CHAPTER I

INTRODUCTION

EVER since the physiological side of botany began to emerge from obscurity, the question of the relation between the nutrition and the growth of the plant has occupied a foremost position. All kinds of theories, both probable and improbable, have been held as to the way in which plants obtain the various components of their foods. But quite early in the history of the subject it was acknowledged that the soil was the source of the mineral constituents of the plant food, and that the roots were the organs by which they were received into the plant.

A new chapter in the history of science was begun when Liebig in 1840 first discussed the importance of inorganic or mineral substances in plant nutrition. This discussion led to a vast amount of work dealing with the problem of nutrition from many points of view, and the general result has been the sorting out of the elements into three groups, nutritive, indifferent, and toxic. Thus calcium, phosphorus, nitrogen and potassium are classed as nutritive, arsenic, copper and boron as toxic, and many others are regarded as indifferent.

Closer examination, however, shows that this division into three classes is too rigid. Now that experiments are more refined it has become evident that no such simple grouping is possible. It has been found that typical nutrient salts are toxic when they are applied singly to the plant in certain concentrations, the toxic power decreasing and the nutritive function coming into play more fully on the addition of other nutrient salts. For instance, Burlingham found that the typical nutrient magnesium sulphate in concentrations above $m/8192$ ($m =$ molecular weight) is toxic to most seedlings, the degree of toxicity varying with the type of seedling and the conditions under which growth takes place. It will be shown in the following pages that even such a typical poison as boric acid may, in certain cases, prove to be an essential element for the nutrition of the plant. A review of the whole subject leads one to conclude that in general both favourable and unfavourable conditions of nutrition are present side by side, and only when a balance is struck in favour of the good conditions can satisfactory growth take place. As indicated above, experiments have shown that the very substances that are essential for plant food may be, in reality, poisonous in their action, exercising a decidedly depressing or toxic influence on the plant when they are presented singly to the roots. This toxic action of food salts is decreased when they are mixed together, so that the addition of one toxic food solution to another produces a mixture which is less toxic than either of its constituents. Consequently a balanced solution can be made in which the toxic effects of the various foods for a particular plant are reduced to a minimum, enabling optimum growth to take place. Such a mixture of plant foods occurs in the soil, the composition of course varying with the soil.

While the earliest observations set forth the poisonous action of various substances upon plants, it was not long before investigators found that under certain conditions these very substances seemed to exert a beneficial rather than an injurious action. The poisons were therefore said to act as "stimulants" when they were presented to the plant in sufficiently great dilution. This stimulation was noticed with various plants and with several poisons, and a hypothesis was brought forward that attempted to reconcile the new facts with the old conceptions. Any poison, it was suggested, might act as a stimulant, if given in sufficiently small doses. It will be seen in the following pages that this is not universally true, such substances as copper, zinc, and arsenic failing to stimulate certain plants even in the most minute quantities so far tested.

Of recent years investigators in animal physiology have brought into prominence the striking effect of minute quantities of certain substances in animal nutrition, as for example iodine in the thyroid gland (see E. Baumann, 1895). This and other work has rendered it imperative to re-examine the parallel problems in plant physiology.

The words "stimulant" and "stimulation" themselves need more precise definition. As a matter of fact, the "stimulation" noticed by one observer is not necessarily held to be such by another. Stimulation may express itself in various ways—the green weight and the general appearance of the fresh plant may be improved, the dry weight may be increased, the transpiration current may be hastened, entailing increased absorption of water and food substances by the roots, assimilation processes may be encouraged. But these benefits are not of necessity correlated with one another, e.g. a plant treated with a dilute solution of poison may look much healthier and weigh far more in the green state than an untreated plant, whereas the latter may prove the heavier in the dry state. To a market gardener to whom size and appearance is so important, stimulation means an improvement in his cabbages and lettuces in the green state, even though the increased weight is chiefly due to additional water absorbed under the encouragement of the stimu-

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lative agent, whereas to a scientific observer the dry weight may give a more accurate estimate of stimulation in that it expresses more fully an increased activity in the vital functions of the plant whereby the nutritive and assimilative processes have gone on more rapidly, with a consequent increase in the deposition of tissue.

While stimulation expresses itself in the ways detailed above, poisoning action also makes itself visible to the eye. Badly poisoned plants either fail to grow at all or else make very little or weak growth. Even when less badly affected the toxic action is well shown in some cases by the flaccidity of the roots, and in others by the formation of a "strangulation" near the crown of the root, which spreads to the stem, making it into a thin thread, while the leaves usually wither and die. If such plants as peas are able to make any shoot growth at all, the roots show marked signs of the failure of the laterals to emerge. The primary root gets much thickened and then bursts down four sides, owing to the formation and thickening within the short root of a large number of laterals which fail to develop further owing to the influence of the poison. Most curious malformations of the root arise from this response of the plant to adverse conditions of growth and nutrition.

While all the inorganic substances examined in this monograph are toxic in high concentrations, some lead to increased growth in lower concentrations, while others apparently have no effect. In this sense all substances could be classed as toxins, even the nutrients. Thus the old distinction between toxin and nutrient has now lost its sharpness, but it does not lose all its significance. The old "nutrients" had certain definite characters in common, in that they were essential to plant growth, the growth being in a great degree proportional to the supply, a relatively large amount of the nutrients being not only tolerated but necessary. The substances dealt with more particularly in this book have none of these characters. Even those that cause increased growth or that may be essential for nutrition (as boron) are not required in such quantities as potassium, phosphorus, nitrogen, etc., while there is no evidence that growth is proportional to supply. The substances fall into two groups:

(1) Those that apparently become indifferent in high dilutions and never produce any increase in plant growth.

(2) Those that are either essential for growth, or at least cause increased development, when applied in sufficiently small quantities.

The former group may be legitimately regarded as toxins; the latter present more difficulty and even now their function is not settled. It is not clear whether they stimulate the protoplasm or in some way hasten the metabolic processes in the plant, whether they help the roots in their absorbent work, or whether they are simple nutrients needed only in infinitesimal quantities. The two groups, however, cannot sharply be separated from one another. Indeed a substance may be put into one of these classes on the basis of experiments made with one plant alone and into another when a different plant is used, while it is quite conceivable that further experiments with other plants may abolish the division between the two groups altogether. It is even impossible to speak rigidly of toxicity. The addition of the inorganic food salts to solutions of a poison reduces the toxicity of the latter, so that the plant makes good growth in the presence of far more poison than it can withstand in the absence of the nutrients. This masking effect of the inorganic food salts upon the toxicity of inorganic plant poisons is paralleled by a similar action on organic toxic agents. Schreiner and Reed (1908) found that the addition of a second solute to a solution decreases the toxicity of that solution; further the plant itself may exercise a modifying influence upon the toxic agent. Water culture experiments were made upon the toxicity of certain organic compounds, with and without the addition of other inorganic salts. Arbutin, vanillin, and cumarin were definitely toxic and the toxicity decidedly fell off after the addition of sodium nitrate and calcium carbonate, especially with the weaker solutions of the toxins. Rothamsted experiments showed that peas and barley grown in a strong nutrient solution are able to withstand the toxic action of higher concentrations of hydrocyanic acid and various phenols than plants grown in weaker solutions (Brenchley, 1917, 1918), again illustrating the masking effect of inorganic salts on the toxicity of organic compounds.

Another important problem has come to the front with regard to these toxic substances—How do these substances get into the plant? Are they all absorbed if they occur in the soil, or is there any power of discrimination on the part of the root? In other words, do the roots perforce take in everything that is presented to their surfaces, or have they the power of making a selection, absorbing the useful and rejecting the useless and harmful?

Daubeny (1833) described experiments in which various plants, as radish, cabbage, *Vicia faba*, hemp and barley were grown actually on sulphate of strontium or on soils watered with nitrate of strontium. No strontium could be detected in the ash of any of the plants save barley, and then only the merest trace was found. Daubeny concluded that the roots *were* able to reject strontium even when presented in the form of a solution. "Upon the whole, then, I see nothing, so far as experiments have yet gone, to invalidate the conclusion...that the roots of plants do, to a certain extent at least, possess a power of selection, and that the earthy constituents which form the basis of their solid parts are determined as to *quality* by some primary law of nature, although their *amount* may depend upon the more or less abundant supply of the principles presented to them from without." Some years after, in 1862, Daubeny reverted to the idea, stating "I should be inclined to infer that the spongioles of the roots have residing in them some specific power of excluding those constituents of the soil that are abnormal and, therefore, unsuitable to the plant, but that they take up those which are normal in any proportions in which they may chance to present themselves[1]." This, however, was not held to apply to such corrosive substances as copper sulphate. De Saussure had found that *Polygonum persecaria* took up copper sulphate in large quantities, a circumstance which he attributed to the poisonous and corrosive quality of this substance, owing to which the texture of the cells became disorganised and the entrance of the solution into the vegetable texture took place as freely, perhaps, as if the plants had been actually severed asunder[2]. Daubeny concluded that a plant is unable to exclude poisons of a corrosive nature, as this quality of the substance destroys the vitality of the absorbing surface of the roots and thus reduces it to the condition of a simple membrane which by endosmosis absorbs whatever is presented to its external surfaces, so that whenever abnormal substances are taken up by a living plant it is in consequence of some interference with the vital functions of the roots caused in the first instance by the deleterious influence of the agent employed.

In spite of the enormous amount of work that has been done on this subject of toxic action and stimulation, it is yet too early to discuss the matter in any real detail. A voluminous literature has arisen round the subject, and the activity in this direction may be indicated by the fact that since the publication of the first edition of the present volume over two hundred papers have appeared dealing with the effect of manganese

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[1] This idea of a selectivity of the roots has been revived by Colin and Lavison (1910) who found that when peas were grown in the presence of barium, strontium or calcium salts no trace of barium could be found in the stem, strontium only occurred in small quantities, while calcium was present in abundance. They concluded that apparently salts of the two latter alkaline metals could be absorbed by the roots and transferred to the stem and other organs, but that this is not the case with salts of barium. They obtained similar results with other plants, beans, lentils, lupins, maize, wheat, hyacinth. Their proof is not rigid, and exception could be taken to it on chemical grounds.

[2] Vide Daubeny, *Journ. Chem. Soc.* (1862), p. 210.

alone on plant growth. In the present discussion some selection has been made with a view to presenting ascertained facts as succinctly as possible. No attempt has been made to notice all the papers; many have been omitted perforce, as it would have been impossible to deal with the matter within reasonable length otherwise. A full and complete account would have demanded a ponderous treatise. This widespread interest on the part of investigators is fully justified, as the problems under discussion are not only of the highest possible interest to the plant physiologist, but hold out considerable promise for the practical agriculturist.

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CHAPTER II

METHODS OF WORKING

I. DISCUSSION OF METHODS

IN the course of the scattered investigations on plant poisons and stimulants, various experimental methods have been brought into use, but these all fall into the two main categories of water and soil cultures, with the exception of a few sand cultures which hold a kind of intermediate position, combining certain characteristics of each of the main groups.

The conditions of plant life appertaining to soil and water cultures are totally different, so different that it is impossible to assume that a result obtained by one of the experimental methods must of necessity hold good in respect of the other method. A certain similarity does exist, and where parallel investigations have been carried out this becomes evident, but it seems to be more or less individual, the plant, the poison and the cultural conditions each playing a part in determining the matter.

1. *Water cultures.*

This method of cultivation represents the simplest type of experiment. Its great advantage is that the investigator has maximum control over all the experimental conditions. Nutritive salts and toxic substances can be supplied in exact quantities and do not suffer loss or change by interaction with other substances which are beyond control. Any precipitates which may form in the food solution are contained within the culture vessel and may be utilised by the plant. The results are thus most useful as aids in interpreting the meaning of those from the field experiments, the results of the one method frequently dovetailing with those of the other in a remarkable way. The disadvantage of the water culture method is that it is more or less unnatural, as the roots of the plants are grown in a medium quite unlike that which they meet in nature, a liquid medium replacing the solid one, so that the roots have free access to every part of the substratum without meeting any opposition to their spread until the walls of the culture vessel are reached. The conditions of aeration are also different, for while the plant roots meet with gaseous air in the interstices of the soil, in water cultures they are dependent upon the air dissolved in the solution, so that respiration takes place under unusual conditions. It is possible that the poverty of the air supply can be overcome by regular aeration of the solution, resulting in decided improvement in growth, as L. M. Underwood (1913) has shown in experiments on barley in which continued aeration was carried out.

2. *Sand cultures.*

This method has the advantage over water cultures in that the environment of the plant roots is somewhat more natural, but on the other hand the work is cumbersome and costly, while the conditions of nutrition, watering, etc. are less under control than in the water cultures. Sand cultures represent an attempt to combine the advantages of both soil and water cultures, without their respective disadvantages. Generally speaking, perfectly clean sand is used varying in coarseness in different tests, and this is impregnated with nutritive solutions suitable for plant growth. The sand is practically insoluble and sets up no chemical interaction with the nutritive compounds, while it provides a medium for the growth of the plant roots which approximates somewhat to a natural soil. It is probable, however, that a certain amount of adsorption or withdrawal from solution occurs, whereby a certain proportion of the food salts are affiliated, so to speak, to the sand particles and are so held that they are removed from the nutritive solution in the interspaces and are not available for plant food, the nutritive solution being thus weakened. The same remark applies to the poisons that are added, so that the concentration of the toxic substance used in the experiment does not necessarily indicate the concentration in which it is presented to the plant roots. The adsorption in most sands, however, is relatively small, and also the adsorbed material is not permanently removed, but returns to the solution as the concentration of the latter is weakened by the gradual removal of the salts by the plant. On the other hand, undue concentration of the solution is apt to occur by excessive evaporation from the surface, owing to the large size of the sand particles, a condition that does not apply in soil cultures. In practice this disadvantage can be overcome by weighing the pots regularly and adding water to make up the evaporation loss.

3. *Soil cultures in pots.*

In this case the conditions of life are still more natural, as the plant roots find themselves in their normal medium of soil. But the investigator has now less control, as more bacterial and other actions come into play, while the nutrients and poisons supplied may set up interactions with the soil which it is impossible to fathom. This method is useful in the laboratory, as it is more convenient for handling and gives more exact quantitative results than plot experiments. Also the pots can be protected from many of the untoward experiences that are likely to befall the crops in the open field. The conditions are somewhat more artificial, as the root systems are confined and the drainage is not natural, but on the whole the results of pot experiments are a useful complement to those obtained in the field by similar tests.

4. *Field experiments.*

These make a direct appeal to the practical man, but of the scientific methods employed the field experiments are the least under control. The plants are grown under the most natural conditions of cultivation it is possible to obtain, and for that reason much value has been attached to such tests. Certainly, so far as the final practical application is concerned, open field experiments are the only ones which give information of the kind required. But from the scientific point of view one very great drawback exists in the lack of control that the investigator has over the conditions of experiment. The seeds, application of poison, etc. can all be regulated to a nicety, but the constitution of the soil itself and the soil conditions of moisture, temperature and aeration introduce factors which are highly variable. No one can have any idea of the composition of the soil even in a single field, as it may vary, sometimes very considerably, at every step. Further, no one knows the complicated action that may or may not occur in the soil on the addition of extraneous substances such as manures or poisons. Altogether, one is working quite in the dark as to knowledge of what is going on round the plant roots. It is impossible to attribute the results obtained to the direct action of the poison applied. While the influence may be direct, it may also happen that certain chemical and physical interactions of soil and poison occur, and that the action on the plant is secondary and not primary, so that a deleterious or beneficial result is not necessarily due to the action of the toxic or stimulating substance directly on the plant, but it may be an indirect effect induced possibly by an increase or decrease in the available plant food, or to some other physiological factor. Consequently great care is needed in interpreting the results of field experiments without the due consideration of those obtained by other methods.

II. DETAILS OF METHODS

Many details of the sand and soil culture methods have been published by various investigators, e.g. Hiltner gives accounts of sand cultures, while the various publications issued from Rothamsted deal largely with the soil experiments. As this is the case, and as the technique of water culture work has much to do with the success of the experiments, full details of this method only are appended.

The great essential for success in water culture work is *strict attention to detail*. Cleanliness of apparatus and purity of reagents are absolutely indispensable, as the failure of a set of cultures can often be traced to a slight irregularity in one of these two directions. Purity of distilled water is perhaps the greatest essential of all. Plant roots are extraordinarily sensitive to the presence of small traces of deleterious matter in the distilled water, especially when they are grown in the absence of food salts. Ordinary commercial distilled water is generally useless, as the steam frequently passes through tubes and chambers which become incrusted with various impurities, metallic and otherwise, of which slight traces get into the distilled water. Loew (1891) showed that water which contained slight traces of copper, lead or zinc derived from distilling apparatus exercised a toxic influence which was not evident in glass distilled water. This poisonous effect was removed by filtering through carbon dust or flowers of sulphur. Apparently only about the first 25 litres of distilled water were toxic, as in the later distillate the deleterious substance was not evident.

The best water to use is that distilled in a jena glass still, the steam being passed through a jena glass condenser. For work on a large scale, however, it is impossible to get a sufficient supply of such water, while the danger of breakage is very great. Experiments at Rothamsted were made to find a metallic still that would supply pure water. While silver salts are very injurious to plant growth, it was found that water that had been in contact with *pure* metallic silver had no harmful action. Consequently a still was constructed in which the cooling dome and the gutters were made of pure silver without any alloy, so placed that the steam impinged upon the silver dome, condensed into the silver gutter and was carried off by a glass tube into the receptacle. Such water proves perfectly satisfactory and the same silver condensing dome has been in use for fifteen years, having recently been rebuilt with new external parts into an enlarged still. In emergency a new tinned copper still has been employed with good results, but this is somewhat dangerous for general