impairment of the photosynthetic mechanism.

To test this, sugar beet plants grown in sand culture with addition of sodium but no potassium salts were sprayed daily with a 10 per cent solution of sucrose. Though the sugar content of the leaves was increased by spraying, indicating that sucrose was absorbed, there was no appreciable effect on growth. It appears, therefore, that the effect of potassium deficiency on carbohydrate production by photosynthesis does not account for the decreased growth of the plant, but that some other part of the growth process must also be affected.

EFFECT OF WATER POTENTIAL ON GERMINATION AND WATER UPTAKE OF WHEAT SEEDS

The results of Dr. P. C. Owen's work on this problem have now

been prepared for publication (29, 30). As the work has now been discontinued it is appropriate to summarize the conclusions, although some of them have already been given in previous Reports.

Germination

The critical level of water potential necessary to inhibit germination of wheat seeds completely is much lower than was expected. After 15 days, 20 per cent of the seeds germinated at a potential of —320 metres of water or a pF of 4·5, well below Permanent Wilting Point which is generally accepted to be at pF 4·2, or a potential of —160 metres of water. Under very extreme conditions, air drying can produce a soil pF of 6, equivalent to a relative humidity of 50 per cent, but this would not normally occur in the field in a temperate climate except at the surface of the soil. Recent Danish work has shown that the relative humidity in the soil rarely falls as low as 98 per cent, therefore the moisture conditions corresponding to a pF of 4·5 or a R.H. of 97·7 per cent can be considered as extremely dry.

In the soil moisture conditions of any normal seed-bed there appears to be no reason connected with water supply why emergence of the radicle from the seed should not occur eventually, but this does not imply that subsequent growth will always be satisfactory. Low potentials delay germination, and there is evidence that they reduce the viability of the seeds by increasing their susceptibility to fungal and bacterial infection. It follows that failures of crop establishment in the field during drought periods are probably not attributable to inhibition of germination, but may be the result of subsequent failure of the young seedlings to withstand low water potentials or of a high death rate of seedlings due to attack by pathogenic organisms.

Water uptake

At water potentials near to —250 metres of water (R.H. 98 per cent) the uptake of water by wheat seeds from air dryness to equilibrium moisture content can be satisfactorily represented by a curve of form :—

$$y = y' (1 - e^{-at})$$

where y = water content at time t and y' = equilibrium water content. If the initial water content of the seed is y° this becomes :—

$$y' - y = (y' - y^{\circ}) e^{-at} \quad \ldots \qquad \ldots \quad 1$$

After the onset of active growth of the embryo, the subsequent increases in water content over the short times studied may be expressed by :—

$$y - y' = (y' - y^{\circ}) e^{bt} \quad \ldots \qquad \ldots \quad 2$$

At these low water potentials, curves of the form given by equation 1 fitted to the data for living and for dead seeds are nearly identical indicating that water uptake in the initial phase is due to physical rather than physiological causes. The second phase of water uptake, represented by equation 2, is presumably due to water absorption by the embryo as its size increases.

The parameter a in equation 1 represents, or is directly proportional to, the diffusivity of water in the seed, and would therefore

be expected to be independent of water potential. However, as noted in the 1950 Report, curves fitted to the data obtained from seeds held at different water potentials gives values of a that decrease with increase in potential from —250 metres to zero.

Consideration of the results for dead seeds or, more strictly, seeds the germination of which was inhibited by exposure to propylene oxide vapour, suggests that for water potentials near to zero, the simple exponential relation given by equation 1 is inadequate to represent the initial physical phase of water uptake, because the water content did not approach a constant value within the experimental period but continued to increase. It is therefore postulated that for water potentials near to zero, the curve of water content is the sum of two components, (1) a curve of the form given by equation 1, and (2) a curve showing exponential approach to a constant rate of uptake. The water content y and time t can then be expressed by the equation :—

$$y - y^\circ = \frac{A - B}{a} (1 - e^{-at}) + Bt \quad \ldots \quad \ldots \quad 3$$

where A = initial rate of uptake when $t = 0$, B = constant rate of uptake reached when t is large, and a has the same significance as before. Curves constructed on this hypothesis fit the observed values satisfactorily when the same value for the diffusivity a is used over the whole range of water potential tested, and the anomalous variation of a with water potential disappears.

It is suggested that the component (2) of the total uptake curve is attributable to some change within the seed that is initiated at water potentials near to zero, but not at low potentials near to —250 metres, within the duration of the experiments. This change may be the production of sugar by starch hydrolysis, and its failure to develop at low potentials may partly account for the retarded germination observed at low potentials.

BIOLOGY OF WILD OATS

Miss J. M. Thurston's work on wild oats has dealt with the following problems :—

Germination and dormancy

It was previously noted (1950 Report, p. 58) that a higher proportion of wild oats seeds germinated in the first season when they were sown in farmyard manure than in soil. In the second season, this result was reversed ; many fewer seeds germinated in farmyard manure than in soil. Thus, farmyard manure not only tended to break the dormancy of the seeds in the first season, but it also greatly reduced germination in the subsequent season, and the total viability of the seeds. Both these effects may have practical value.

To find out whether viable seeds can be spread in animal excreta, a calf, bedded on peat in a loose-box, was fed 2,000 seeds of *A. ludoviciana* mixed with its food. The manure and peat were collected, spread in trays, and kept moist in a glasshouse. In the first 11 months only seven wild oat seedlings have appeared. This suggests that the risk of spreading wild oats by farmyard manure

applications is small. The material is being kept, as viable but dormant seeds may still remain in it.

In the field experiment started in October, 1950, to give information on seasonal germination and the period of survival of wild oats seeds in the soil, germination in the first season was low, ranging from 3 per cent to 15 per cent for different treatments. There was a differential response of the two species to depth of sowing ; more seeds of *A. fatua* germinated when harrowed in on the surface than when buried 6 in. deep, but for *A. ludoviciana* this result was reversed and the deeper-sown seeds showed the greater germination.

Attempts to work out the temperature relations of germination have been hampered by lack of equipment for providing controlled temperatures within the appropriate range. A series of germination tests of whole spikelets of *A. ludoviciana* was made at fluctuating or fairly constant temperatures between 30°F and 90°F. First and second seeds germinated most readily at steady temperatures between 45°F and 55°F and more slowly at temperatures varying between 50-70°F or 30-70°F. All the first seeds of the spikelets germinated at these temperatures but only about 50 per cent of the second seeds germinated at 45-55°F and about 10 per cent at 50-70°F and 30-70°F. At just above freezing point, 95 per cent of the first seeds, but none of the second seeds, germinated between three and four months from sowing. No seeds germinated at constant temperatures of 30°F, 68°F, 85°F or 90°F or at temperatures fluctuating between 50°F and 90°F. After two months all seeds held at 90°F were dead, but nearly 100 per cent of first seeds held at the other temperatures germinated in three weeks when transferred to the more favourable temperature range of 45-55°F.

Diagnostic value of seed characters

Wild oats seeds received from various parts of England in 1950 (1950 Report, p. 58) varied considerably in appearance and some differed from those occurring at Rothamsted. Twenty-two selections of *A. fatua* and seven of *A. ludoviciana* were therefore sown in pots in spring, so that the plants grown from them in similar conditions could be compared at all stages of development.

In general, plants of *A. fatua* bore seeds similar in husk-colour and hairiness to those from which they were grown. Differences in plant characters were small, and were not closely correlated with seed characters. This throws doubt on the validity of sub-dividing the species *A. fatua* into a number of varieties based only on seed characters.

No morphological difference in the growing plants was found that could be used to distinguish between plants of *A. fatua* and the normal brown-husked type of *A. ludoviciana* before the flowering stage. However, three grey-husked selections of *A. ludoviciana* type differed from all the others in a number of respects, and could easily be picked out from among the randomized pots of the experiment at all stages. They had narrower and more drooping leaves and a greater number of shoots, and the ears emerged later. The later flowering and ripening of this grey-husked type may have some agricultural importance, but the normal season of germination of these seeds in the field is not known, and if it is autumn or winter

the ears may be produced at about the same time as those of later germinating but quicker ripening sorts. However, the late date of collection of two of these selections suggests that in field conditions they ripen later than other wild oats.

Distribution of A. fatua *and* A. ludoviciana *in England and Wales*

A survey of the distribution of wild oats, covering almost the whole of England and Wales, was made possible by the co-operation of the National Agricultural Advisory Service. Officers of the National Agricultural Advisory Service collected nearly 600 samples and a few were received from other observers.

Almost all samples contained *A. fatua*. The range of this species covers all parts of England where wheat and barley are grown, from Berwick in the north, all down the east side between the Pennines and the coast, all the Midlands as far as the eastern borders of Staffordshire, Derbyshire and Shropshire, and all southern England east of Exeter. Wales was reported free of wild oats except for a small area of *A. fatua* in Monmouthshire.

A. ludoviciana has a much more restricted range. It occurred in about 70 samples from an area roughly within 80 miles radius of Oxford, reaching from Somerset in the west to Essex in the east, and from Warwickshire in the north to the Isle of Wight. The highest concentrations of samples were between Faringdon and Oxford, between Leamington and Rugby and on the plain west of the Chilterns from Bedford to Aylesbury.

Information on the soil type, on the density of the infestation and on the agricultural history of the land was supplied with each sample, but this has not yet been analysed.

PHYSIOLOGICAL EFFECTS OF VIRUS INFECTION

In co-operation with the Plant Pathology Department, a pot culture experiment on broccoli was made to investigate the effect of nutrient supply on the symptoms caused by infection with broccoli mosaic and cabbage black ringspot viruses. The results are not yet analysed. It was also intended to measure the effects of infection on growth and yield, but natural spread of infection from outside sources interfered with this.

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