SOME ASPECTS OF PLANT NUTRITION

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The usual starting point for inaugural lectures seems to lie between 350 and 300 B.C. About this time Aristotle argued that since there was no obvious excrement from plants, their food must be absorbed from the soil in a perfectly prepared condition. The plant itself was quite passive and the growth resulting from the absorption of this food was merely a process of crystallisation unaccompanied by any chemical change. His own translated words "As many sayours as there are in the rinds of fruit, so many it is plain prevail also in the earth" summarise the results of his observations and thought on plant nutrition. This view remained unassailed until the end of the sixteenth century and the beginning of the seventeenth century, when the first recorded experiment on plant nutrition was performed by van Helmont. This well-known experiment consisted of growing a willow tree in a pot of soil for five years during which time only water was supplied. The original weight of the cutting was 5 lbs., and 5 years later it weighed 164 lbs., but the soil in the pot had lost only 2 ozs. Thus there was a gain of 159 lbs. by the plant, but only a loss of 2 ozs. by the soil. It was clear that the Aristotelian theory could not be upheld and the only conclusion possible at the time was that the tree made all of its substance from the water supplied. No doubt 80 to 90% of the increase in weight was water, but there still remained 10 to 20% of this increase to be accounted for. Nothing was known of the absorption of carbon dioxide and photosynthesis, so that no other conclusion could be drawn from the results of this experiment. In 1771 Priestley reported that sprigs of mint confined in an atmosphere rich in carbon dioxide (fixed air) produced in the course of several days large quantities of oxygen (dephlogisticated air). Scheele, in 1777, on the other hand, found that germinating seeds produced carbon dioxide (fixed air) when confined in a

certain volume of air. These two opposing observations were not completely reconciled for nearly thirty years, during which time Ingen-Housz. Senebier and de Saussure were investigating the relations between plants and the atmosphere. Ingen-Housz, a Dutch physician, showed in 1779 that green plants were able to purify the air by the liberation of oxygen, only when they were exposed to sunlight. In the shade, or at night, green plants vitiate the air by giving out carbon dioxide in the same manner as animals and non-green plants in light and darkness. Senebier, a Swiss cleric and librarian, came to the same conclusion in 1782, and was bold enough to suggest that the increased weight of the willow tree in van Helmont's experiment came from the fixed air (carbon dioxide). De Saussure, a Geneva intellectual. carried out experiments on the same lines as the two previous workers, but used quantitative methods. He determined the amount of matter taken up and given off by the plants and thereby ascertained what it retained. He showed in 1804 that water and carbon dioxide are fixed by the plant at the same time, that no normal growth and development of plants took place without the uptake of nitrates and mineral matter, that the source of nitrogen to plants was from the soil and not from the air, and lastly, that green plants in the dark respire, that is, they give out carbon dioxide and take in oxygen.

These contributions of de Saussure were, during the next 40 years, sadly neglected. The major contribution in the light of our present knowldge to the problem of plant nutrition was made by Dutrochet, who realised that the capacity for absorption of carbon dioxide on the part of the green plant in the light was directly dependent on the presence of chlorophyll. The general outline of the process of plant nutrition as accepted to-day was known before 1840. But the general acceptance of the view that the food of plants is composed only of carbon dioxide, water and mineral salts, was hindered by those who believed that plants obtained their carbon from the decomposition products of the organic matter or humus in the soil.

Liebig, the father of Agricultural Chemistry, in 1840 attacked the humus theory, and established by means of calculations that humus could not possibly supply all the carbon needed by plants for any length of time, whereas the carbon dioxide of the air was sufficient to support the vegetation of the earth for countless generations. As regards the mineral matter and nitrogen, he claimed that for a soil to remain fertile it was necessary to return, in the form of manure, the mineral constituents and nitrogen that had been removed. Liebig established the essential facts of plant nutrition beyond doubt. But even Liebig, like the plant physiologists he so strongly criticised, made mistakes, for he denied plants any respiratory activity because the process involved the loss of carbon dioxide, and was contradictory to the absorption process he advocated—but then he was a chemist and no plant physiologist.

The outstanding figure of the next fifty years was Julius Sachs, the "Father of Plant Physiology". It was Sachs (1887) who first indicated the significance of the respiratory process in plants. He compared the giving out of carbon dioxide by plants to a burning process accompanied by the liberation of energy. To quote Sachs: "in a word, respiration is the source of the energy from which all phenomena of life derive their vital forces; while assimilation in the organs which contain chlorophyll supplies the materials which are subsequently to be set in motion for the purpose of life. This, expressed generally, is the physiological significance and object of respiration, and it is certainly not too dearly bought by a relatively small loss of substance".

Sachs also provided the first evidence that the formation of a carbohydrate in the green cells is a product of the carbon dioxide and water absorbed, and he visualised a carbohydrate as the percursor of all the carbon-containing compounds in plants. In the light of recent work on photosynthesis, Sach's view was not very different. For the majority of plants the first easily recognised product of photosynthesis is a carbohydrate, but the mechanism involved for the formation of this product can also account for the formation of fats and proteins.

Another contribution which Sachs made to the study of plant nutrition was the development of the technique of growing plants in dilute aqueous solutions of various salts. He concluded that so long as the culture solution contained salts involving the elements nitrogen, sulphur, potassium, phosphorus, calcium, magnesium and iron, a perfectly healthy plant would result. This result was supported by Knop who developed the same technique and came to the same conclusion as Sachs. Thus by the end of the nineteenth century it could be said that the food of plants consisted of carbon dioxide from the air, water and mineral salts containing at least seven essential elements.

It soon became evident that other elements were essential for normal growth and development. With production of very pure chemicals it became possible to prepare culture solutions containing specific quantities of particular elements. Plants grown in such solutions containing only the known seven essential elements were not normal. A search for others followed (see Stiles, 1946). In 1905, Bertrand discovered manganese to be essential for the growth of oats. In 1914 Mazé proved zinc essential for maize. Later still in 1923 Dr. Warrington of Rothamstead found boron necessary for the normal growth of beans. In 1931 Sommer showed that copper in small quantities was important for sunflowers, flax and tomatoes. It was not until 1939 that Aron and Stout of Berkeley, California, found molybdenum necessary for tomatoes. These five elements have been designated the micronutrients or trace elements because they occur in in such small quantities in plants. These results have been confirmed many times by independent workers, and many plants have been shown to require all of them. It is fairly safe to conclude that all plants need a supply of all these elements all the time. Thus of the 90 odd elements composing the universe, only 15 or so are essential for plant growth and development.

The discovery of the essentiality of a particular element stimulated biochemists, physiologists, soil scientists and agriculturalists to undertake investigations into:—(1) The functions of the elements in the plant, (2) the factors affecting the absorption of the element, (3) the availability of the element in the soil, and (4) the effect of fertiliser treatments containing the element. It will be impossible to discuss all these aspects of plant nutrition in connection with all the fifteen essential elements (see Annual Review of Plant Physiology), but by considering manganese it will be possible to get some idea of the problems involved in a study of plant nutrition. Manganese in the plant cells is directly concerned in such essential processes as photosynthesis, protein metabolism, respiration and iron metabolism.

The importance of the photosynthetic process cannot be over-emphasised for it is the sole basis of our food supply and the main factor in supplying both raw materials and the energy of industry. Thus the rôle of manganese or any other element in this complex process is of major importance. It has been calculated that plants over the whole surface of the world manufacture annually by photosynthesis organic matter equivalent to 270,000,000,000 tons of glucose. As regards the rôle of manganese it has been shown by Gerretsen that manganese deficient oat leaves assimilate only 1/3 as much carbon as normal leaves. This estimate was obtained when the chlorophyll content of the normal and deficient leaf samples was the same. Similar results were obtained with a primitive green plant (Ankistroresmus) in 1950. The rate of photosynthesis of these microscopic organisms was quadrupled in $1\frac{1}{2}$ hours on the addition of a minute quantity of manganese sufficient to bring its concentration in the nutrient medium up to 0.5 parts per million.

The formation of the essential compound chlorophyll may be disturbed by the presence of high concentrations of manganese. On the chocolate brown manganiferous soils of the Transvaal, citrus has been reported to suffer from manganese toxicity, the symptoms of which are a yellowing of the leaves. A similar condition has been observed on pineapples in Hawaii. The yellow condition of the leaves indicates that the normal formation of the chlorophyll is disturbed. However, from the practical point of view, there is no real problem since the toxic condition induced by excess manganese can be cured by spraying with iron salts. This indicates that for the normal formation of chlorophyll, iron and manganese must be in balance. In view of this interrelationship, I should like to discuss the results of certain experiments designed to elucidate the interaction of these elements (Twyman, 1951). These involved growing plants in culture solutions containing varying proportions of iron and manganese, and as a result of carrying out a number of these experiments, it was possible to recognise the following four different reactions to the various levels of supply:—

- 1. When both elements were in low supply, very small chlorotic plants were produced (Treatments 1—4, Table 1).
- 2. With adequate or low iron and high manganese supplies, manganese toxicity developed (Treatments 5 and 6, Table 1).
- 3. When manganese was low and iron high, manganese deficiency developed (Treatments 7 and 8, Table 1).
- 4. When manganese and iron were supplied in adequate quantities normal high-yielding plants were obtained (Treatment 9, Table 1).

| | | Concen in me | tration dium | (| Concer in tis | ntration ssues | |
|--------|-----------------|-----------------|-----------------|---------|------------------|-------------------|--------------|
| Treat- | | | | Mean - | | | |
| ment | Description of | Mn | Fe | dry wt. | Mn | Fe | |
| No. | supplies | (p.p.m.)* | (p.p.m.) | (g.) (p | .p.m.) | (p.p.m.) | |
| 1 | Low Mn and Fe | 0.005 | 0.005 | 0.85 | 34 | 203 | Chlorotic |
| 2 | Low Mn and Fe | 0.010 | 0.005 | . 0.40 | 53 | 368 | Chlorotic |
| 3 | Low Mn and Fe | 0.005 | 0.010 | 0.71 | 30 | 191 | Chlorotic |
| 4 | Low Mn and Fe | 0.010 | 0.010 | 0.55 | 54 | 277 | Chlorotic |
| 5 | Adequate | | | | | | |
| | Mn and low Fe | 0.250 | 0.005 | 0.51 | 529 | 255 | Chlorotic |
| 6 | Adequate | | | | | | |
| | Mn and low Fe | 0.250 | 0.010 | 0.70 | 454 | 193 | Chlorotic |
| 7 | Low Mn, high Fe | 0.005 | 3.000 | 4.72 | 8 | 157 | Mn deficient |
| 8 | Low Mn, high Fe | 0.010 | 3.000 | 8.07 | 6 | 138 | Mn deficient |
| 9 | Adequate Mn and | | | | | | |
| | Adequate Fe | 0.050 | 0.500 | 14.12 | 34 | 82 | Normal |
| | | * par | ts per m | illion. | | | |

TABLE 1

In addition to these observations several other points emerged when yield and analytical data were examined. It was noticed for instance, that the yields of normal plants appeared to be governed by the balance between the amounts of iron and manganese in the culture solution. In Table 2 the results of two experiments are shown. It is clear that in 1944 the maximum yield of oat plants (49.8 grm.) was produced when the ratio of iron to manganese was 0.6:1, while in 1947 the highest yield was 16.18 grm., and the corresponding ratio was 12:1. The yield of normal plants therefore appears to be controlled by the balance of iron and manganese in the culture solution, but the value of the ratio may vary according to other factors (temperature, light and humidity), which vary from season to season.

TABLE 2

Oat plants 1944 and 1947. Iron to manganese ratio, in the culture solutions producing normal plants in relation to the dry weight yields in grams

| | | | 1944 | | | |
|-------------|-------|--------|--------|---------|-------|--------|
| Fe/Mn | 0.1:1 | 0.25:1 | 0.60:1 | 1.5 : 1 | 2.0:1 | 12.0:1 |
| Dry wt. (g) | 41.53 | 42.38 | 49.80 | 46.36 | 40.89 | 39.66 |
| | | | 1947 | | | |
| Fe/Mn | | 2.0:1 | 10.0 : | 1 1 | 2.0:1 | 60.0:1 |
| Dry wt. (g) | | 10.07 | 14.12 | 1 | 6.18 | 13.44 |

TABLE 3

Manganese concentrations (p.p.m. dry weight) in the stem and leaf tissues of oat plants (1944) grown with various iron and manganese concentrations in the culture solution.

| In concentration | Fe concentration in medium | | | | |
|------------------|----------------------------|--------|--------|--|--|
| in medium | 0.005 | 0.5 | 3.0 | | |
| p.p.m. | p.p.m. | p.p.m. | p.p.m. | | |
| 0.000 | 0*† | 5* | 4* | | |
| 0.002 | 23† | 7* | 6* | | |
| 0.010 | 37† | 9* | 8* | | |
| 0.250 | 318‡ | 68 | 42 | | |
| 2.000 | 635‡ | 166 | 114 | | |
| 5.000 | 780‡ | 233 | . 135 | | |

* With manganese-deficiency symptoms.

† With iron-deficiency symptoms.

‡ With manganese-toxicity symptoms.

TABLE 4

The mean manganese concentrations in the stem and leaf tissues of lettuce and oat plants supplied with 0.250 p.p.m. manganese and various iron concentrations in the culture solution

| Lett | uce | Oa | ts |
|---------------------|----------------------|------------------|----------------------|
| Fe in the medium | Mn in the tissues | Fe in the medium | Mn in the tissues |
| (p.p.m.) | (p.p.m.) | (p.p.m.) | (p.p.m.) |
| 2.0 | 150 | 0.05 | 444 |
| 10.0 | 97 | 0.50 | 77 |
| 30.0 | 57 | 2.00 | 66 |
| 50.0 | 34 | 25.00 | 56 |

Other points of interest arose from an examination of the analytical data, for instance from Tables 2 and 3 it became apparent that iron suppressed the absorption of manganese thus favouring the development of manganese deficiency. On the other hand, an examination of Tables 5 and 6 shows that the converse was true, manganese retarded the entry of iron but to a lesser extent than iron retarded the entry of manganese. These are some of the results which illustrate the interaction of two essential elements outside and inside the plant. Similar interrelationships exist between other essential elements. From the practical point of view it is clear that balanced inorganic manuring is essential for maximum yields.

TABLE 5

Iron concentrations (p.p.m. dry weight) in the stem and leaf tissues of oat plants (1944) supplied with various iron and manganese concentrations in the culture solution

| Mn concentration | Fe concentration in medium | | | | |
|------------------|----------------------------|----------|----------|--|--|
| in medium | 0.005 | 0.500 | 3.00 | | |
| (p.p.m.) | (p.p.m.) | (p.p.m.) | (p.p.m.) | | |
| 0.000 | 84*† | 150* | 95* | | |
| 0.002 | 76† | 108* | 130* | | |
| 0.010 | 61† | 69* | 82* | | |
| 0.250 | 68† | 77 | 83 | | |
| 2.000 | 65‡ | 92 | 75 | | |
| 5.000 | 70‡ | 130 | 71 | | |

* With manganese-deficiency symptoms.

† With iron-deficiency symptoms.

‡ With manganese-toxicity symptoms.

TABLE 6

| fron c | once | innu | nons (p | .p.m. ur | y weigh | i) in | the stem | i unu | ieuj |
|---------|------|------|---------|-----------|----------|--------|-----------|-------|------|
| tissues | of | oat | plants | (1947) | grown | with | various | iron | and |
| | mai | ngan | ese con | centratio | ns in th | e cult | ure solut | ion | |
| M | | | | E | | +h | | | |

| Mn concentration | | e concentration | | |
|------------------|----------|-----------------|----------|----------|
| in medium | 0.005 | 0.01 | 0.500 | 3.00 |
| (p.p.m.) | (p.p.m.) | (p.p.m.) | (p.p.m.) | (p.p.m.) |
| 0.000 | 146*† | 173*† | 234* | 258* |
| 0.002 | 165† | 112† | 110* | 165* |
| 0.005 | 203† | 191† | 158* | 157* |
| 0.010 | 368† | 277† | 127* | 138* |
| 0.050 | 344† | _ | 82 | 141 |
| 0.250 | 255† | 193 | 91 | 126 |
| | | | | |

* With manganese-deficiency symptoms.

† With iron-deficiency symptoms.

As regards the effect of manganese on the respiration of plants, it was Lundegardh in 1939 who first provided direct evidence that manganese was concerned in this process. He found that the oxygen uptake by wheat roots was increased from 155 to 470% by adding manganese to the culture solution to raise its concentration to nearly 3.0 p.p.m. Since this date several enzyme reactions concerned in the respiratory process in animals and fungi have been found to be activated by manganese. If these enzyme reactions can be retarded or stopped altogether by controlling the manganese supply, is should be possible to obtain information confirming or otherwise the hypotheses put forward to explain the cycle of events believed to take place during respiration in animals and lower plants.

Let us now consider another aspect of the study of plant nutrition; I refer to the ability of the soil to supply an essential element to plants. This problem is not only of academic interest, but has an important practical application in ascertaining the nutrient potential or fertility of a given soil. As far as manganese is concerned no satisfactory method has yet been discovered for extracting the so-called available manganese. Although a great deal is known of the factors influencing the amount of available manganese in the soil, the actual mechanism by which soils supply this element to plants has not vet been elucidated. Acid soils supply an abundance of manganese, sometimes so much as to cause toxicity, while alkaline soils supply very little, often causing the deficiency disease to appear. Well drained and well aerated mineral soils of neutral reaction tend to supply much less manganese than similar soils which are periodically water-logged. The soil organic matter forms unknown complexes with manganese rendering the element unavailable. Thus neutral to alkaline soils containing abundant organic matter are most likely to produce manganese deficient crops. A chemical method of differentiating between manganese deficient and normal soils would be most acceptable.

In connection with the supply of manganese to higher plants we must not forget the influence of micro-organisms. The soil is teeming with bacteria and fungi all of which are probably making demands on the small quantities of manganese present, while others, by a process of oxidation, cause simple soluble salts of manganese to be precipitated as manganese dioxide which cannot be utilised by higher plants. The problem of availability is an intricate one involving the inter-relationships between the soil, plant and micro-organisms, and necessitates the co-operation of chemists, plant physiologists, bacteriologists and mycologists.

We will now consider the more practical aspects of the problem of plant nutrition. It is apparent to us all, as it was to Liebig in 1840, that if the fertility of the soil is to be maintained the nutrients removed by the crop must be replaced by some means or other. It is, however, not always realised how much of the nutrient elements is in fact removed. As an example, it has been found (by Dr. T. D. Hall, Dr. D. Meredith, and R. E. Altona, of African Explosives and Chemical Industries Ltd., S.A.) that a crop of maize yielding 7 bags per morgen (the average yield for the Transvaal in 1946-47) removes 35 lbs. of sulphate 170(NH) So of ammonia, 11.2 lbs. of phosphorus (equivalent to 56 lbs. of superphosphate) and 35 lbs. of potash (equivalent to 75 lbs of potassium sulphate). Thus a total of 301 lbs. of mixed and balanced fertiliser per morgen would replace these nutrients removed. The amounts actually added ranged from 70 lbs. to 241 lbs. with an average of only 123 lbs. of mixed fertiliser per morgen in the Transvaal in 1946/47. However, when one takes into consideration that the average efficiency of nitrogenous and potassic fertilisers is only 50% and that of phosphatic fertilisers only 20%, it is clear that to re-establish the original fertility, the quantities mentioned for sulphate of ammonia and potash can be doubled, and that for the superphosphates multiplied by five. It is clear that even for this small yield of 7 bags per morgen, the fertility of maize lands is being drained away. The target for maize production in South Africa is 20 bags per morgen; to achieve this it would be necessary to supply correspondingly greater quantities of fertiliser. It has been stated (Dr. Meredith, 1953) that for every ton of potassium removed, only 2/3 of a ton is returned, and for every ton of nitrogen removed, barely 500 lbs. are put back. Merely increasing fertiliser applications will not of course solve the problem of maize production, but it is an important aspect of the general problem which also involves the maintenance of soil structure, the conservation of the soil,

crop rotation, green manuring and the genetic constitution of the maize itself. In practice, of course, the level of fertilisation must be ruled by financial considerations, but some means must be found to ensure an adequate profit to the farmer and at the same time to maintain soil fertility.

Fertility is difficult to estimate, but attempts to this end have resulted in the evolution of several methods for diagnosing nutrient deficiencies. The methods available are: (a) Field trials, (b) Soil analysis, (c) Plant analysis, (d) Injection methods, (e) Visual diagnosis. Before considering these methods individually it will be well to have a clear idea of the aim of a method of deficiency diagnosis. What the farmer requires of any method is a forecast of the increase in the value of the total final product which may be expected as a result of certain fertiliser applications. This then must be the ideal aim of any method (see Goodall and Gregory 1947).

The field trial is obviously the best diagnostic method. The yields can be directly related to the amounts of the nutrient elements supplied. Unfortunately field trials are expensive and time-consuming, and because of this more rapid methods have been sought. However, the fact remains that for a particular locality the field trial represents the ultimate test to which the findings of any other diagnostic method must be submitted. Except for nitrogen, phosphorus and potassium, little or no adequate standardised information has accumulated for the other nine essential elements. It is only by the development of these more rapid standardised chemical methods of diagnosis that the results of field trials can be quickly and effectively utilised for ensuring maximum crop production with the minimum of outlay, on arable land in proximity to the trial.

The chemical analysis of a soil involves the extraction of the nutrients from the soil followed by their estimation in the extract. The methods adopted for the extraction of plant nutrients involve the use of dilute solutions of mineral acids, organic acids such as acetic and citric and various salts, which are supposed to imitate the action of the plant roots on the soil. Thus even with the most accurate chemical methods of analysis, the estimate obtained is only an approximation which may or may not represent the amount of nutrient available to the plant. However, methods for potassium and phosphorus have been successfully evolved and accurate forecasts of the yield of some crops (e.g. sugar beet) can be made on the basis of a soil analysis. Thus for these two elements and for some crops and soils the requirements of the ideal method of diagnosis are fufilled. The results of soil analysis for the other plant nutrients either bear no relation to their level of supply and crop yield, or as in the case of calcium and nitrogen, the interpretation is complicated by other factors.

The realisation that solutions of chemical substances are rather poor substitutes for plant roots in extracting nutrients from the soil led some workers to evolve biological means of extraction. One such method which has proved successful for copper, molvbdenum and magnesium has been developed using a common mould. Aspergillus niger, as the test organism. In the case of molybdenum (Nicholas and Fielding, 1950) it has been possible to estimate 0.01μ grm. (i.e. one hundred millionth part of a gram) of this element in a gram of dry soil. By this method it was shown that molvbdenum deficient soils contained 0.01 to 0.03μ grm. of molybdenum while normal soils contained more than 0.5μ grm. molybdenum per gram of air dry soil. The sensitivity of this bio-assay method makes it preferable to chemical methods and they may well be further developed to give precise data relating crop yield to nutrient concentration in the soil, particularly in respect to the trace elements.

The third method of diagnosis is that of plant analysis. Most of the published data compare the concentration of a nutrient in the leaves of normal plants with that in deficient plants (see Table 7).

TABLE 7

Manganese content in parts per million of dry matter of normal plants and those showing deficiency symptoms (from Goodall and Gregory, 1947).

| | | ontent in p.p.m. | |
|------------------|------------------|------------------------|---------------------|
| | Part of | Showing | Normal |
| Name of Plant | plant sampled | Deficiency symptoms | without symptoms |
| Apple | Ieaves | 5.0 | 54.9-124.6 |
| Orange | ,, | 7.0-10.0 | 18.0-20.0 |
| ,, | ,, | 4.4-11.1 | 20.8-29.4 |
| Grapefruit | ,, | 8.8-10.5 | 34.7 |
| Lemon | " | 2.0-4.0 | 14.0-75.0 |
| Oats | plants | 4.8-9.9 | 8.9-56.7 |
| Spinach | " | 51.8 | 56.1-103.0 |
| Tung | leaves | 58.0-81.0 | 638—3110 |

Although data of this kind are valuable for routine advisory work, they fall short of the full requirements of an ideal diagnostic method.

There is evidence, however, that plant analysis can provide more precise information than this. With barley grown in sand culture, Gregory has shown that the nitrogen and phosphorus contents of the seedlings two weeks after germination reflect the concentration of these nutrients in the rooting medium, and it would, therefore, be possible to apply dressings of nitrogen and phosphorus containing fertilisers at this stage if necessary. Further, Crowther, working with cotton under irrigation in Egypt, has shown that the nitrogen content of leaves within the first two months after germination could be used to forecast fairly accurately the crop yield. Lundegardh's experiments with oats have also demonstrated that the nitrogen, phosphorus and potassium contents of these plants can be used to forecast the probable increase in yield of grain expected by the application of certain fertiliser combinations.

Plant analysis, therefore, promises to give the nearest approach to an ideal diagnostic method provided that the necessary standardisation through field trials is performed and the plant organs sampled are of known physiological age and morphological position.

The injection and visual methods are purely qualitative and are used in survey and routine advisory work. The injection method devised by Dr. Roach of the East Malling Research Station (England) involves the presentation of solutions of the essential elements to plant organs in such a way that absorption of the solution occurs. There are various ways of doing this, two of which are (a) by intervenal injections of the leaf, and (b) by leaf stalk injections (Roach and Roberts, 1945). By carrying out trial injections with a dye the areas of the leaves that receive the nutrient element solution above and below the site of the injection can be determined. It is in these areas that a response to a particular nutrient is looked for. A positive response is indicated by an intensification of the green colouration and/or an increase in growth of the injected areas as compared with the uninjected areas. There are a few problems to be solved in order to make injection methods useful to all crops; for instance in 1945 Roach and Roberts wrote of citrus: "No positive response was obtained in any of the few score injections of nutrient carried out during a visit to the Union of South Africa". But during his visit to the Eastern Cape in 1952, quite definite responses to intervenal leaf injections of phosphate, copper and iron were obtained. There is therefore a need to establish beyond doubt the best time and method of injection in citrus, and also to observe whether the responses obtained are related to increased yield of crop when the appropriate nutrients are supplied.

The visual method consists of learning the signs and symptoms of deficiency conditions; this is usually done by growing crops under controlled conditions of nutrient supply in sand culture, and observing whether the same symptoms appear in the field (see Wallace, 1951). This method is of course not quantitative.

So much for some of the immediate fundamental and practical problems in plant nutrition. What of the rather more distant future? I would like you to consider the following statements:—

- 1. By Dr. Milner of the Carnegie Institute of Washington in May, 1952: "It has been said that half of the people in the world now are hungry all of the time".
- 2. Sir William Ogg (1951): "It appears that there are known reserves of rock phosphate which will last at least 1,000 years and probably longer".

The facts are that the present food production is not sufficient to feed adequately the whole world population, but even if this problem was solved by the introduction of modern agriccultural methods into the vastly over-populated backward areas, or by solving the economic problems of agriculture and distribution of food products, the source of supply of at least one of the major plant and animal nutrients is drving up even at the present rate of consumption. It must be remembered that the amount of land utilisable for arable crops is not unlimited, but if all possible land were utilised the rate of consumption of the world reserves of phosphates would be greatly increased. These considerations, together with the fact that the world population is ever increasing, indicate, amongst other more drastic solutions, that some way must be found of growing plants more efficiently, particularly plants synthesising a high proportion of fat and and protein.

Since plants only need a supply of the simple salts of the essential elements, water, carbon dioxide and sunlight to synthesise carbohydrates, fat and protein, a method must be devised to ensure the maximum utilisation of sunlight and the complete absorption and utilisation of the salts. These conditions are best satisfied by growing plants in solution cultures. Experiments in the U.S.A. (Milner, 1951 and 1952) suggest that the most suitable plant is a unicellular, microscopic, freshwater organism called Chlorella. It reproduces itself rapidly in dilute salt solutions and the proportion of the fat and protein can be controlled by varying the amount of potassium nitrate supplied. photosynthetic efficiency can be increased by supplying the culture with air containing 5% carbon dioxide instead of the normal 0.03% in the atmosphere. Pre-pilot experiments on the large scale production of this organism have already been performed using in one case trays (8' x 4' x 8" deep) covered by

transparent tops of plastic material. The culture solution, with an atmosphere of 5% carbon dioxide above it, is rocked to and fro in the tray, and in this way, a successful culture of the alga has been obtained. Many fundamental problems of the physiology of this organism, however, will have to be solved before its large scale culture can be contemplated.

What contribution can the culture of this organism make towards the world food shortage- Greater utilisation of the sun's energy is possible by this method, for by conventional agricultural methods, only 0.1 to 0.5% of the solar energy is utilised by the crop plants, whereas *Chlorella* cultures can achieve a 2.5% efficiency, an increase of 5 to 25 times. The production is calculated at about 40 tons of dry high protein *Chlorella* culture per acre per year. There is therefore a possibility of increasing the production of high protein vegetable matter very efficiently from water, carbon dioxide and mineral salts in any area of the world where there are long periods of continuous sunlight. South Africa may well be one of these places.

A technical achievement that would make this project, as well as many others even more efficient would be the large scale selective removal or sodium chloride from sea water. If this were possible, desalted sea water could be diluted with fresh water to provide the necessary very dilute solution for the growth of *Chlorella*. The supplies of nutrient salts in the sea are almost inexhaustible. A rough estimate of the amount of phosphate in the sea allows one to calculate that at the present rate of consumption of phosphate, 21,000,000 tons per year, the supply in the sea alone would last at least several million years, instead of the few thousand that surface deposits can supply. How many more millions of years then would this last if the efficient factoryfarming of *Chlorella* became adopted?

On this speculative note I will conclude, and hope that I have given you some idea of the interests and work of a crop physiologist.

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