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Presidential Address

Experimental Plant Biology in Pre-Linnean Times.

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On this occasion I propose to devote my address to a subject which has interested me very much during the last 20 years, and which has been much neglected by historians of science. Although my title may suggest a somewhat specialized biological dissertation, I do not intend to enter into technical details, but rather to give a brief general survey which will show that the subject has some historical implications, and that it presents a promising field of study for future investigators.

The growth of an interest in the experimental investigation of natural phenomena in the 17th century has been studied by many historians of science, but few writers have paid attention to the experiments performed with plants during this period. Canon Raven has expressed the view that artists and gardeners played a great part in the Scientific Renaissance, but this opinion has not received universal approbation. It is, however, well founded on ample material which has never been properly studied in relation to its historical background. The experiments performed and the results obtained have generally been regarded as trivial, or as only of horticultural interest, but they show the process by which a knowledge of plant physiology, a difficult branch of science, gradually developed. Some writers, too, seem to have forgotten that a young science may be developed by the labours of a number of relatively obscure persons, and that its growth is not only due to the labours of men of outstanding ability, like Harvey, Newton, Boyle, Hooke and Hales. Many experiments could be made on plants without laboratories or special apparatus, and their importance was often, not so much in the results obtained, as in the pleasure and interest gained from the investigation of the mysteries of Nature. It seems likely that during the 17th century far more experiments were being tried on plants than on other scientific subjects.

From very early times man has relied on plants for his food and drink. They provide fodder for his domesticated animals; trees gave wood for his buildings and furniture, as well as being the main source of his fuel. The beginnings of plant science were in the recognition of those species which were edible and those that were poisonous. Then came the discovery that certain plants had medicinal properties, consequently a closer study of the plant world became necessary so that officinal species could be recognized.

The Greeks placed on record much of what was then known about the characters and properties of the forms with which they were acquainted. Their philosophers pondered over their nature as living objects, and, as such, on their

mode of nutrition. The Romans recorded many of the practical details of the growth of plant crops, while in the Mediaeval period men were content with the fragments of information that had come down to them from ancient times.

With the renaissance of science, intelligent men first turned their attention to the careful study and description of the plants growing around them and in Western Europe. They found that many of them were not identical with the Mediterranean forms described by classical authors, and that a large number of other forms could be recognized. Later they tried to test by experiment the views of the classical authors on plant nutrition.

It is not easy to obtain any knowledge of the vital processes which go on in the plant body, this cannot be got by direct observation and can only be deduced from the results of experiments. The Greeks, having recognized that plants were living things, speculated about the food necessary for their growth and compared them with animals. Aristotle taught that plants receive their food in an elaborated form from the earth. Having no intelligence they were unable to distinguish between wholesome and unwholesome food, but by means of water they obtained perfectly prepared nutrition from the earth, and this went directly to the building up of their bodies.

Jung, a native of Lubeck, and a contemporary of Galileo, Kepler and Descartes, is said by Sachs to have been the first to question Aristotle's dicta, but he does not seem to have made any experimental study of the matter. Van Helmont, in the early years of the 17th century attempted a test experiment. He completely dried a quantity of soil and weighed out 200 lb., which he placed in a pot. In this he planted a young willow shoot weighing 5 lb., covered the soil to prevent the addition of dust, and watered it daily with rain water. After five years the willow had increased in weight by 164 lb., but when the soil was dried once more, its weight had only decreased by 2 oz. From this he concluded that all the material used in the growth of the plant had come from the water.

Boyle in the *Sceptical Chemist* described similar experiments on the growth of pumpkins. He was very careful to get his soil quite dry, and in one experiment it showed no loss in weight, but in a second it had lost $1\frac{1}{2}$ lb. probably due to some accident. He also found the Spear Mint could be grown in water, and that it put out new roots and leaves in water cultures.

These experiments are of interest since they were attempts to investigate the classical views of plant nutrition. But most of the early plant biologists seem to have ignored the ideas of the ancient philosophers and their descriptions of plant life and growth in the terms of scholastic philosophy. There was at work a much stronger influence than the desire to test ancient doctrines, and which encouraged experimentation in several branches of plant physiology. This was the practice of horticulture.

The 17th century saw the spread of a great interest in the laying out of flower and kitchen gardens, the planting of orchards and trees. Although at this time some horticultural practice, largely based on the Latin authors, was doubtless established, yet much of the work of growing plants in England was experimental to a considerable extent. Experiments of a simple kind were necessary to find out what plants could be grown in our climate, to discover whether they were best propagated by seeds or by vegetative means, to determine how much water they needed in summer and what protection was necessary in winter. The establishment of orchards needed grafting and budding, involving the careful manipulation of the scion and stock: unless these operations were skillfully carried out failure would result. It is clear from the early parts of the *Philosophical Transactions* that there was much uncertainty about the treatment that should be given to many cultivated plants.

The extent of the popular interest in these matters, and in the application of new knowledge to agriculture is shown by the books on horticultural topics which were produced during the 17th and early years of the 18th centuries. My incomplete bibliography shows that 80 books by 43 authors were published between 1593 and 1735, several of these works went through a number of editions. A number of them specify in their titles or sub-titles that they give information about new experiments or new improvements. If they were all examined in detail we should learn a good deal about the way in which an elementary knowledge of some aspects of plant physiology was built up. Doubtless many of the experiments described were crude and some were probably fictitious. With our present knowledge, still far from complete, we may be inclined to regard some of the work described as so simple or so inconclusive as to be unworthy of notice. But these simple observations of the effects of environmental conditions on plant growth were a necessary preliminary to the more elaborate, exact and decisive experiments that were made later. When a branch of scientific enquiry is young it is not clear where investigation may most effectively be pursued; much effort may be expended on matters which later are seen to be of little importance; observations may be made or problems envisaged which are not followed up, though they might have led to important results. It is easy for us with our superior knowledge to see what should have been done, but the men of the 17th century had a background of ideas very different from ours. These considerations are often neglected by the historians of Botany.

Among those who appear to have carried out experiments on plants in the 17th century, Francis Bacon must first be mentioned. His posthumous *Sylva Sylvarum* contains two chapters devoted to experiments on plants in which many results are briefly described and other experiments suggested. This work is commonly derided, and is scarcely mentioned by the historians of botany, but, taken as a whole, his experiments gave some idea of plant physiology, especially from the point of view of the practical horticulturalist. It may be mentioned that Bacon was probably the first person to conceive of the possibility that plants might take in air and convert it into a dense substance. In one of his experiments on plant nutrition he took up a standard rose tree and kept it with its roots in a pan of water in a chamber without a fire for some time. He found that its growth continued and that new leaves were produced from the buds; but he also noticed that these leaves were paler in colour than the leaves of the same plant when grown outside.

Sylva Sylvarum was reprinted several times and probably became widely known since some later investigators refer to Bacon's experiments, and a number of them were repeated towards the close of the century.

Robert Sharrock, Fellow of New College, Oxford, produced a little book about 1660 called *The history of the propagation and improvement of vegetables by the concurrence of art and nature*. Its second edition, published at Oxford in 1672, was dedicated to Robert Boyle. The preface commences with a quotation from Bacon, and among the experiments subsequently described is one which Bacon suggested. This book is noteworthy as containing a description of the first known experiment on phototropism, the growth of stems towards a source of light. He had placed a pot containing seedlings at a window, probably one that was never cleaned, from which one quarry was missing and he found that the seedlings all grew towards the hole till they were almost horizontal. On turning the pot round and replacing it at the window the direction of growth changed, growth being always towards the hole. This growth curvature was attributed to the fresh, cool air which the plant received from outside. Following up

Bacon's experiment with the rose tree, Sharrock grew plants from seed in what he described as a close room, and he found that their stalks and leaves were white or pale green in colour. He compared this with the change in colour of grass when covered with any weighty body. He attributed these changes in colour to the lack of fresh air and does not appear to have thought that they might be due to lack of illumination, which is the real cause. He also carried out an experiment, suggested by Bacon, of weighing onions, sedums, and other plants and then hanging them up in the air; they grew well but always lost weight.

Sharrock's work, some of which was carried out in 1658, is an indication of the experimental outlook on the study of plants at the time when the Royal Society was founded. But there were still some who retained the Scholastic approach. Sir Kinelm Digby gave a discourse in 1660, at a meeting of the 'Society for promoting Philosophical Knowledge by Experiments', concerning "The vegetation of plants". This was printed in the following year; it makes interesting reading though almost completely devoid of any reference to experiments. It might well have been written some 200 years earlier. Thus he says, "As to the bean, although the swelling and bursting forth of the fiery and viscosse parts of it be towards all sides, according to the Nature of fire which streameth out from the centre every way to the circumference, yet it will be efficacious upwards towards the Aire, because it meeteth less resistance that way than any other". He concludes, "Upwards then, and towards the Air must be the speediest and greatest concourse of these hot and viscosse streams which coming into the Air, contract themselves into a circular stalk." Later there is a wonderful description of the results of freezing a decoction made from the ashes of calcined nettles. In the ice there appeared an abundance of nettles, only they were white and not green, and they disappeared when the ice melted.

It is clear from the histories of the Royal Society by Spratt and by Birch that the experimental study of plants occupied the minds of the early Fellows very considerably, and that several of the more influential and active men took part in formulating proposals for experiments, and in the discussion of results. Spratt in describing the activities of the Fellows says "they have composed *Queries and Directions* what things are needful to be observed in the production, growth, advancing, or transforming of vegetables. Later in dealing with experiments, he says "the fifth kind is of the growth of vegetables in several kinds of water; of hindering the growth of seed corn in the earth by extracting the air, furthering their growth by admitting it; of steeping seeds of several kinds; of inverting the positions of roots and plants set in the ground; to find out whether there are valves in the pores of the wood that only open one way; of the decrease of the weight of plants growing in the air; of the growing of some branches of Rosemary by only sprinkling the leaves with water; . . . ; of the reunion of the bark of trees after it had been separated from the body". From Birch and the *Philosophical Transactions* we find that these experiments were carried out by Boyle, Merrett, Goddard, Pell, Moray, Blount and Hooke. At a meeting in 1665, Wilkins moved that a committee might be appointed to draw up a list of experiments about vegetation, etc. to be distributed for making experiments. It was ordered that Mr Howard, Mr Evelyn, Dr Wilkins and Col. Blount constitute this committee. At the following meeting Mr Daniel Coxe produced, at the request of the Society, his "Inquiries touching Vegetation". These were 74 questions concerning plant growth on which information or further evidence was required. When we examine these questions we must remember that the formulation of experiments, or the

choice of subjects for investigation, arises mainly from previous knowledge or existing theory. Coxe's questions were mainly based on the problems and observation of those who grew plants in their gardens, but they include some of the fundamental problems of plant growth. He begins by saying that the nature of the ground, as a matrix wherein plants are conceived and whence they draw their nourishment, must be understood. Later he asks, "If the whiteness of most roots arises from their being secluded from the air", noting that the covered leaves of cabbage and lettuces are white. Another question was whether plants can be raised in water, and what substances these plants afford, exposed to chemical analysis. Other problems related to the perplexing variation in plants of the same kind grown from seeds, both in the rate of growth of the seedlings and in the colours of the flowers. A few of the questions related to current problems, now known to be without foundation, such as the relation of plant growth to the phases of the moon, and spontaneous generation.

In the *Philosophical Transactions* for 1668 there was published "Queries concerning Vegetation, especially the motion of the Juyces of Vegetables, communicated by some curious persons", perhaps the results of the deliberations of the committee appointed three years earlier. These relate to polarity, the ascent of sap, bleeding of trees, the role of roots, together with many questions relating to the culture and use of the plants of kitchen gardens. They show the strong influence of the idea that the physiology of plants might be closely similar to that of animals, and that the circulation of the blood had a parallel in the supposed circulation of the sap. Experimental work on this subject may well have been in progress at the time, for three months later answers to some of the questions, communicated by Dr Beale and by Dr Tongue, were printed. These two men produced additional answers in the *Transactions* during the next few years. In 1669 there was a paper by John Ray and Mr Willugby giving the results of experiments by the latter in the Spring of that year on the bleeding of trees and the ascent of sap*. These distinguished naturalists made some ingenious experiments, contributing to knowledge, but the problem was an exceedingly difficult one, which even now is not completely elucidated. Bleeding was found to show a periodicity which varied with different species. Different experimenters, working with different trees at different times of the year, obtained discordant results, the discussion of which is recorded in the *Transactions*.

In the same publication we find the records of other experiments, the first being by Christopher Merrett. He was evidently trying to find out how similar plants were to animals, and in 1667 published a paper recording how he had cut a strip of bark on an apple tree, presumably not severing it above, and then replaced it and bound it in place. During the growing period of the year the strip became reunited, but this did not take place in the winter. However, when a branch was cut through and replaced, it withered within three days. The same paper records the results of keeping a plant of an Agave (or Aloe) hung up in a kitchen and weighed periodically. It grew for five years, producing two new leaves each year, and steadily losing weight.

Martin Lister communicated to the *Transactions* the results of his experiments on the bleeding of trees in which he discovered the relations between bleeding and temperature. He added much confusion to the problem by regarding the exudation of latex from certain plants as a form of bleeding; it has actually nothing to do with the normal ascent of sap. He made some experiments on the physical nature of latex, obtaining evidence of differences in its constitution in different species.

* It would appear from the *Historia Plantarum* that Ray also made experiments on other subjects.

In 1687 there was an account, communicated by Hooke, of the experiments made from 1671–1686 by a certain Thomas Brotherton on taking off a ring of bark from the stems of the crab and fir. These anticipated some of the work of Stephen Hales. Brotherton showed that the sap ascends in the wood of the tree and not in the bark, as had sometimes been supposed. He made a very interesting experiment by leaving a bridge of uncut bark across the ring, and found that this allowed normal growth to continue above and below the ring, moreover the bark grew again and covered the exposed wood. Hooke added at the end of the paper conclusions which seem to have been his own, viz. : that increase in the girth of a tree is by the descent of the sap ; that sap circulates through all the summer season (not merely in the spring, as some thought) ; that plants are nourished by a double food, one part being impregnated water. the other impregnated air. I may say that each of Hooke's conclusions is substantially correct.

About this same time Nehemiah Grew was communicating to the Royal Society the results of his researches on the anatomy of plants. His collected papers were republished in a finely illustrated book in 1682, which is of outstanding importance in the history of botany. He had much to say about the physiology of plants, but like many others after him, his ideas were deduced from the structural features he observed rather than from the results of experiments. As might be expected, many of these ideas were incorrect. He does, however, mention briefly a few experiments, including one showing the curvatures of root and shoot on a bean plant grown in an inverted position. I believe that this was the first published demonstration of geotropic curvature. Grew's major experimental work lay in what we may call the field of plant biochemistry. At the end of his book on the anatomy of plants there are printed seven lectures given to the Royal Society, the result of great experimental activity. These lectures have been rather neglected by botanists, though I have no doubt that they are well known to some historians of chemistry. In his first lecture on the nature, causes and power of mixture, he states his theory of atoms, the simplest of bodies. The experiments in the second lecture include the trial of the effects of different acids and other substances upon a variety of plant structures. In the third lecture are the results of calcining different plants and finding the proportion of lixivial salts in their ash. He found considerable variation in the amounts extracted, and made the interesting observation that wild Sea Scurvy Grass gave four times the quantity of salt which was yielded by the plant from a garden. The next lecture gives further experiments on the soluble salts obtained. By evaporation and other means, he showed that more than one salt was present. Lecture five, on the colours of plants, shows that he adopted Sharrock's belief that air was essential for the formation of chlorophyll. He went on to determine the effect of putting coloured flowers in different liquids. He repeated Ray's earlier observation of the change in colour of some flowers from blue to red when they were immersed in acids. His last lectures were on tastes and on the solution of salts in water. Grew's experiments show considerable industry, most of his results were neglected, and many were rediscovered some 200 years later.

Most of the experiments I have mentioned were described in brief communications, or often in short paragraphs of a few lines. But the *Philosophical Transactions* for 1699 contains a paper on a specific subject occupying 34 pages and giving full quantitative data of experiments lasting through the summer and autumn of two years. This was by Dr John Woodward, better known for his writings on Geology, and founder of the teaching post in the University of Cambridge which now bears his name. Under the title "Some thoughts and experiments concerning vegetation" Woodward returned to the old question of

plant nutrition. After pointing out the probable inaccuracies in the methods used by Van Helmont and Boyle, he described the experiments he had made in 1691 and 1692. He grew plants in vials containing water and covered with parchment to prevent evaporation. The species used were kept growing for some months, a known weight of water being added from time to time; at the end of the experiment the increase in the fresh weight of the plant was found, and the ratio of this to the weight of water used was calculated. In the first year he used plants of three different species and grew each of them in rain water, spring water and river water from the Thames. In the next year he added some garden soil to the water. He found, of course, that after a time the water became turbid owing to the growth of bacteria and unicellular algae, he regarded this as due to the precipitation of earthy matter from solution. From his results he drew eight conclusions, giving a discussion of the evidence which led him to them. The most important of these was that the greater part of the fluid mass that is drawn up by the plant passes through its pores and exhales into the atmosphere. This was the first demonstration of Transpiration. He thought he had proved that the food of plants was not water but the mineral substances dissolved in it believing that water acted only as a vehicle by which terrestrial matter passed into the plant. The part really played by water in the formation of carbohydrates was not discovered until another century had passed. The climate of thought at the end of the 17th century is shown in the concluding words of Woodward's paper: "There's a procedure in every part of Nature that is perfectly regular and geometrical, if we can but find it out, and the further our researches carry us the more shall we have occasion to admire this and the better twill compensate our Industry".

We find few communications on plant biology in the *Philosophical Transactions* in the 18th century. But in 1718 the Rev. Stephen Hales was elected a Fellow, and a few days later informed the Society that he had lately "made a new experiment upon the effect of ye sun's warmth in raising ye sap in trees." Hales was a product of the new education provided at Cambridge at the end of the 17th century. Although destined for the Church his education included Arithmetic, Algebra, Geometry, Astronomy, Trigonometry, Physics and Natural Philosophy. He was at Corpus Christi College during the last four years of Newton's tenure of the Chair of Mathematics, and also at the time when the teaching of chemistry by Vigani commenced. He held a Fellowship from 1703 to 1709, and during this period seems to have devoted most of his time to Natural Science. His approach to biological studies, is indicated in the introduction to his book on "Vegetable Statics," where he wrote: "The most likely way to get any insight into the nature of those parts of the creation which come within our observation must in all reason be to number, weight and measure". In this book he gave the results of three years of assiduous experimentation on the sap in vegetables, on the growth rate in plants, and on what he called the analysis of air, which was in reality the study of gases. He described 124 experiments and illustrated them by 46 finely engraved figures.

It is unnecessary for me to say more about this work, which has been described by a number of authors, and which may be said to be the beginning of modern plant physiology. Nor have I time to speak again about the experiments of Richard Bradley, whose work lay in different fields of plant biology. But even in Bradley's lifetime the interest in experiments on plants was becoming diminished. Hales, who lived until 1761, turned his attention to other subjects after 1727. On the death of Newton in 1727 Hans Sloane became President of the Royal Society; he, with William Sherrard, dominated the

study of botany, and both of them having collected plants in foreign countries were mainly interested in the description and naming of exotic forms. John Martyn succeeded Bradley at Cambridge and lectured on the plants described by classical authors; he is known chiefly for his translations of Vergil's 'Georgics' and 'Bucolics'.

The regression of interest in plant biology was intensified by the influence of Linnaeus. The great Swede was essentially a field naturalist of the older type, and was probably little influenced by the movements of thought of the 17th century, or by the new development of science. He seems to have had no interest in experiments, and though he termed his system of plant classification the sexual system he appears to have made no attempt to prove that the stamens and carpels of plants had such functions as would entitle them to be regarded as sex organs. His activities were centred round the naming and recognition of organisms. His simplified system of nomenclature and his artificial system of classification were especially welcome at a time when plants of all kind were being brought to Western Europe from foreign lands. By 1762 his system was being used in Britain, and for the next 130 years botany in England meant the naming of plants and the recognition of their differences. Even when attention became once more turned to the problems of plant nutrition by the work of Priestley and afterwards of Ingenouosz. The advances in knowledge were regarded as of interest in agriculture rather than in botany.

I do not think that we can account for the general cessation of experimental work on plants for some fifty years by saying that progress in plant biology had to wait for the fuller development of chemical knowledge. There were so many problems which might have been elucidated by careful experiment and observation. Some of the earlier workers had disclosed curious facts which had never been properly examined. But for some reason the urge to try experiments had faded.

Both the anatomy and the physiology of plants received little more attention in Britain until about 1870. But eventually the wheel turned through the full circle, and early in the 20th century British botanists were again leading the world in the investigation of the fundamental processes of plant life.

