WARD HARRY MARSHALL

DISEASE IN PLANTS

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Содержание

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PREFACE

It has often been represented to me that the cultivators of plants, among whom are to be included planters and foresters, as well as agriculturists and gardeners of every kind, are more particularly concerned with, and interested in, the maladies themselves of the plants they grow, than in the life-history of the fungi, insects or other organisms to which they are due, or in the physiological processes which are involved; and although it is impossible to really understand any disease unless we also understand the processes by which it is brought about, there is room for sympathy with the point of view of the cultivator. He says, in effect, "I do not want to know all about the biology of the fungus of wheat-rust, or of the *phylloxera*, nor do I want to learn what experts can tell me about the action of bacteria in soil, or the process of starch-formation in the leaves: I have neither the time nor the means to master these details. What I want is guidance as to what is wrong with my tomatoes, apple trees, chrysanthemums, fir trees, turnips, etc., and what I am to do to set things right." Just so. With the latter part of this cry one must sympathize, much as a doctor does with the wail of the parent who calls him in to cure his sick child—we need not stop to classify or compare the motives of the parent and the cultivator, and perhaps I had done better to select a breeder of sheep with his flock and a veterinary doctor in the illustration, but we will let it pass; and as regards the former part of the cry, I do not know that the plant-doctor can expect the cultivator to be initiated in the aetiology of the disease any more than the physician expects the parent to understand the biology of the typhoid bacillus. That both the cultivator and the parent would be the better for a real knowledge of the disease in either case must be admitted—nay insisted on, provided the knowledge *is* real—but we have to deal with facts, and it is a fact that the clients of both doctors are impatient of the details of the case.

Now, of course, I am aware that no short cut or "royal road" to science exists, and if a man is going to train up trees or other plants, he ought to know all about them in health and in sickness, in youth and in old age, and he ought to learn everything about the soil they grow in, the air that surrounds them, the enemies that beset them, and all the multifarious relations of these one to another; but when I look at my boy and reflect how much his nurse, his schoolmaster, his tutor, his doctor, and his parents *ought* to know successively and simultaneously about him in sickness and in health, and about his surroundings, etc., I begin to wonder whether there is not after all something to be said for the cultivator's point of view.

Moreover, the cultivator knows a good deal about his plants which I do not know, and although I should much like to know it, his plea of want of time rings in my ears and the conviction strikes home that one ought to try and meet his views, and tell him something about disease as manifested in plants without insisting on his becoming a professional mycologist, entomologist, agricultural chemist, and philosopher.

Of course, beyond a certain point, it is his lookout how much the information is worth, and its educational value—a very different matter—is sure to suffer from any restrictions imposed on the treatment of the subject; but if the theme of disease in plants, treated from a general point of view—I was about to write "treated in a popular manner," but that is impossible until physiology and mycology are more widely taught—enables him to understand better the questions he puts to himself, and, still more, if it stimulates him to enquire further into the inexhaustible field of science glimpsed at, something may come of it.

The purpose of these essays is to treat the subject of disease in plants with special reference to the patient itself, and to describe the symptoms it exhibits and the course of the malady, with only such references to the agents which induce or cause disease as are necessary to an intelligent understanding of the subject, and of the kind of treatment called for. Consequently I have avoided any unnecessary classification or elaborate descriptions of parasitic fungi or insects, histological details of the tissues of plants, chemical and physical details regarding the soil, and even matters purely physiological as far as possible. Several admirable works on these subjects are already available, and must be referred to for further details.

It is, however, quite out of the question to avoid technicalities, though I have chosen the simpler course wherever it was found feasible, and have tried to so employ the examples selected that the student who wishes to go further into the matters dealt with may turn to special treatises for further information. For one eminently technical section I ought perhaps to apologise, but the temptation to try and set forth, in concrete form and suitable for the purposes of this book, some account of what is known of the most essential and profound factors concerned in the difficult question of the nature of life and death, health and disease, was great. Probably my apology should go further, and apply to what after all must be failure to explore this mystery to the bottom: my only excuse must be that it may stimulate others to go further.

It was an afterthought to add, in Part I., the considerations on the factors which influence the plant regarded as a living machine, so to speak, in order that the student may the better apprehend the point of view taken of the bearings of the matters discussed in Part II.

With regard to references, it seemed a better plan to give, in the form of notes after each chapter, the titles of the principal books and papers on which a student may base a further course of reading, than to overweight the pages of what is, after all, merely an introductory sketch to a huge subject, with detailed quotations from the numerous sources of information made use of. I have freely expressed my own opinions, but the sources for others are, I hope, as freely given. It will, however, be understood that I have not aimed at a complete bibliography, and, particularly, I have only given foreign references where it seemed that adequate treatment of the subject could not be found in English.

My sincere thanks are due to Mr. F. Darwin, F.R.S., who has kindly looked through many of the proofs, and given me the benefit of several suggestions: and to my wife for the very material aid she has afforded me in the preparation of the index.

H. MARSHALL WARD.

Cambridge,
November, 1900.

PART I.
SOME FACTORS

CHAPTER I.
THE PLANT AND ITS SURROUNDINGS

The plant the central object of study—soil, climate, atmosphere, etc., are factors of its environment. Agricultural chemistry. The plant a machine. Physiology.

If I were asked to sum up the most important result of the numerous advances made during the past decade in agriculture and forestry, I should reply—the clearer and wider recognition of the fact that the plant itself is the centre of the subject, and not the soil, climate, season, or other factors of its environment. Until comparatively recent times it was the habit of farmers, foresters, planters, and gardeners, all the world over, to look upon the plant as a mere item or as a mysterious if important one in their calculations, and to regard the soil as the chief factor in their studies.

Now all is changing, and the world is gradually awakening more and more to the recognition of the truth that the soil and the clouds and the atmosphere are merely reservoirs of more or less inert materials, from which the living plant draws its supplies, and works them up, by means of energy focussed from the sun, into new plant substance.

In other words, the more far-seeing pioneers of scientific agriculture and forestry, etc., are recognising that agricultural chemistry is not the be-all and end-all of agricultural science; but that, in place of the study of the chemical analyses of dead soil, water, air, and plant-remains, which has so long held sway, largely owing, I think, to the influence of Liebig, the student should have his attention more concentrated on the living plant itself and on the physiological actions which make up its life. He must regard the living plant as a sort of working machine —infinitely more complex than any machine made by man, but a machine nevertheless—the purpose of which is to store up energy from the sun, and so to add to our wealth on this planet, at the expense of the extra-terrestrial universe.

It is not, be it noted, that the new study proposes to ignore or abandon the old studies: modern physiology owes too much to the physics and chemistry on which it is partly based, and to the labours of De Saussure, Ingenhousz, Priestley, and others, for that. But it is that the new study recognises that the central point, to which all views must be focussed, is not the one that it was formerly supposed to be. The student is still taught that the chemistry of soils yields valuable information, and that lessons of importance are derived from comparisons of the analyses of the ashes, etc., of plants; but he is no longer able to cherish the hope, however remotely, that such studies solve his most important problems.

The scene—or rather the point to which attention is now directed—is the living, working, energy-accumulating plant itself, and not the dead store of materials in the soil. The reason for the change is not far to seek: it is due to the enormous strides made in the study of the physiology of plants during the last quarter of a century, and the subject abounds in examples illustrating the marvellous advances that have been made, and at the same time showing how, in the progress of researches, made for their own sake—*i.e.* in pursuit of satisfaction for the intense curiosity of the scientific man—all kinds of side issues turn up which prove to be of value in practice, and suggestive of further thinking.

At the beginning of the nineteenth century—*i.e.* about 1820—the best thinkers were giving up the old ideas that the environment supplied food, as such, to plants, and had recognised that the plant takes up substances from without and rearranges these in its own body.

The next twenty years or so form a very dark interval in plant physiology, chiefly owing to the influence of the assumption of a special "vital force," an assumption which was not allowed merely to serve as a hypothesis put forward to stimulate research and suggest better ideas, but which gained a hold over men's powers of reasoning to an extent which now appears monstrous and phenomenal.

Many errors crept in during this reign of terror, one of the most fatal of which was De Candolle's revival of the idea of "spongioles"; and another, equally disastrous in many of its effects, was the conception of a sort of vegetable food-extract, humus, existing in the soil in a form peculiarly suitable for direct use by plants. It was during this period that the confusion between the processes of respiration and carbon-dioxide assimilation arose, and exerted its effects for evil into our own day.

The now astounding statement that oxygen-respiration in plants did not occur, laid the foundation of many subsequent difficulties, and so did the positive and authoritative views on the uses of minerals to the plant. Liebig, in fact, stood in the invidious position of being a high authority on purely chemical questions, who was impelled to give opinions on matters which can only be solved by physiological experiments: his great service was to clear up mistakes as regards the chemistry of soils and of plants—his great mistakes were due to his pronouncing on physiological matters; and it may be doubted whether his great services to the purely chemical side of subjects connected with agricultural matters are the more to be admired, or the disastrous influence of his statements on subjects which do not belong to the domain of chemistry should be the more deplored. Be that as it may, he handed on to succeeding generations some weighty errors as regards plant-life, and taught the agriculturist to regard chemical analyses of soils and plant ashes with a reverence which obstructed progress for some time. As a set-off to this we must place his contributions to the destruction of the bugbear vitalism, which was simply preventing enquiry, and his services in bringing together and sifting with power and originality all that had been then acquired as regards the chemistry of the plant, the soil, and the atmosphere.

That Liebig was indispensable in 1840-1850 is one thing; but that his influence should extend to the present day is quite another, and his inevitable mistakes were almost as powerful for future evil, as his clear exposition of the chemistry of his day was productive of immediate good.

Boussingault, working at the same time, 1837-1855, but experimentally with the living plant, taught us more about these matters than any investigator of the time, though it is very probable that the stimulus of Liebig's speculations, good and bad, had its effect in impelling Boussingault to devote his splendid methods to problems of plant-nutrition. Boussingault's contributions to our knowledge of the composition of the dead plant cannot be over-estimated; but he did more than this, because he so clearly apprehended the necessity for asking his questions directly of the living plant, instead of deducing from chemical principles what might be supposed to occur in it; and although future researches showed that even so careful an investigator solved a problem of first importance—viz. the question of the fixation of free nitrogen—the wrong way, it will be found that so far as he did go his conclusions were sound, and well calculated to inspire the confidence with which the world received them. As we are here concerned more especially with the botany of agriculture, however, it is unnecessary to dwell longer on these matters, or on the similar and even more extensive experiments, of world-wide reputation, carried on for so many years, and still being carried on under the liberal auspices of Sir John Lawes, at Rothamsted. Moreover it may be necessary to return to some of these points later on.

Notes to Chapter I

The reader will find a further general account of these matters in Sachs' *Lectures on the Physiology of Plants*, especially Lectures I. and XII., Engl. ed., Oxford, 1887. He may then proceed to Pfeffer's *Physiology of Plants*, Engl. ed., 1899, chapter I., and to the account of the history of the subject in Sachs' *History of Botany*, Oxford, 1890, especially pp. 359-375 and 445-524. References to more special literature will be found in Pfeffer.

CHAPTER II.
THE PLANT AND ITS FOOD

The food of plants—"Vital force"—Other errors—Liebig and Boussingault—The botany of agriculture. The synthesis of carbohydrates—The physiology of plant-nutrition. The persistence of misconceptions.

The year 1860 may be regarded as a landmark of importance in the history of plant physiology, for it was in that year that Sachs discovered that the bringing together of water and carbon-dioxide, in the green chlorophyll-corpuscles of the plant exposed to sunlight, results in the formation of the grains of starch found in these corpuscles.

Previous to this date Dutrochet (1826-37) had introduced the then crude idea of osmosis into physiology; vegetable anatomy had improved, and the modern conceptions of the living cell, protoplasm, nucleus, etc., were slowly looming; sieve-tubes had been discovered, and the proteids and starch in various parts of the plant examined; and the suggestion was abroad, replacing Liebig's idea that plant acids were the first products of carbon-assimilation, that some substance, of a slimy nature, was manufactured in the cells of the leaves and thence distributed as the formative material from which the plant constructed its parts. Davy and Boussingault had even surmised that a carbohydrate might be the first-formed product in assimilation.

There can be little doubt that Sachs' classical proof, by direct physiological observation and experiment, first brought forward the truth of organic synthesis in the plant in a concrete and convincing form.

But it did more than that. It laid the foundation of the modern physiology of plant-nutrition on ground already prepared by De Saussure and the earlier workers; for, in addition to emphasising the truth of organic synthesis—a truth which had been gradually impressing itself on the world for some years—Sachs' discovery showed clearly the real meaning of carbon-assimilation as a process for obtaining combustible food, which the plant then proceeds to make use of.

Many points were rapidly cleared up at once, or if not explained were at least put into a strong light for further enquiry, and plant-nutrition soon ceased to be the mysterious subject for all kinds of wild conjectures that it had hitherto been.

The meaning of thin leaves, with numerous stomata and finely ramified or divided vascular bundles, became more apparent, as also did the significance of the ascending transpiration current; the storage of starch-grains in tubers, medullary rays, roots, seeds, etc., obtained meanings not understood before; the spread of roots in the soil, and the gradually discovered properties of the finer rootlets and of the root-hairs, fitted naturally into their places; and, in short, a thousand facts, otherwise isolated, became collated into an intelligible system, full of suggestions for new work, such as has since gone on and is now being pursued with an activity and success never before realised in the history of science.

As time went on, while the general truth of Sachs' views was confirmed, a number of detailed discoveries were made which seemed to contradict them in certain points. It was found that not all leaves form starch, for some contain sugar or oil; but Holle and Godlewski proved experimentally that this oil may be replaced by starch if the conditions of assimilation are slightly modified. More recently Hébert discovered that the stalks and leaves of grasses contain a peculiar form of gum, which was formerly confounded with starch, a substance not abundant in them. Then came Schimper's discovery of starch-forming corpuscles, which, if supplied with sugar, are able to form starch-grains in the dark, as in tubers, etc., underground; and as subsequent researches have proved that the chlorophyll-corpuscles—which are morphologically the same as the starch-forming corpuscles and can be replaced by them—are also able to form starch-grains from sugar, as proved by the experiments of Boehm, Acton, Meyer, Laurent, Bokorny, Saposchnikoff, and others, it soon became evident that nothing essential needed altering in Sachs' view that starch is the first visible product of carbon-dioxide assimilation, only it became clearer that the starch-grains are built up by the protoplasm from glucose or some similar body, and represent so many packets of reserve materials put by for the present because not required for the immediate needs of the cell.

Boussingault showed, about thirty years ago, that assimilation soon stops in green leaves if cut off from the plant, not because the leaves die, but owing to some "maximum capacity" being attained. Sachs had shown that the starch passes down to other parts of the plant in solution as glucose.

Neither time nor space will permit me to go into the enormous field of research and results opened up by these and similar observations made between 1860-70. It must suffice to say that they led to the discovery and study of the diastatic and other enzymes in the leaves and other green parts of plants, and to a clearer understanding of what was already known of them in seeds, and this knowledge reacted at once on our insight into the processes of transport of reserve materials and constructive materials from one part of the plant to another, matters which will be referred to later on.

It remains to explain Boussingault's difficulty as regards the cessation of assimilation. Recent researches confirm the view that at least three causes are at work to bring about the inhibition of the carbon-assimilation: first, the chlorophyll-corpuscles become filled to excess with starch, which cannot get away because all the passages are full and the products are inhibiting the further action of the enzymes which should dissolve the solid granules; secondly, the leaf being detached from the plant explains why the soluble products cannot get away, for this makes a great difference in the rate of exhaustion of the leaf; and, thirdly, the same fact involves that the leaf can obtain no further supply of salts of potassium, etc., without which elements the processes in question cannot go on.

These and numerous other deeper insights into the process of assimilation, obviously strengthen the force of Sachs' discovery; though it by no means necessarily follows that starch-grains are always the resting form of the products of assimilation, and we now know that such is often not the case: we now have much deeper glimpses into the initial products of carbon-assimilation than Sachs had in 1860, but this enhances rather than detracts from the importance of his splendidly worked-out discovery. Put more generally, we may now say that the process of carbon-dioxide assimilation in green leaves under the influence of light is a process of synthesis—photo-synthesis—resulting in the building up of a carbohydrate such as sugar, inulin or starch from the elements carbon, hydrogen and oxygen.

But it must not be supposed that the importance of Sachs' discovery, and the rapid consequent extensions of our knowledge, did their work forthwith in disabusing men's minds of old and erroneous notions. To say nothing of numerous smaller misconceptions which still held their ground owing to the stupendous ignorance of plant-physiology which prevailed, we find incompetent teachers and text-books were still propagating ideas worthy of ancient times. The confusion between oxygen-respiration and the gas interchanges in carbon-assimilation was by no means eliminated even recently, though it can no longer withstand the deliberate onslaughts now made on it. That the roots take up food as such from the soil, and that that food is directly employed by the plant for its nutrition is even yet implied in daily conversation around us; and although matters have advanced so far that everyone now knows that the substances at the roots must be in solution, ere they can be received into the plant, it sometimes leads to astonishing replies, if we press the question very far as to how the absorption takes place, in an elementary examination of agricultural students. That manures are foods to the plant, that sap circulates, that transpiration is of use to keep the plant cool, and wood is a "porous body," etc., are only a few of the misconceptions still current, in a decade that has found publishers for a work advocating that roots are congealed sap, and that the leaves of plants absorb the moisture and dust of the air, and so provide the plant with food, and for a paper explaining the action of root-hairs as tubes with open pores at their tips. But the gravest misapprehensions current among us are due to the crude ideas as to what a plant really is: this, I take it, is owing to the difficulty of grasping what physiologists mean by organised structure, and leads to regarding the living being either as a mere aggregation of chemical compounds, built up by the ordinary play of chemical forces, as we know them, acting on dead matter, or, as in the days before organic chemistry, as a mysterious entity endowed with "vital force," and with properties not amenable to scientific investigation. The mistaken notions as to the powers of roots to "select" those substances which the plant requires, and to reject useless ones was merely an expression of this belief.

The rock on which all are liable to come to grief—the chemist or physicist who requires all his facts in terms of analyses and proportions by weight, and therefore takes too mechanical a view of the subject, or the man who is not scientifically trained at all, and therefore is more liable to go to the other extreme and regard the plant as a mysterious something which grows and has poetical associations and traditions—is the great fact of organised structure, and it is the recognition of this fact and some of its consequences which has altered the whole position of the subject, and brought the study of the plant into the domain of physiology. The living plant, its structure and organisation, the functions of its mechanism, and its relations to the environment, thus forms a subject apart from that which concerns the chemical composition of the plant and its environment, and this distinction designates, in a word, as it were, the change which has been brought about by modern biology.

A point to be emphasised to the utmost where agricultural students are concerned is that the essential process of feeding is the same in a green plant, a fungus, and an animal; the greatest confusion still exists with regard to this matter, owing to misconceptions as to the real meaning of the functions of the chlorophyll-corpuscles when supplied with carbon-dioxide and water and the energy of the sun's rays. The plant does not feed on carbon-dioxide, any more than it feeds on oxygen—it feeds on the organic material after it has been constructed, and the chlorophyll-function is merely one mode of obtaining supplies of such organic substance.

Notes to Chapter II

In addition to the references in the last chapter, the student should consult Sachs' *Lectures*, XVII.-XIX., and Pfeffer's *Physiology*, pp. 287-329, for the further development of this subject. An excellent résumé, with new facts and points of view, will be found in Dr. Horace Brown's "Address to the Chemical Section," *British Association Reports*, Dover, 1899; and "Chemistry and Physiology of Foliage Leaves" in *Trans. Chem. Soc.*, 1893, p. 604. See also Blackman, "Experimental Researches on Vegetable Assimilation and Respiration," *Phil. Trans.*, 1895; and Parkin, "Formation, etc., of Carbohydrates in Monocotyledons," *Phil. Trans.*, 1899.

CHAPTER III.
THE PLANT A LIVING MACHINE

The plant a machine into which energy and material are taken—Carbon assimilation—Feeding—Accumulation and transformations in the plant. The action of light—The chlorophyll-function.

The relations of the plant to the environment can only be understood by taking into account the results of modern physiological discoveries. These teach us that the living plant is a highly complex machine, the details of its organisation and structure being much more numerous and much more closely correlated at numerous points, than the parts of any other machine known to us.

They also teach us that it is supplied with energy from without, as any other machine; and that when so supplied, and properly working, the living structure or machinery does work, also as other machines. But modern physiology goes further, in that it renders some account of the ways by which the external energy is taken into the plant, and there applied to do work, or stored up for a time in order that it may be used to do work at some future time.

The accumulation of energy thus ensured is associated with corresponding changes of material substance, and the principal means for bringing this about is recognised in the assimilation of carbon-dioxide—photo-synthesis.

In this process energy enters the chlorophyll-corpuscle in the form of the radiant energy of the sun, it is there directed in the mechanism of the protoplasm, so as to do work on the molecules of water and carbon-dioxide which have also been brought into the machinery; this it does, breaking asunder their stable structure into unstable bodies, which then re-combine in different ways to form a carbohydrate, such as starch, and this starch is temporarily stored as grains, while oxygen escapes.

Each starch-grain, therefore, is to be regarded as a packet of matter and of potential energy, as it were, capable of yielding up the latter at any future time, when put under such circumstances that it must do so. Such stores of energy-yielding substance, if I may use the much-abused phrase, form the principal food of the plant—or of an animal, if it steps in and takes them—and we now see that the process of carbon-dioxide assimilation, as it has perhaps unfortunately been called, is not the same thing as the process of feeding, for the *feeding*—*i.e.* the nutrition proper—of the plant does not begin until the *food* has been thus obtained.

We now see what the real position of the plant is, to its environment, whether the latter be living or dead. From our point of view, the plant serves as a centre for bringing together the substances obtainable from the soil, and those derived from the atmosphere, and so focussing and directing the radiant energy of the sun upon these substances, that they are broken up, and some of their constituents synthesised, with absorption of energy, into a body, such as starch, containing more energy than did the original substances taken together or separate. It matters little whether the actual carbohydrate thus synthesised is starch, or sugar or inulin: the point is that energy has been gained from outside and bound up with the acquired material for further use. But modern physiology has carried matters much further than this, and especially in the three following directions.

In the first place, it has shown that much of the energy thus stored from without in the plant is again liberated in the process of oxygen respiration, and expended partly as appreciable heat and partly as driving force for stimulating the machinery of the living plant to further activities.

In the second place, part of it is rearranged with the rearrangement of the molecules with which the energy is bound up, as it were, so that work of various kinds is done *in* the machinery of the plant: I refer to various metabolic and surface-actions resulting from the peculiar mode of presentment of the resulting substances, for instance the production of osmotic pressures in the cell.

And, thirdly, part of the synthesised substance is worked up into higher bodies, by processes which obviously entail the further doing of work on the constituents.

The further pursuit of this theme would evidently carry us beyond the more immediate subject of this book; but I want to make clear that recent researches render it more and more certain that the living plant is a complex piece of co-ordinated machinery which brings together matter and energy from the external universe, and then gets work out of these.

This proposition is the more important because the whole question of the enrichment of our planet with new food, new building materials, and new fuel, to compensate the daily losses, depends on it, and is of course to be referred fundamentally to the acquirement of new supplies of energy from the sun. Enormous activity has been displayed by physiologists, since 1860, in attempting to solve the question, which of the many different rays known to proceed from the sun are absorbed by the chlorophyll-corpuscle, and directed to the performance of the work above referred to.

The names of Draper, Sachs and Pfeffer stand forth prominently as pioneers in this; while those of Lommel, Engelmann, Timiriazeff and Langley have been among the most active in making important contributions to the subject, and in attempting to answer the further questions connected with the mode in which the chlorophyll is concerned in utilising the energy of the solar radiations. The point is one of supreme importance, because it goes on all fours with modern questions as to the rays of light absorbed or dispersed in our atmosphere at different seasons of the year, or in special climatic conditions, to say nothing of its other scientific aspects. Unfortunately, however, we have no satisfactory explanation of the actual rôle played by the chlorophyll substance itself, in spite of much industrious work which has been done in the subject in this country and elsewhere. As regards the rays employed, it was first proved that the most effective belong to the red end of the visible spectrum, and that the effect as measured by the amounts of oxygen given off, and of starch formed in given periods of time, is more or less proportionable to the intensity of the solar light. Then it was established that no monochromatic light is so powerful as the white light from which it was obtained, though the relative numbers expressing the activity in the red and yellow regions may stand to those in the blue as something like 12:1. The latest results place the maximum assimilation in the red-orange, and this coincides with the maximum absorption in the chlorophyll. If we may accept the current views as to the distribution of energy in the spectrum of solar light, which depends on the complete absorption of all the rays by a black body, where they are estimated as heat, we have the interesting result that the agricultural or forest plant is adapted to catch and retain, broadly speaking, just those particular rays which possess most energy.

The probability is increasing that the protoplasmic machinery is the really effective mechanism in the process, and we may figure this machinery as so holding or presenting the molecules of carbon-dioxide and water to the impact of the light-vibrations, that the latter are enabled to undo the molecular structure; the atomic combinations thereby liberated may then be supposed to form a body like formic-aldehyde, which by polymerisation becomes a carbohydrate of the nature of a sugar such as glucose, which the protoplasm then builds up into its substance and subsequently deposits as starch, and stores temporarily in the form of grains or as amorphous material.

This is partly hypothetical, and is largely due to the careful deductions of the chemists, but there are very many facts now to hand which bear out its probability, especially the recent advances in our knowledge of the sugars, and the experimental feeding of leaves and plants deprived of starch with such substances as dextrose, levulose, maltose, and other sugars, as well as glycerine and other bodies which should be convertible into, or yield them, if the theory is true. In this last connection, the careful and extensive experiments of Acton, A. Meyer, Boehm, and Laurent should be mentioned. It would be interesting to enlarge upon Engelmann's beautiful physiological experiments in connection with this subject of absorption of solar energy, where the maximum accumulation of oxygen-loving bacteria at those parts of a green alga which lie in the red-orange of the spectrum, are used as indicators of the maximum oxygen evolution (and therefore of the maximum carbon-dioxide assimilation), but space will not admit of this. For a similar reason I must also pass over the same observer's experiments with plants which assimilate in protoplasm behind a red instead of a green substance, and which absorb chiefly other rays between the yellow and blue, with the remark that they also seem to imply that it is the protoplasmic machinery which turns the energy on to the carbon-dioxide molecule, the coloured screen being secondary in the matter. Recent experiments which show that green plants will not assimilate carbon-dioxide in a light which has passed through a solution of chlorophyll—and therefore left its red rays behind; nor behind a screen of iodine dissolved in carbon-dioxide—which lets no visible rays between the red and blue pass—should be noticed, as showing the importance of the chlorophyll and the special rays referred to, however; and I ought at least to mention Timiriazeff's beautiful proof, published in 1890, that if, on the leaf of a plant left in the dark long enough to render it free of starch, a bright solar spectrum is steadily projected for 3-6 hours, the chlorophyll then removed by alcohol and the decolorised leaf placed in iodine, the image of the spectrum is reproduced by the different intensities of the starch bands, blue with iodine, in the different parts. Here, again, the maximum coloration coincides with the maximum absorption in and near the red.

Microscopic observations and photo-chemical experiments alike convince us that the chlorophyll-corpuscle is itself a complex piece of protoplasmic machinery, working for and with the rest of the plant, and there can be little question as to the greater accuracy of our reasoning on the whole question I am discussing, since Meyer, Schimper, Pringsheim, and others have established the importance of its structural peculiarities.

I must now pass on to consider another aspect of the question of carbon-assimilation.

Notes to Chapter III

In addition to the references in the last chapter, the reader may be referred to Sachs' *Lectures*, XXV., and Pfeffer's *Physiology*, pp. 329-356, where the voluminous literature is given.

CHAPTER IV.
METABOLISM

Quantities of starch formed, and their significance for the plant. The absorption of energy—the conversion of energy in the plant. The plant is a complex machine for concentrating and storing energy and material from without.

Sachs measured the increase in dry weight (due to the carbohydrates formed in the chlorophyll-corpuscles) per square meter of leaf-surface, exposed for a definite period, by drying rapidly at 100° C. equal areas of the leaves concerned, and comparing the weights.

Of course the results are not to be pushed too far, in view of the fact that some of the starch is continually passing away to be utilised, and of the difficulties of comparing the weather, the intensity of light, currents of air, hygroscopic conditions of atmosphere, and other variable factors which influence the matter. For instance, the stomata open and close to different extents according to the conditions of light and moisture, and this affects the whole mechanism of transpiration especially, and therefore the supplies of water and mineral salts. Nevertheless, some interesting and valuable results have been obtained in connection with this important subject.

It was found, for instance, that the foliage of a sun-flower or of a vegetable-marrow may be forming starch at a rate of considerably over a gram per hour in every square meter of leaf-surface exposed on a fine day; while in particularly clear and warm sunny weather Sachs obtained as much as 24 to 25 grams per square meter per diem.

When one reflects that 200 square meters is not an extravagant estimate for the area of leaf-surface exposed on a tree, for a period which even in our latitudes may be considerably over 100 days of, say, ten hours' light, we need no longer wonder at the rapidity with which wood is produced in the stems, and similar estimates (which I have purposely kept lower than the estimates for continental and tropical climates) may suffice to show how quickly potatoes or the ears of corn, etc., may fill up with the starch or other carbohydrates which render them valuable as crops. We want more measurements in these connections, moreover, for there are several ways in which they are of scientific value and practical importance.

It is evident from what has been said that every grain of starch formed represents so much energy, packed away for the moment in the storehouses of the plant; and we know that—quite apart, however, from intermediate transformations of the energy thus stored—this energy reappears in the kinetic state eventually, when the starch is burned off, in presence of oxygen, and transformed into carbon-dioxide and water. It matters not how quickly or how gradually this combustion occurs, or whether it is accomplished by burning in a fire, or by slow and complex stages in respiration or metabolism: the point is that the unit of weight of starch yields so many units of heat when its structure tumbles down to the original components, carbon-dioxide and water.

Clearly, if we know how many units of heat are yielded by the combustion of one gram of starch, we can obtain an estimate of the amount of energy, measured in terms of heat, which the foliage gains and stores up—an estimate which will approach the truth in proportion as our estimate of the total assimilative activity is correct.

A word of warning is necessary here, however, for those best acquainted with physiology recognise that however useful such calculations as the above may be, and undoubtedly are, to give a general idea of the fact that the energy represented is large, it would be a mistake to suppose that such estimates give even an approximate measure of the energy of potential which may be got from the carbohydrate, and still less of the amount of work that may be got from its employment, according to the way it is employed or presented in the plant. To take a single instance only. If the carbohydrate is rapidly burned off to carbon-dioxide and water, very little is got out of it in the way of work—most, if not all, of the energy set free escapes as heat: whereas if the carbohydrate is slowly and gradually oxydised, passing through various stages and giving rise to powerfully osmotic bodies in the process, or if it is built up into protoplasm, or into the structure of a cell-wall, relatively enormous quantities of work may be got out of its surface-energy, and heat may be absorbed. Whence it follows that we cannot measure the power for physiological work of a body by merely obtaining its heat of combustion, any more than we can infer its significance in metabolism from its chemical properties.

The general conclusion that the plant stores large quantities of energy may of course be arrived at by simply estimating the enormous quantities of food-material which we obtain annually from agricultural plants.

Modern physiologists have attempted to proceed further than this, however, in their essays to form an estimate of the relations between the available energy in the solar rays and that used and stored in the plant.

If we reflect on such phenomena as the cool shade of a tree, and the deep gloom of a forest, and on experiments which show that an ordinary leaf certainly lets very little of the radiant energy of the spectrum pass through it, it becomes evident that many of the rays which fall on the leaf are absorbed in some form, and it becomes very probable that much of the solar energy, other than that we term light, is retained in the leaf for other purposes than assimilation—or, at least, no other conclusion seems possible in view of all the facts. Engelmann's researches with purple bacteria are almost conclusive on this point, and we may regard it as extremely probable that the plant makes other uses of rays, perceived by us as heat-rays, as sources of energy. Researches on the influences of temperature on assimilation and other functions point to the same conclusion; and Pfeffer and Rodemann definitely state that heat is converted into work in the osmotic cells. And the study of the absorption bands in the spectrum of the living leaf becomes more intelligible in the light of these conclusions. Moreover, the fact that a plant still carries on processes of metabolism when active transpiration has lowered its temperature below that of the surrounding air—and the plant therefore receives heat from the environment—points to similar conclusions.

The importance of the conclusion is immense, for even if the plant had no other sources of energy than the darker heat rays of the solar spectrum, it is clear that it ought to be able to do work.

The above may suffice for the general establishment of the conclusion that the plant absorbs more radiant energy than it employs solely for assimilation, and emphasises our deduction that it is a machine for storing energy.

The question now arises, how is this relatively enormous gain in energy employed by the plant? Our answer to the question is not complete, but modern discoveries in various directions have supplied clues here and there which enable us to sketch in some degree the kinds of changes that must go on.

Not the least startling result is that, important as carbon-assimilation is as the chief mode of supplying energy, it is not the only means that the plant has of obtaining such from the environment, and it is even possible—not to say probable—that energy from the external universe may be conveyed into the body of the plant in forms quite different from those perceptible to our eyes as light.

In the most recent survey of this domain, it is pointed out that we may distinguish between radiant energy, as not necessarily or obviously connected with ponderable matter, and mechanical energy, which is always connected in some way with material substance. All mechanical performances in the plants depend on transformation of some form of these, evident either as actual energy doing mechanical work, or as energy of potential ready to do work.

In so far as molecular movements are concerned, we have the special form of chemical energy. The evolution of heat, light and electricity by plants are instances of radiant energy, and so on.

Many transformations of energy in the plants are due to non-vital processes—*e.g.* transpiration, warping actions, etc., but we cannot always draw sharp lines between the various cases. Nor can we directly measure the work done in the living machinery; but from the effects of pressures and strains, the lifting of heavy weights, driving of root-tips into soil, osmotic phenomena, etc., it is certain that the values may be very high.

The following classes of processes in living protoplasm and cells may be taken as indicators. First we have transformation of chemical energy, without which continued life is impossible: in many cases—*e.g.* the processes connected with oxygen respiration—these result in the development of heat. Secondly, we have those remarkable manifestations of energy known as osmotic processes, which depend on surface actions, and with which may be associated other surface effects, such as imbibition, secretion, etc., and in connection with which heat may be evolved or absorbed. It is true the substances which exhibit the properties here referred to may be produced, or placed in position, by chemical energy, or they may be absorbed by roots, etc.; but the proximate energy exhibited by them is not derived from chemical energy, and may be out of all proportion to the chemical energy of the substance or substances concerned. Moreover it is significant to note that a highly oxydised body may develop much osmotic energy, as well as a highly combustible one.

It is of the greatest importance to realise the truth that much work can be, and is done in the living plant, by conversions of energy of potential independent of and out of proportion to the chemical energy available by decomposing the substances concerned; even the heat of respiration may be superfluous here, for the plant may absorb heat from without, and convert it into work.

Tensions often arise in the plant, and do work expressed as movements—*e.g.* the springing of elastic Balsam fruits, stamens of *Parietaria*, etc.

Osmotic energy not only results in enormous pressures and tensions, but causes movements by diffusion and diosmosis, and any given osmotic substance which carries this energy with it is not necessarily formed always in the same way in the cell—*e.g.*

glucose may arise from starch, or from carbon-dioxide, or from oil.

Surface-energy is also expressed in the powerful attractions for water exhibited in imbibition, swelling, capillarity, absorption, surface tensions, etc.

Transpiration induces relatively enormous disturbances of equilibrium, and does work in moving water quite independent of chemical energy.

Again, what may be termed excretion-energy, as expressed in the separation of a solid body—*e.g.* a crystal—from a solution, may be for our purposes regarded separately. Any change in the condition of aggregation of a substance in the plant may result in movements and the overcoming of resistances.

It will be evident from this short digression—and this is the point I wish to emphasise—that in the interval between the securing of a grain of starch, representing so much energy won from the external universe, and the reconversion of this grain into its equivalent carbon-dioxide and water, by respiration, resulting in the loss of the above energy as heat, the starch referred to may have undergone numerous transformations in the living machinery of the plant, and have played at various times a rôle in connection with the most various evolutions of energy.

If we try to picture a possible case, we may take the following. A given starch-granule, after being built up in the chlorophyll-corpuscle, is decomposed, and yields part of itself as glucose, which passes down into other parts of the plant in solution. Part of it is merely re-converted into starch, and temporarily stored: another part passes into the arena of oxydation-processes, the sum of which constitute respiration, and may serve for a time in the molecules of an organic acid: yet another part may be converted into a constituent of the cellulose cell-walls; while part may be brought into play in the reconstruction of protoplasm.

In this last connection a discovery made by Schulze about 1878, and followed up later by Pfeffer, Palladin, and others is of importance. Seedlings growing in the dark, or in an atmosphere devoid of carbon-dioxide in the light, become surcharged with nitrogenous bodies known as amides, formed during the breaking down of the proteids in the destructive process preceding and accompanying respiration: if the seedlings are allowed free access to light and carbon-dioxide, however, the amides disappear. The explanation is that they are combined with some of the materials of the carbohydrates, and again built up into the material of the living protoplasm.

Returning to our hypothetical starch-grain—or, rather, its parts—we have some of it retained as starch, in excess, simply because it is not needed at the moment: another portion gives up its energy in respiration, and this does work on the spot, or is lost as heat; or in the body of an organic acid, or its salt, the part in question may do lifting or pressing work by osmosis, or cause diffusion-currents from one cell to another. In the constitution of the cell-wall we may have part of our starch-grain aiding in imbibition or in the establishment of elastic tensions in turgidity:

and, finally, parts may be built up into the living protoplasmic machinery of the plant.

What is true for the starch-grain is also true for any particle of salt, or water, or gas which enters into the metabolism of the living plant, regard being paid to the particular case, and circumstances in each case.

Enough has been said to show that the plant cannot be properly studied merely as the subject of chemical analysis or of physical investigation; you might as well expect to understand a watch by assays of the gold, silver, steel and diamonds of which its parts are made up, or to learn what can be got out of the proper working of a lace machine by analysing the silk put into it, and the fabric which comes out, and by taking the specific gravity of its parts and testing the physical properties of its wheels and levers.

This is not the same thing as denying the value of such knowledge, in the case of either the dead machine or the living plant: it is merely emphasising the supreme importance of the study of the structure and working of the active machinery in both cases.

Nor is it pertinent to remark on the apparent hopelessness of physiology being at present able to explain the seemingly infinite complexity of the living machinery of protoplasm and its activities. The modern locomotive is also a complex affair in its way, but it is profitable to investigate it and to know all one can of its working and possibilities, for obvious reasons: a little reflection will convince us that it is also worth while to investigate that complex machine, the plant—the working organism which alone can really enrich a country. Moreover, we ought to be encouraged by the satisfactory progress now being made, and the splendid practical results which are accruing, rather than dismayed by the prospect of unflagging labour which will be required in the future.

Enough has perhaps been said to establish the general truth that the plant is a complex machine for storing energy and material from outside, and we have seen that modern research has at least gone a long way towards determining how the living machine works.

It is hardly necessary to point out that important practical consequences may result from these phenomena of the accumulation of surplus starch or other carbohydrates in the leaves during the day, and of their disappearance during the night into the lower parts of the plant. For instance, foliage cut for fodder in the morning is far poorer in starch than if cut in the evening, and it would be very instructive to have experiments made on a large scale to test the result of feeding caterpillars or rabbits, for instance, with mulberry, vine, or other leaves in the two conditions.

Again, we now see what complications may arise if a parasitic organism gains access to the stores of carbohydrates in process of accumulation, or attacks and injures the machinery which is building up such materials, etc.

Notes to Chapter IV

The student who desires to pursue this subject further should read Sachs' *Lectures*, XX. and XXV., and Pfeffer's *Physiology*, pp. 442-566, but he will hardly arrive at the best that has been done without consulting Pfeffer's "Studien zur Energetik der Pflanzen" in the *Abhandl. der Math.-Phys. Classe der Kgl. Sachss. Gesellsch. der Wiss.* (Leipzig, 1892), p. 151; and Kassowitz, *Allgemeine Biologie* (Vienna, 1899), Bk. I., pp. 1-127.

CHAPTER V.
ROOTS AND ROOT-HAIRS

Older views as to root-hairs—Root-hairs and their development—Surface—Variations—Conditions for maximum formation—Minute structure—Adhesion to particles of soil—Functions.

On the roots of most plants are to be found delicate, silky-looking, tubular prolongations of some of the superficial cells, known as root-hairs. Malpighi (1687) seems to have been the first to observe them, and he took them for capillary tubes. Grew (1682) seems to have been responsible for the view that the roots act like sponges in taking up water.

Simon (1768) was probably the originator of the idea that these root-hairs were excretory tubules, a view that became very popular at the beginning of this century.

Meyer (1838) was perhaps the first to give a comparative account of them, and he supposed them to be delicate prolongations of the root-surface to facilitate the absorption of water.

The real importance of these organs, however, has only become apparent since Sachs, in 1859, recognised their relations to the particles of soil between which they extend and to which they cling.

In 1883 Schwarz made a very thorough study of their biological character, and in 1887 Molisch gave us new facts as to their physiology. Our knowledge of them has been rendered very much more intimate by the researches of Pfeffer and De Vries on osmotic and plasmolytic phenomena, and they serve as an excellent study of some of the best results of modern physiology.

In the normal case, such as is exemplified by a seedling wheat or bean, the root-hairs arise some distance behind the growing tip of the root, an obvious adaptation which prevents their being rubbed off by the soil, as they would be if developed on parts still actively lengthening. As those behind die off, new ones replace them in front, and so we find a wave of succession of functionally active root-hairs some little distance behind the tip of the root: the same order of events holds for each new rootlet as it emerges from the parent root, and so successive borings in the soil, made by the diverging root-tips, are thoroughly explored by these root-hairs.

Measurements have shown that in various plants the surface of root on 1 mm. of length is increased by the root-hairs in proportions given in the following table:

PLANT.	Area of surface without root-hairs.	Area of root and hairs.	No. of times greater.
Maize,	4.52 sq. mm.	25.13 sq. mm.	5.5
Pea,	4.71 sq. mm.	58.33 sq. mm.	12.4
Scindapsus,	14.02 sq. mm.	261.90 sq. mm.	18.7

—which sufficiently establishes the general proposition that the area of the root-surface is enormously increased by these hairs.

But this does not give us any definite idea of the length of the cylinders of soil explored by these surfaces, until we find that plants such as an ordinary sunflower, hemp, or vegetable-marrow may have roots penetrating into a cubic meter of soil, in all directions, and so closely that probably no volume so large as a cubic centimeter is left unexplored. Clark found by actual measurement that the roots of a large gourd, if put end to end, extended over 25 kilometers, and Nobbe gives 520 meters for the roots of a wheat. Vetches may go nine feet deep, and oats more than three feet. The Sal, a tree of the forests of India, has roots which penetrate to a depth of 50 to 60 feet.

Some rough notion of the lengths, superficies and penetrating capacities of the roots of a large tree may be gathered from the above, but it is doubtful whether we can form any adequate ideas as to the millions of root-hairs which must be developed along the course of these subterranean boring organs.

One of the most striking results of modern enquiry into these matters, is the discovery that the number and superficial area of these root-hairs, on one and the same plant, may vary to a large extent according to the structure, as it were, of the soil, and the degree of moisture it is capable of retaining; or, with the same soil, according to the amount of water which it receives and holds. Correlations have also been observed between the development in length and surface of the rootlets themselves.

The following illustrations will suffice to show this:

Six young wheat-plants in soil kept constantly wet, developed roots the total length of which measured 365 mm. each, on the average, and almost devoid of root-hairs.

Six similar plants in soil only moderately moist, averaged 668 mm., and were well furnished (though not densely covered) with root-hairs.

Six similar plants in soil which would be termed dry, averaged 371 mm., but were densely covered with rich crops of root-hairs.

Further researches have shown that the conditions which rule the development of the root-system and root-hairs in the soil are very complex, and not always easy to trace. The most general statements we can make are the following:

There is an optimum degree of moisture in the soil which promotes the maximum development of root-hairs. If the soil is too wet they are not developed.

These facts are of importance as correlated with the ease or difficulty experienced by the roots in obtaining water, and plants such as our ordinary agricultural plants show this very distinctly.

Although, as shown in the experiments with wheat, the short roots in dry soil were more densely covered with root-hairs than the much longer roots in moderately moist soil, subsequent closer investigation shows that the total quantity and area of root-hairs is less in the former case than in the latter.

The greatest number of root-hairs are developed on roots which are growing at their best: too much moisture may prevent the formation of root-hairs: too little may induce dense growths of root-hairs locally, but the total number is reduced.

Another set of events which exerts influence on the development of root-hairs is the composition of the dilute solution—water containing dissolved salts—which surrounds them in the soil.

Thus, Schwarz found that when similar oat and wheat plants were grown with their roots in solutions of various salts, the results differed as follows:

Oats in a 15 per cent. solution of calcium chloride developed no root-hairs, though they formed in a 5 per cent. solution, and were very numerous in a 0.5 per cent. solution, or in water alone. In a 10 per cent. nutritive solution the plants developed no root-hairs, though they were abundant in a 1 per cent. solution.

Wheat plants with their roots in a 15 per cent. solution of potassium nitrate bore no root-hairs, but they were numerous in a 2 per cent. solution of the same salt.

These are extreme cases, for, although the roots were not killed, they were strongly inhibited in their growth by the more concentrated solutions. However, experiments of this kind at least bring vividly before us what variations are possible, and suggest that similar events on a smaller scale may occur in a soil which yields large quantities of soluble substances, *e.g.* when freshly manured. Obviously these facts have a practical significance as regards kind of soil, drainage, season (*e.g.* drought or wet), etc.

But there are other factors which rule the development of root-hairs, and some experiments by Lesage show that the correlations between the development of root-hairs and roots are probably much more complex than had been suspected; for he finds that if the lateral rootlets of a Bean, in a water culture, are suppressed, the main rootlet develops numerous and very long hairs to compensate the loss in surface, a matter of obvious importance in the discussion of cases where roots have been injured in the soil.

Before proceeding further it is necessary to look a little more closely into the structure of a single hair.

It is a tubular prolongation of a single cell of the external covering of the young root, usually about 1 to 3 mm. in length, and 0.01 to 0.10 mm. in diameter. In special cases the root-hairs of some water plants may reach 5 to 18 mm. in length, but of course I am referring to the ordinary land plants of agriculture and forestry. This tubular prolongation is closed and rounded off at the distal free end, and opens at the proximal end into the cell of which it is a protrusion.

The whole structure is bounded by an extremely delicate and elastic wall of cellulose, which Frank says is of special composition, almost too thin to measure in many cases, but often somewhere near 0.005 to 0.001 mm. in thickness. This thin membrane is remarkably permeable by water, or dilute solutions, as is shown by the rapidity with which a root-hair collapses if exposed to evaporation, or with which dense solutions abstract water from it, or with which solutions may be seen to penetrate it under the microscope.

Overlying the thin cell-wall proper, on the outside, is a thin gelatinous layer, a product of alteration of the outermost lamellæ of the former.

Closely lining the proper cell-wall on the inside, is an extremely thin layer of living protoplasm, and somewhere in this protoplasm is a distinct cell-nucleus.

The interior of the tube is filled with cell-sap, and it is the osmotic pressure of this cell-sap which keeps the whole living instrument tense and rigid, and the thin protoplasmic film close pressed against the cellulose cell-wall.

Nothing whatever can pass into the cell-sap, or out from it, without traversing both the lining of living protoplasm and the cell-wall.

If we gently pull a living root, of wheat, pea, mustard, etc., from a normal soil, we find particles of soil so closely adherent to the root-hairs that they cannot all be washed off without tearing the hairs: the root-hairs establish relations of contact with these particles, so close that they are cemented to the solid surfaces by means of the gelatinous layer already referred to. This peculiarity has the following consequences. In the first place, the enormous holdfast, ensured by the millions of points of adherence, enables the plant to withstand even powerful lever actions from above, and provides fixed points against which the root-tips can work as they drive deeper into the soil. In the second place, the intimate contact of the root-hairs and particles of soil, ensures that the films of water held by surface-action on the soil-particles and root-hairs shall be in continuity with the water saturating the cell-walls of the latter, and therefore with the protoplasm and cell-sap in their interior. The importance of this at periods when the soil is "dry" will be obvious, when we reflect that no soil is ever naturally so dry that surface-films of water are absent from the particles.

The fact that the root-hair contains living protoplasm, enables us to understand to a certain extent the results of the following experiments.

If we have a leafy and healthy plant, with roots, bearing numerous root-hairs, properly established in suitably moist soil in the pot, the roots cease to absorb water if the temperature of the soil falls below a certain minimum, though they recommence to do so if the temperature is raised again: this has nothing to do with the temperature of the upper parts of the plant, or of the air, and the latter may be so high that the plant rapidly droops from loss of water at the leaves, which is not being compensated owing to the inactivity of the roots.

Similarly we may have the air so cold, at a time when the soil is warm enough to keep the root-hairs actively at work, that the plant becomes surcharged with water, which escapes from the leaves like drops of dew. The temperatures necessary to cause these disturbances in the action of the living root-hairs vary for different plants, and even for different varieties of the same species.

Similar arrestation of the functions of the roots may be brought about by removing the oxygen from the soil around the root-hairs, and replacing it by carbon-dioxide, or the vapour of chloroform. If not kept too long in such a condition, the plant recovers rapidly on admitting atmospheric oxygen, which is always present in a normal well-drained soil both as gas in the capillary interspaces, and dissolved in the water on the surfaces of the particles. If the access of oxygen is delayed, however, as often happens in rainy seasons and in wet soils, the root-hairs are killed, and rot sets in. A good instance of this has lately been given by Heinricher in the case of potatoes.

Notes on Chapter V

For the further pursuit of this subject the reader should consult Sachs' *Lectures*, II. and XV.; Sorauer, *A Popular Treatise on the Physiology of Plants*, 1895, chapters II. and IV., and Pfeffer's *Physiology*, pp. 149-163. The principal paper on root-hairs referred to in the text is Schwarz, "Die Wurzelhaare der Pflanzen," in *Unters. aus dem bot. Inst. zu Würzburg*, I. Heft 2, 1883, p. 140, where a very exhaustive account of these organs will be found.

CHAPTER VI.
THE FUNCTIONS OF ROOT-HAIRS

Excretions from root-hairs—Osmotic phenomena—Turgescence—Plasmolysis—Control of the protoplasm in absorption, etc. Selective absorption.

We see then that the root-hairs are the active living instruments in absorbing the water (containing small quantities of dissolved substances) of the soil.

If the living root-hairs are so numerous and so active, however, a natural inference is that they must exert some influence on the composition or arrangement of their environment. All the teachings of modern physiology go to show that such a living cell as I have sketched cannot carry on its life, brief though it be—the root-hairs are active for about four or five days—without forming substances of the nature of excreta, and we should expect some of these to pass out to the soil.

Sachs showed, in 1860, that roots growing in contact with polished marble corrode the surface of the mineral, and Nobbe, in 1876, showed that the roots of seedlings reduce potassium permanganate, a fact which Molisch confirmed in 1887. The latter observer also proved that living root-hairs secrete substances which colour a solution of guaiacum blue, oxidise pyrogallic acid and other organic substances, and rendered it probable that they excrete some substance which inverts cane-sugar, and in some cases even small quantities of a diastatic enzyme.

Molisch also confirmed an old observation, that roots excrete carbon-dioxide; and he and Czapek showed that the root-hairs excrete acids more permanent in their nature than carbonic acid, and published a method for showing this by means of a dilute solution, slightly alkaline, of phenolphthalein.

Molisch declared that the substances secreted by root-hairs may even be observed, dissolved in drops which ooze from the surfaces of the root-hairs.

That these root-excretions, and particularly the acids, may be of service in dissolving and rendering more available various constituents of the soil is an obvious suggestion, and it is borne out by Sachs' discovery of the corrosion of marble, and by Molisch's observation that living roots slowly corrode ivory if continuously kept in contact with it.

But a deeper insight into the physiology of these organs was only possible when the meaning of the phenomena of osmosis had been rendered clearer by the researches of Pfeffer and De Vries in 1877.

De Vries showed that the turgescence of the living cell can be diminished, and even reduced to nothing, by placing the cell in contact with solutions of substances which attract water from the cell-sap: as the turgescence diminishes, the cell contracts, owing to the elasticity of the cell-wall, which was previously distended;

if the abstraction of water continues, the living protoplasmic membrane lining the cell-wall contracts away from the latter. He then proved that no injury need accrue to the cell by this process of plasmolysis, since the turgescence can be restored by washing out the salt with a more dilute solution, or with pure water; and the cell may go on living and even growing as before. These phenomena can only be produced in cells where the protoplasmic lining is intact and alive.

Pfeffer showed that the whole matter depends on the properties of the living protoplasmic membrane, which, so long as it is alive, has the power of governing the entrance or exit of dissolved substances, but is as a rule freely permeable for water. If, then, substances with a powerful attraction for water are formed in the cell cavity, and of such a nature that the protoplasm does not permit their free diffusion to the exterior, they attract water, and hold it fast, and so set up the condition of hydrostatic pressure known as turgescence, the limit of which depends on the attainment of a state of equilibrium between the elastic reaction of the cell-wall and the distending power of the absorbed water. When this limit is reached, water begins to filter back again through the cell-wall. Numerous researches during the last fifteen years have shown that the sap of such a living cell as the root-hair is charged with substances of various degrees of osmotic power; bodies like sugars, amides, vegetable acids and their salts, being formed by the metabolic activity of the protoplasm and accumulated there. Moreover, we now know that the salts of the vegetable acids in particular are effective, and the researches of Warburg and Palladin in 1886 have placed it beyond reasonable doubt that these acids are continually being developed and destroyed in the living cell during normal growth and respiration, and that great variations as to quantity may be brought about by alterations in the conditions of the environment—*e.g.* temperature, oxygen, etc.

If, now, we bring a solution of some salt, such as potassium nitrate, which has a powerful attraction for water, on the outside of the living root-hair, the question whether the water remains in the cell, or passes out of it, merely depends on whether the substances inside or that outside have the most powerful attraction on the water in the sap, since the protoplasm allows water to pass freely.

But the protoplasmic lining may affect the whole matter in another way; for it may allow the dissolved salt, or other substance, in the solution outside or inside the cell to pass through it also, or it may take it up and fix it, or break it up or otherwise alter it.

More recent researches, and especially those of Pfeffer, have shown that these diosmotic properties of the living protoplasm are of the utmost importance in the whole matter of absorption of substances from the soil.

Let us suppose the following case. A root-hair, in full vigour, is allowed to bathe freely in a dilute solution of various substances, such as sugar, potassium nitrate, phosphates, sulphates and carbonates of iron, soda, lime, magnesium and others known by experiment to be harmless to its life.

Now it turns out to be by no means a foregone conclusion that all or any of the substances, even though freely soluble in the water, can pass through the protoplasm into the interior of the cell. Some may be allowed easy access, others may only be permitted to pass in small quantities, and others, again, may be absolutely refused access by the delicate living filter, so long as it is vigorously alive. Nor, as proved by numerous experimental cultures since De Saussure's time, is the entrance of a salt, etc., ruled by its indispensability or otherwise in the economy of the plant. And it is important to notice that only experiment can prove the point and determine which substances are absorbed and which refused by the root-hair.

If we now suppose the protoplasm to give rise to powerfully osmotic substances which accumulate in the sap-vacuole, but which are not permitted free egress through the protoplasm (and the formation of such bodies will occur if the protoplasm is actively respiring), the conditions for absorption of water, with or without any dissolved salts, which the protoplasm allows to traverse it, are set up.

But the above supposed case is realised, as Pfeffer showed in 1886, when he found by a series of beautiful experiments that certain aniline dyes can accumulate in living root-hairs, and other living cells, whereas others cannot pass the living protoplasm. After accumulating for some time, the dye may either remain stored there, or may eventually diffuse out.

Pfeffer made another discovery, of equal importance, namely, that under the influence of dilute organic acids, such as citric acid, the permeability of the living protoplasm may be altered, so that it allows substances to pass which could not otherwise have traversed it. De Vries had also shown that the condition of the protoplasm affects its power of retaining the colouring matter in the sap of the Beet: so long as the protoplasm is alive, the crimson sap is retained, even when the cell is plasmolysed, but immediately it begins to die the colour escapes through it. A similar case exists when the chlorophyll-corpuscles retain their colour in living cells known to be charged with acids: so long as the protoplasm is alive and normally active the green bodies are protected.

These, and numerous other experiments of the same kind, prove that the healthy root-hair is a living instrument for taking up dilute solutions out of the soil, and holding them in the sap-cavity for a time. If killed, by frost for instance, it loses these powers.

The researches of the last ten years have also shown that a time comes when the turgid cell, if an isolated one, and if sufficient supplies of water are present, is so tightly distended that the surplus water begins to diffuse out again under the pressure proper to the hydrostatic conditions set up.

Now we arrive at a very critical point.

When the water, or dilute solution of various substances, begins to exude under pressure from the living root-hair, what is to prevent its escape into the soil? And if it thus diffuses out, where is the object of absorption?

The questions are obviously pertinent, and they may seem the more so in that the cells adjoining the root-hair on its inner side are also turgid, and possess similar properties to those of the root-hairs. To establish a condition of things which shall bring about the inward flow of the absorbed water, one of the three following cases is conceivable. (1) The cells, as we pass radially into the root, have different properties on the wall of the two sides; or (2) they are more and more greedy of water owing to some process of extraction of their water by tissues in the centre of the root; or (3) these successive series of cells possess osmotically more powerful contents at periods coincident with the escape of the water from the now osmotically weaker root-hairs.

A little reflection will show that where we have a group of such cells as the above, all capable of absorbing water and dilute solutions and of becoming turgid, movements of the absorbed water must go on until all the cells are in equilibrium, as regards their osmotic pressures.

Now the living rootlet is just such a system, the various cells of which are in different conditions of osmotic pressure at any given time: some of these cells are old, and their protoplasm is allowing sap to filter out under pressure: others are in the height of their vigour, and their protoplasm extremely impervious to the highly osmotic sap-constituents which it itself is forming actively: others are too young to have attained their full turgescence: while others again are in stages intermediate between the above.

There is another point of importance, however, to explain some peculiarities in the absorption of these dilute solutions of salts, etc., by the root-hairs from the soil, and by cells lying deeper in the plant from these root-hairs.

It is easy to understand that if a root-hair absorbs a given substance—say calcium sulphate, for illustration—and hands it over to other cells unchanged, a time must be supposed to arrive when, the sap of all the cells being equally charged with calcium sulphate, no more could be absorbed: the rate of absorption of this particular substance, and the quantity absorbed, up to the hypothetical point of equilibrium chosen, would then depend simply on the ease with which its molecules traversed the living protoplasmic membrane, and the degree of their solubility in the sap.

But now suppose the following new factor to come in. Suppose that calcium sulphate undergoes decomposition in some one of the internal cells of the system of absorbing cells, or that it is even merely crystallised out in such a cell, or in any other way removed from solution (*e.g.* by deposition in cell-walls). This alters the state of affairs considerably. The separation of the molecules from the sap-solution is itself a cause for the flow of more of the solution to the cell concerned, and such causes of diffusion are very common in the plant.

The importance of this principle consists in that it lies at the base of the whole question of selective absorption, application of manures, and the rotation of crops; and those who are acquainted with the excellent analytical results of De Saussure, Boussingault, Wolff, Trinchinetti, Gödechen, etc., and the water-culture experiments of Sachs, Nobbe, and others, will understand what an illuminating effect on these points was produced by the above generalisation, which we owe especially to Pfeffer's splendid researches into the nature of osmotic phenomena.

It will now be clear, I hope, why we regard the living root-hairs as instruments—as pieces of living machinery—for the active absorption of water, with substances dissolved in it, from the soil; and it will also be evident, I think, that no one can form a proper conception of this matter of absorption, so important in all agricultural questions, unless he pays attention to these biological phenomena. It was hopeless to expect to understand these matters merely in the light of chemical analyses of plants and soils, and one expression of this hopelessness was the belief in the power of roots to select only the substances useful to it. We now know that the expression "selective power of roots" has a totally different meaning from that implied in the minds of the last generation of agriculturalists, and it would be easy to devise experiments, with solutions of different strength, where the plant should be made to take up relatively large quantities of harmless, but useless minerals, etc., and to starve in the midst of plenty of the elements proper to its structure, simply because the former are offered in a form in which they easily traverse the protoplasm of the root-hairs, while the latter are presented in a form unsuitable for absorption. That all these matters are of importance in regard to manuring and choice of soils, etc., needs no emphasising.

These remarks, of course, do not detract from the value of good comparative chemical analyses, when viewed in the light of physiological knowledge, as I need hardly say; but they do, and emphatically so, attack the position that such analyses alone can explain the problems of agriculture.

On the other hand, we must not rest satisfied with the suggestions so far put forward to account for the processes referred to, since it is impossible to overlook the fact that in their present form they merely afford proximate explanations, and are too crudely mechanical for finality.

Notes on Chapter VI

In addition to the works referred to in the last chapter, the student should consult Pfeffer's *Physiology*, pp. 86-149, and pp. 410-441. With reference to water cultures, Sachs' *Lectures*, XVII., may also be consulted. The standard work on ash constituents of plants is Wolff, *Aschen-analysen*, 1871 and 1880, an indispensable book of reference in this connection, though there are others, quoted in Pfeffer, where further literature may also be found.

CHAPTER VII.
THE BIOLOGY OF SOIL

> Soil not a dead matrix—Organic materials—The living organisms of the soil—Their activities—Their numbers and importance. Abandonment of the notion that chemical analysis can explain the problem.

It is customary to regard the soil, between the particles of which the root-hairs of plants are distributed, as if it were merely a dead matrix of smaller or larger pieces of rock, such as sand, gravel, stones, etc., and organic remains, such as bits of wood, leaves, bones, etc., with water and air in their interstices. As matter of fact, however, soil is a much more complex body than was suspected until comparatively recent times.

It is, of course, beyond the scope of this book to go into the different varieties of soils, their structure or arrangement, and the chemical nature of their constituent rocks and the débris mingled with the latter. For the same reason I must pass over the curious properties of soils in relation to the solutions they yield to water in contact, the manner in which they retain some of these solutions and allow others to pass easily, and the remarkable double decompositions which go on in them. Moreover, I must assume as known the chief physical properties of ordinary soils with respect to the phenomena of capillarity, absorption of heat, action of frost, and so forth.

But all ideas as to the nature of soil based merely on the study of its chemistry and physics are misleading, and it is in just the establishment of this truth that modern discoveries in Agricultural and Forest Botany have played so important a part.

From the facts that organic débris is found chiefly at the surface of the earth, and that the smallest particles are held in suspension by the water near the surface, it is comprehensible why such organic remains abound in the upper parts of the soil, where the rootlets with their absorbing root-hairs are also found, because they must have oxygen. The rule is, therefore, that an ordinary soil consists of upper strata, rich in organic materials and in oxygen, and a subsoil, poorer in these substances.

Among these organic materials are countless myriads of living beings, especially fungi and bacteria, which require oxygen and organic materials for their subsistence, and it depends on the open or close, moderately moist or damp, warm or cold nature of the soil, and on some obviously connected factors, how far down these aërobic organisms can thrive. As we go deeper down they become fewer and fewer, and gradually disappear, and (neglecting certain anaërobic bacteria of putrefaction) they are rarely found in marked abundance more than a few inches below the surface soil.

These aërobic fungi and bacteria are the great agents of continued fertility of a soil, and it is they which, living and multiplying in the moist and well-aerated warm interstices of a rich open soil, carry out the useful destruction of organic matter, breaking it up into mineral and gaseous bodies, which are then dissolved in the water bathing the root-hairs or escape into the atmosphere. In this work of destruction they are aided by the oxygen of the air and the solar heat: their own fermentative action is also accompanied by a marked rise of temperature, and the carbon-dioxide and other products of their activity all go to complicate the chemical changes going on in the soil around the roots.

Duclaux has calculated that *Aspergillus niger*, a common mould fungus, can break down organic substances, such as carbohydrates, at such a rate that a metre cube of the fungus would decompose more than 3000 kilogr. of starch in a year, and this may serve as an example giving some idea of the possibilities in soil.

Analyses of waters containing large quantities of organic matter, as they enter such open soils as those referred to, compared with the drainage water after passing through the upper strata, show that the carbonaceous and nitrogenous materials are broken down to more or less completely oxidised simpler compounds, and that the following chief changes result. The ammonia and some other nitrogenous bodies remain behind in the soil, as also do the phosphoric acid and much of the potash; whereas large quantities of nitric and nitrous acids, together with much sulphuric acid, chlorides, and calcium salts pass away in the drainage. These facts are obviously highly important in agriculture.

Experiments on sewage farms have shown also that the upper soil retains most of the bacteria of the sewage. Koch found at Osmont, near Berlin, that whereas the different sewage waters contained numbers so enormous that each cubic centimeter probably held 38,000,000 germs, the different drainage waters held only 87,000 per c.cm.; and the whole process of water-filtration through sandy soils depends on these well-known facts.

Recent experiments in connection with soil-filtration, however, bring out the further facts that the oxidations which organic matters undergo in the soil—and without which they are useless to the higher plants—are enormously enfeebled if the upper layers of soil are sterilised, so as to deprive them of the myriads of aërobic bacteria, fungi and yeasts which they normally contain, and there can no longer be any doubt as to the importance of the biology of the soil in connection with the preparation of materials suitable for absorption in solution by the root-hairs of agricultural and other plants.

The researches of the last ten years have brought to light a long list of forms, comprising yeasts, such as Hansen's *Saccharomyces apiculatus*, fungi and bacteria which live and grow in the soil, finding their water and food supplies in the interstices, and under conditions which we now know to be very diverse. They are usually more numerous, in species and individuals, in cultivated farm and garden soils than in woods, prairies, and untilled lands; but the geological nature of the strata, the closeness and otherwise of the soil, its damp or dry character and its average temperature (which depends on many things besides latitude or altitude) and other factors co-operate to rule their distribution and numbers. The fact that cultivated land is so well supplied with manures, air, etc., is of great importance in relation to their relative abundance there, and it is extremely probable that the use of artificial manures lessens their numbers considerably as compared with land on which stable and other animal manures are employed.

A list of the soil-bacteria which have been isolated and more or less carefully cultivated and examined would comprise about fifty species; but it is certain that, as at present classified and named, many more species are to be discovered in any ordinary soil.

The fungi are apparently even more numerous than the bacteria, and we may rest satisfied for the present with the general statement that the life-actions of the myriads of individuals of these organisms in the soil completely alter the question of soil-water as understood by the last generation of agriculturalists.

But there is another aspect of this question of soil-organisms which has grown in importance of late to such an extent that we are more than ever justified in regarding the biology of soil as far more vital to the interests of the plant than its physical or chemical properties. With many of the fungi in the soil the roots of plants have to compete—just as plant competes with plant—

for water, salts, and other food-materials. The toadstools which are so conspicuous in fields and forests spring from mycelia which ramify in the ground, and are busily breaking down the remains of other organisms, and just such fungi are known to store up relatively large quantities of salts of potassium and phosphorus—the very salts which are so valuable to crops and occur so sparingly in most soils, but which the extensively spread fungus mycelia can gradually accumulate. Some of these fungi, moreover, are more active in their antagonism, and actually attack and pierce the roots as destructive parasites, but I pass these by for the present, as they form the subject for further consideration when we come to the diseases of plants.

It is obvious that the competition of fungi with root-hairs for mineral salts, oxygen, etc., may be at times acute, and it is extremely probable that cases of so-called sterility of soil, where a particular soil is found unsuitable for a crop, may sometimes be due to this over-competition.

The researches of recent years, however, and especially those of Frank, Winogradsky, Hellriegel, and Stahl, have brought to light a series of relationships between certain of these soil-organisms and the higher plants which place the matter of soil-biology in quite new lights.

On the one hand it has been discovered that groups of bacteria are the active agents in bringing about the destruction of organic nitrogenous matter with the formation of ammonia, in oxidising this ammonia to nitrous and to nitric acids, which combine with bases in the soil to form the corresponding salts; while, on the other hand, other forms can decompose the nitrates and reduce them to nitrites, or set free ammonia or even nitrogen from them. Moreover, there are certain species which can fix the free nitrogen of the atmosphere, and start the cycle of up-building of this inert element into the complex higher compounds we term organic. It is impossible to over-estimate the importance of these processes of nitrification and denitrification going on in the soil about the root-hairs of the higher plants.

But, in addition to this circulation of nitrogen in the soil, it turns out that the life-actions of bacteria, and not mere chemical decompositions, are largely responsible for the circulation of carbon, of iron, of sulphur and other elements formed from the decomposition—also by bacterial and fungal agency—of animal and vegetable remains in the soil.

Even more startling are the biological relations in the soil between the absorbing roots of the higher plants and some of these bacteria and fungi, for it has now been established beyond all doubt that certain fungi enter the living roots and there flourish not as mere destructive parasites, but as messmates not only tolerated by the plant, but even indispensable to its welfare. It is probable that nearly half the plants of our fields, moors, and forests entertain such fungi in their root-tissues. The curious, and long-known nodules on the roots of leguminous plants—peas, beans, clover, etc.—are filled with bacteria which enable these plants to avail themselves of the free nitrogen of the air, and so enrich the soil with nitrogenous substances.

The roots of most forest trees, orchids, and plants of the moorlands, meadows and marshes are similarly occupied by fungi, which in some way convey salts—probably especially phosphates and potassium compounds—to the plant in return for the small tax of organic carbon-compounds it exacts from the latter. In some cases at any rate, as Bernard has lately shown, the very existence of the plant depends on its seedling roots obtaining this advantageous attachment and co-operation (symbiosis) of the fungus immediately on germination.

These remarks must suffice to illustrate this part of my subject, and to emphasise the statement that the question whether a given plant can be grown in a given soil, is by no means one of simply the physical and chemical constitution of the latter. The plant will have to run the gauntlet of a long series of vicissitudes brought about by the presence or absence, relative proportions and vigour, and specific nature of the organisms in the soil at its roots, and it is easy to see that many cases of disease may be due to the absence of advantageous bacteria or fungi, or to circumstances which disfavour their life, as well as to the predominance of competing organisms.

It will now be evident that the old points of view must be abandoned, and with them, especially, the widely prevalent notion that chemical analyses of the plant and soil can explain the real problems of agriculture.

It was of course an enormous advance in the science when, thanks to the splendid labours of the chemists, at the end of the last century and the beginning of this, we obtained that preliminary knowledge of the constitution of the air, and of the composition of the water, acids and salts, etc., which plants require for their food-materials and life-processes. Much was gained by De Saussure's establishment of the fact of oxygen respiration, though we now understand by the term something very different from, and much more complex than, what he understood by it, as, also, much had been gained by the previously acquired knowledge of the gas-exchanges in carbon-assimilation: nor must we forget the services of those who proved, by laborious analyses, continued for long periods, what chemical compounds are found in the tissues of plants, and in the soils at their roots and the atmosphere which surrounded them. We must also remember many other contributions which have been furnished, and are still being furnished by the chemist; and I for one hope that his labours will continue to go hand in hand with those of the physiologist.

But, when all due honour is paid to the scientific chemist, it must still be allowed that his problems are different from the real problems of agriculture. To take one set of instances alone. The chemist can analyse a given soil or a given manure, and can even go a long way towards making them, but his analyses do not tell us what conditions are necessary in order that their ingredients may be presented to the roots so as to be absorbed and become built up into the plant. Chemistry told us that carbon was fixed from the air, but physiological experiments determined how this meant the synthesis of certain definite carbohydrates —this, too, in the face of the powerful authority of the chemist Liebig, who supposed that the vegetable acids were the results of the assimilation of carbon. Wolff, De Saussure, and other chemists have done yeoman service in showing that different plants, growing in the same soil, contain different proportions of mineral substances; but it was by means of water-cultures, and other physiological researches, such as those of Pfeffer on osmotic phenomena and of Schwarz and Molisch on root-hairs, that the puzzling question of selective absorption, by means of the living root-hairs, came into the arena of our knowledge.

In every case—and, as already said, I am not undervaluing the work done—the chemist has left us only on the threshold of the real problem. He has stood outside the factory in which the real work we want to know about is being carried on, and has told us of so many tons of this material being carried in at the gates, and of so many tons of that coming out; he has even burnt down the factory, and all its contents and machinery, and has then told us how many tons of the various materials were there at the time; but this is not what we want, valuable as the information is, and still more will be. What we want, and what we expect to obtain, is more information regarding what is done with the materials in the factory: what machinery they are put into, and how they are put in: what stages they go through, and how the stages follow one another: what wear and tear has to be endured, and how we can step in and stop the working of the machine for our own benefit at the best possible time.

Конец ознакомительного фрагмента.