THE SCIENTIFIC STUDY OF PLANTS

Inaugural Lecture of the
Professor of Botany
delivered at the College
on 27 October 1955
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IN its Second Session the University College of Swansea founded a Department of Biology under the leadership of Dr. Florence A. Mockeridge. The dual post of Head of the Department of Biology and Professor of Botany was created in 1936 and from that date until 1954 was occupied with distinction by Professor Mockeridge. My predecessor, now an Emeritus Professor of the University, gave thirty-three years of devoted service to the College and to the Department which she nurtured from its foundation. Her pioneer work and that of her staff, particularly of Dr. P. A. Little who since 1927 has been responsible for the teaching of Zoology, has established in Swansea a high standard of teaching in Biology, culminating in the present creation of separate Departments of Botany and Zoology and in the provision of new and more adequate accommodation for teaching and research in these Biological Sciences.

The favourable position thereby created has not come to pass easily and Professor Mockeridge with foresight and persistence began some twenty years ago to urge upon the Council of the College the need for the important developments now initiated. The pioneer biologists at Swansea have, therefore, had to face, at least in some measure, the resistance which biology has always called forth and which arises because its impact on our cherished dogmas and ways of life is more direct and revolutionary than that of any other science. Discoveries in the sciences of Mathematics, Physics, and Chemistry have long been readily accepted and exploited in the advanced countries. By contrast society has endeavoured to evade the implications of biological discovery with the natural consequence that there still exists a widespread lack of understanding of the nature and importance of contemporary biological science and of the facilities and training required by the research biologist.

This situation faces biologists with both an educational obligation and a struggle for the means of self-expression. It is, therefore, appropriate that on this occasion I should endeavour to trace in broad outline the historical development of my subject and indicate its present needs and potentialities. I embark upon this in the full realization that a lecture of endurable length devoted to such an ambitious undertaking must inevitably be open to many serious criticisms.

Science depends for its advance on the individual scientist. The nature of his work is determined by his individuality, by the previous history of his science, by his own previous training and experience, and by the experimental facilities to which he has access. At certain times during the history of biology this combination of mind, knowledge, and facilities has been so powerful as to effect a pronounced qualitative change in the nature of our understanding. I hope to indicate to you the nature of modern botany by describing and placing in their historical setting certain landmarks in the progress of the scientific study of plants.

Systematic Botany and the Concept of Evolution

Herbals and physic gardens

Knowledge of the usefulness of plants is as old as man himself. It was not, however, until the rise of the Greek and Roman civilizations, and then primarily in connexion with the identification of the plants used in medicine, that systematic and detailed descriptions of plants were written down. These descriptions were in Roman times supple-

mented by botanical drawings made directly from nature and executed in many cases with great accuracy. From work of this kind originated the first great Herbal, that of Dioscorides produced in the first century A.D.

A long period, sterile in art and science, was, however, to intervene between the fall of Rome and the Renaissance. Then within that great cultural revival came not only a renewal of interest in the form of living things as exemplified in the paintings of Botticelli and the drawings of Leonardo da Vinci, but also accurate and beautiful reproductions of the texts of the Ancients. This reawakening of interest in plant form, again closely related to the use of plants in medicine, produced the sixteenth-century Herbals and led to the foundation of Botanic or Physic Gardens in the ancient universities of Europe. It was also during this period that explorers first brought to Europe many of the food plants we know today; plants which were to make possible population growth and thereby the development of more highly organized human societies. Out of the ferment of ideas initiated by the Renaissance also came the first important expositions of biological science like Harvey's *Anatomical Dissertation concerning the Motion of the Heart and Blood* published in 1628, and the foundation of scientific societies of which our own Royal Society of London founded in 1662 was one.

Karl Linnaeus and eighteenth-century botany

Stimulated by Bacon's dictum that the essential first step for scientific progress is the accumulation of facts, and aided by Boyle's introduction in 1663 of alcohol as a biological preservative, there arose during this period a group of naturalists which included Tournefort in France and John Ray in Cambridgeshire. These men not only assiduously collected, preserved, and described plants, but sought to *classify* them into species, genera, and families. Here was a recognition not only of the existence of sharply distinct species (a unit first clearly recognized by Aristotle) but of resemblances and affinities between them. The work of these naturalists, and particularly of Tournefort, formed the basis for the outstanding contribution to systematic botany of Karl Linnaeus, whose *Systema Naturae* was first published in 1735 and reached its tenth edition in 1758.

This work of Linnaeus exercised a very powerful influence. Botanists became almost exclusively engaged in the search for new genera and species. They were esteemed within their own circle in proportion to the number of flowering plants whose characters they knew by heart. Their interest only extended to the external features which identified their specimens; only those features of form useful for identification were regarded as important. Their species were static units each dating back to an act of special creation when the total number of plant species was fixed for all time. This narrow concept of the botanist as simply or mainly a collector and identifier of plant species still persists; it is as widespread as it is mistaken.

The origin of species and organic evolution

The static botany of the eighteenth century by stimulating the search for new species was, however, destined to effect its own eclipse. Botanists travelled in the ships of Captain Cook and of Captain Matthew Flinders and in the extensive nineteenth-century voyages of scientific exploration. Knowledge of the living flora and fauna of the world grew rapidly and excited great interest. Geology was developing the basic concepts of palaeontology and paving the way for the study of fossil plants initiated by Robert Brown in 1851.

This rapid increase in biological knowledge during the

century following the publication of the *Systema Naturae* diminished the authority of the criteria of the systematists; particularly of their concept of the fixity of species. The similarities between species, particularly the basic similarity of structure among the warm-blooded animals, suggested a common ancestry. Fossil organisms were clearly related to, but quite distinct from, living species. Domestic animals and cultivated plants were known to have arisen by human selection of the progeny of their wild ancestors; this selection had produced in many cases a range of varieties often sufficiently contrasted as almost to be regarded as new species. In the writings of Buffon, Erasmus Darwin, and Lamarck the static concept of species was rejected; species were regarded as undergoing continuous change; the bewildering variety of living organisms as having evolved from a smaller number of ancestral types and as now undergoing change into the organisms of the future. The scientific climate was ripe for the synthesis achieved by Alfred Russel Wallace and particularly by Charles Darwin in his great work *The Origin of Species by Means of Natural Selection* published in 1859.

Darwin in his *Origin* set forth the immense weight of accumulated evidence that the diverse forms of life are of common descent; that species are continuously changing into new forms. Strongly influenced by the *Essay on Population* written by Malthus in 1798, Darwin explained the process of change by postulating that natural variations were not only transmitted to the offspring but were selected by a 'struggle for existence'. These ideas became linked with the contention of Herbert Spencer that the *direction* of change had been such as to produce higher from lower forms of life. Darwinism and the evolutionary concept of Spencer became synonymous in mens' minds and found eloquent protagonists like Thomas Henry Huxley.

This concept of organic evolution played an important part in the ferment of scientific ideas which characterized the second half of the nineteenth century. The scientific challenge of Darwinism was, however, not fully understood by contemporary biologists. The systematists saw in it a justification for their work and applied themselves even more assiduously to accumulating data on the gross structure of living and fossil species. Thereby they embroidered and extended the systems of classification which now seemed to reveal the evolutionary sequences of the past. Botany became weighed down with an increasing mass of the same kind of knowledge and was principally concerned in constructing genealogical trees depicting the possible ancestries of living species. Such was the spirit of the Darwinian period from 1860 to 1900 that interest was diverted away from a critical examination of the nature and extent of natural variation, of its inheritancy, and of the role of the struggle for existence in evolution. Biologists fully accepted evolution as a fact but failed to analyse *how* it took place. The development of biology, still a science primarily concerned with the study of gross structure as an aid to classification, had reached an impasse —the end of a chapter.

The Study of Cells and of Heredity

The structure of living plant cells and their nuclei

To understand how the scientific study of plants was to move forward beyond this point, we must go back to the seventeenth century; to the publication in 1665 of the *Micrographia* of Robert Hooke. Speaking of Hooke's work, C. D. Darlington in his inaugural lecture as Professor of Botany at Oxford, delivered in 1953, proceeded thus:

> The obstacle to a deeper understanding of plants themselves . . . was ultimately broken down by work of quite another character. . . . It was the young Robert Hooke, working it seems in Boyle's laboratory next to the 'Three Tuns' in the High Street, who put together with his own hands a compound microscope. . . . With this instrument he discovered as he put it 'a new invisible world' in the minute structure of living things. Amongst other things, Hooke observed the compartments into which organisms are divided, or of which they are made up, and he gave them the name we now use of 'cells'.

Almost immediately more extensive investigations of the minute structure of plants were undertaken by Marcello Malpighi in Bologna and by Nehemiah Grew in London. These revealed that the stems, roots, leaves, and flowers of plants are compounded of many different kinds of cells arranged in a pattern of tissues. Though both men failed to understand the true nature of plant cells, they produced, using microscopes magnifying barely 50 diameters, elegant drawings of the anatomy of sections of stems and roots which would compare favourably with the corresponding work of many twentieth-century undergraduate students of Botany!

Further progress in the study of plant cells required more powerful microscopes; microscopes of the kind which did not become available until the nineteenth century. In 1823 Giovanni B. Amici, employing immersion lenses in a microscope of his own construction, observed that pollen grains caught on stigma surfaces of Purslane flowers sent into the stigma tissue minute tubes whose apparently liquid contents showed an active streaming. Robert Brown in 1831 demonstrated that the living cells of plants always contain a highly refractive globular body which he termed the *nucleus*. In 1838 Schleiden noted that the nucleus was always embedded in a cell substance (now termed the *cytoplasm*) which underwent in the living cell an active streaming movement just as had been described by Amici. Later the term *protoplasm* was coined for the cytoplasm and its associated nucleus both of which were found to be constant features of all living cells, plant or animal. Protoplasm was the living matter; the solid structural materials of the plant body were its by-products. The enclosing cell wall which alone had been observed and figured by the seventeenth-century microscopists was not the living unit, the cell as we now visualize it, but simply the envelope of structural material secreted around it by protoplasmic activity.

The development of achromatic lenses and further improvements in microscopic illumination made possible still more detailed studies. By 1878 Abbé microscopes were being manufactured and distributed by Zeiss of Jena. These foreshadowed in all essentials the microscopes of today with resolving powers of 1,000 diameters. As early as 1843 certain minute one-celled plants had been observed undergoing fission into two daughter cells. In 1875 the great German botanist Eduard Strasburger was able to give the first detailed description of this process of cell division, showing it to be a process led and controlled by division of the nucleus. Strasburger's detailed studies were made possible not only by improved microscope design but also by the presence in the nucleus of granular material which stained deeply with basic aniline dyes; and was therefore termed *chromatin* by the contemporary zoologist Flemming. Preparatory to nuclear division, there appeared in the nucleus minute chromatin-rich threads, the *chromosomes*, constant in number and form in the nuclei of each plant species.

During the nuclear division these chromosomes underwent a precise longitudinal division so that each daughter nucleus received its proper complement of daughter chromosomes. Division and separation of the chromosomes to form two daughter nuclei was followed by division of the cell. The chromosomes then lost their definition and the chromatin granules appeared scattered in the 'resting' daughter nuclei. When, preparatory to a further division, the chromosomes were again identifiable they always arose in the same positions and with the same form as recorded prior to their earlier loss of definition—the chromosomes of the nucleus were permanent structures whose microscopic visibility varied with the state of the nucleus.

The cellular basis of sexual reproduction

The new microscopes also made possible study of the process of sexual reproduction at the cellular level. In the introduction to his classical paper of 1855, Nathaniel Pringsheim could write as follows:

> The existence of sexuality in plants is now admitted. In flowering plants, the necessity of conjunction of pollen tube and ovule for the production of the embryo can no longer be denied. The sexual organs of the higher flower*less* plants are also known. But with regard to the manner in which the (sexual) organs participate *materially* in the act of impregnation, and even as regards the necessity for their co-operation, there are but vague surmises.

Then, however, Pringsheim proceeded to describe how he had observed, in his studies of the freshwater alga *Vaucheria*, the entry of the motile male cell into the female cell and had thereby demonstrated for the first time that the subsequent development of the female cell into a new plant was not initiated by some mysterious male essence—the 'aura seminalis' of Aristotle—but by an act of fertilization involving fusion of the sex cells. This discovery, quickly confirmed in other plants, was followed in 1887 by Beneden's demonstration that in *Ascaris* the nuclei of the sex cells contain half the number of chromosomes present in the nuclei of the body cells and of the fertilized egg. Further, since in most organisms the sperm is simply a nucleus with a tail, which is shed as it comes into contact with the female cell, fertilization is to be regarded as a nuclear fusion, the fusion nucleus containing two sets of chromosomes, one of paternal and the other of maternal origin. Clearly in the subsequent development of the sex cells this chromosome number had somehow to be halved. This was found to take place in a special kind of nuclear division, *reduction division*, first observed in plants in 1894 by Eduard Strasburger. In this process the chromosomes do not divide and separate into daughter chromosomes but instead the corresponding paternal and maternal chromosomes pair off, effect some interchange of material between one another, and then separate in such a manner that two sex nuclei with the *halved* chromosome number are formed each containing some chromosomes of paternal and some of maternal origin.

These researches pointed to the chromosomes as the physical agents of heredity. A set of minute thread-like chromosomes, visible only under a powerful modern microscope, was the essential contribution which the male and female made to the fertilized egg from which the new plant or animal arose. Recognition of the significance of this discovery came, however, only after botanists and zoologists, labouring to interpret the results of controlled breeding experiments, had constructed hypothetical concepts which described, at first unwittingly and then with increased consciousness, the nature and behaviour of the chromosomes.

Plant breeding and the theory of the gene

This aspect of our study can and should begin with the work of Gregor Mendel begun in 1857, published in 1865, and then completely neglected until confirmed and acknowledged in 1900 by Correns in Tübingen, by Tschermak in Vienna, and by de Vries in Amsterdam. First Mendel had studied the inheritance of single recognizable characters, for example of the average height of the plants, when 'dwarf' and 'tall' varieties of peas were crossed and the hybrids selfed. To explain the results

he obtained, he had to postulate that the expression of the character (height) was controlled by a pair of factors or determinants (since 1909 these, following the Danish botanist Johannsen, have been termed *genes*), one of maternal and the other of paternal origin, that in the fusion nucleus of the egg, the expression of one of these factors was dominant over the other (in Mendel's experiment the 'tall' gene was dominant) and that the maternal and paternal members of the gene pair suffered random distribution to the sex cells formed in preparation for the next generation. Mendel had then extended his work to study simultaneously the inheritance of two characters and reached the conclusion that the determinants of separate characters were inherited quite independently.

Subsequent work, particularly that with the fruit-fly, *Drosophila*, initiated in 1909 by T. H. Morgan in Columbia University, extended and modified Mendel's findings and led to the deliberate interpretation of studies in the inheritance of characters (genetics) in terms of the structure and behaviour of the chromosomes in reduction division (an aspect of cytology, the study of cell structure); led, that is, to the science of cytogenetics.

It was found that characters were not always inherited independently; rather they arranged themselves into groups such that those within each group were inherited together (as a *linkage group*) and only characters from different groups were inherited independently (i.e. behaved in a typical Mendelian manner). And the number of groups of linked characters was equal to the number of chromosomes in the sex cells. The genes of each linkage group behaved exactly as if they were carried on the same chromosome.

But this was not the end of the story, for linkage was not absolute—if the genes of the linkage group were on the same chromosome then presumably some interchange of material occurred between the paired maternal and paternal chromosomes before they separated to constitute the sex cell nuclei—there was an interchange or *crossing over* of genes between paired chromosomes during the reduction division. This discovery gave genetic significance to the 'chiasmata' which in the early stages of reduction division seemed to the cytologists to tie or loop together the paired chromosomes; such chiasmata presumably marked the points where the interchange was occurring.

Genetical study of 'crossing over' revealed that for any two genes in a linkage group it occurred with a fairly fixed frequency. When cases involving more than two genes were examined, the 'cross-over' frequencies recorded could only be explained by postulating that the genes are arranged in a *linear series* along the chromosomes; just like the beads or granules of chromatin which can be seen, particularly at a certain stage in reduction division, to constitute the chromosomes. The inheritance of genes, the determinants of visible characters, corresponded with the inheritance of the chromatin granules of the chromosomes—chromatin granules were either genes or were the carriers of genes, themselves still smaller material entities. The paired hypothetical determinants of Mendel—the gene pairs—were material entities located at equivalent points on the corresponding ('or pairing') maternal and paternal chromosomes. This in essence is the *Theory of the Gene* from which has stemmed a deeper understanding of the twin problems of the discontinuity of species and of their change into new species during the course of evolution.

Mutation and the nature of natural variation

Now Darwin had postulated that evolution was a process of gradual change; the cumulative effect of successive

small variations over many generations. Hugo de Vries, like others before him, was, however, convinced that series of individual grading from one species into another such as would be expected from Darwin's hypothesis are, in nature, conspicuous by their absence; that each species shows fluctuating variations on either side of a norm but is distinct from other species; that the species concept is an expression of a real discontinuity. In 1886 de Vries, examining a colony of the American Evening Primrose, made observations which he regarded as highly significant; in the colony were variants which on self-fertilization gave rise to quite new and true-breeding forms. Here it seemed was a species disintegrating suddenly (not gradually) into new species. Species were arising by sudden change, or, to use de Vries's term, by *mutation*. Similarly in 1913 Johannsen, although quite unable to alter gradually the mean seed weight of beans by always selecting and replanting the heaviest or the lightest seed, encountered two cases in which the mean seed weights suddenly changed to new and persistent values: encountered mutations in the sense earlier described by de Vries. These mutations were apparently quite unrelated in direction or extent to environmental influences. Their discovery, combined with the recognition that heredity operates through the chromosomes only of special sex cells set aside early in development, led to the rejection of the long-discussed but quite unproved hypothesis of 'the inheritance of acquired characters'. This hypothesis had postulated the inheritance of those changes in form and structure which arise in the body of an organism (i.e. are acquired) as it adapts itself to the environmental influences operating during its lifetime; the progeny were thus little by little, generation by generation, considered to become better adjusted to the environment than their parents. Such a view was superficially very attractive. It seemed to show a purposefulness within the organism. This hypothesis first clearly enunciated by Lamarck has again been temporarily resurrected in recent years by certain Soviet geneticists, including Lysenko; with, one may add, serious consequences for the progress of plant breeding in that country. The overwhelming mass of scientific evidence now supports the view that evolution has proceeded by naturally-occurring mutations, by sudden changes quite unrelated to any acquired characters, but whose survival value is subjected to natural selection or rejection, and there is a preponderance of rejection in the struggle for existence. On reflection comes the realization that this mechanism of nature is more adventurous and more flexible (it makes release from a line of increasing specialization possible), and hence is of greater survival potential than that envisaged in the hypothesis of 'the inheritance of acquired characters'; that the latter arises from a failure to assess analytically the separate roles of heredity and environment in evolution.

The genic basis of variation

It is now logical to ask: how far can this new science of cytogenetics increase our understanding of the origin of natural variation? Now the rapid accumulation of genetic data which followed the rediscovery of Mendel's work not only exposed, as I have indicated, the phenomena of 'linkage' and 'crossing-over' but showed that his concept of dominance was an oversimplification; some characters, although under the primary control of a single gene pair, were modified in their expression by other genes, other characters were controlled not by single gene pairs but by many interacting genes each modifying the effect of the others. The expression of genes is modified by the other genes with which they are associated, genes interact. This gene interaction, together with the independent inheritance of 'linkage groups' and the interchange between these groups called 'crossing-over', clearly could make possible and thereby explain the occurrence of infinite small variations by effecting a reshuffling, during reduction division, of the individual genes of a fixed gene population. No two individuals arising from separate fertilized female cells are exactly alike, nor would they be expected to be.

Inherited variations of the kind we call mutations, the changes important in evolution, have by contrast been shown to involve either quantitative or qualitative change in the gene population. One kind of mutation arises from the very infrequent breakdowns which occur in chromosome behaviour—their frequency can be speeded up by deranging the process of nuclear division with agents like colchicine or mustard gas. They involve deletions or duplications of chromosomes or of chromosome segments; sometimes duplications of whole sets of chromosomes (polyploidy)—such mutations are termed chromosome mutations. The second kind are radical changes affecting individual genes—these are termed gene mutations. These also occur naturally with a very low frequency. Many gene mutations have been induced experimentally by treatment of living cells with X-rays, gamma-rays, and other radiations.

In this second chapter of the history of our science we have traced then, first the development of our knowledge of the fine structure of plants made possible by improved microscopes, then of the adoption of a quantitative approach to the study of the inheritance of definable characters, and finally of the integration of the data from these two different levels of investigation into a unifying concept. From this arose a deeper understanding. It was possible to explain at a more fundamental level—at the *intra*cellular level—the nature of species, of natural variation within species, and of the mechanism of evolutionary change; problems whose recognition I traced in the first section of my lecture.

Plant Physiology and Biochemistry

Spontaneous generation and the study of infectious disease

To complete our survey it is necessary to consider the development of a further and again quite different level of approach to biological problems; a development which, because it involved a different level of approach, produced again a new kind of knowledge.

When the seventeenth-century microscopists had observed that infusions of hay and of other substances, perfectly clear when prepared, became in a few days or even hours cloudy with actively moving microscopic forms (later to be classified as bacteria, fungi, and protozoa), it was natural that they should consider that they had demonstrated the 'spontaneous generation' of life from non-living matter as postulated by Aristotle. The demonstration that such spontaneous generation does *not* occur, that in all cases like the above organisms had reached the suitable source of food and moisture via the air, and had then rapidly multiplied by division, was indeed difficult to prove beyond all unreasonable shadows of doubt. It required the improved microscopes of the nineteenth century, the adoption of a critical experimental approach, and the genius and persistence of Louis Pasteur in France and of John Tyndall in this country. The immediate effects of their researches were the abandonment of the hypothesis of 'spontaneous generation' and the recognition that putrefaction and fermentation in nature were not chemical processes proceeding independent of living organisms; as had been claimed by the chemist Liebig. The long-term effect of their work was that it initiated the

scientific study of infectious diseases in plants and animals. Infectious diseases were shown to be due to micro-organisms, capable of surviving a period of separation from their stricken hosts. Infective fluids, prepared from stricken plants and animals, could be freed from their infectivity, either by killing the micro-organisms by heat or by removing them by passage of the fluid through a sufficiently fine filter (a bacteria-proof filter).

But there were some awkward observations not to be ignored. In 1857 there had been described a disease of tobacco plants later to be termed 'tobacco mosaic'. In 1892 (D. Iwanowski), and again in 1898 (M. W. Beijerinck), it was demonstrated with tobacco plants infected with the mosaic yield a juice which even when passed through a bacteria-proof filter could still convey infection. Here was the first indication of the existence of an infective agent smaller than the visible bacteria. When it became clear that distinct and specific agents of this kind were responsible for many serious plant and animal diseases they were collectively termed *viruses*.

But to return to the filtered juice of the diseased tobacco plant, the infective agent could be precipitated by various chemicals which precipitate protein molecules; by 1926 Mulvania felt able to state that the virus behaved more like a protein than an organism. In 1935 W. M. Stanley succeeded in isolating a crystalline protein possessing the properties of the virus and in the following year F. C. Bawden and his co-workers at Rothamsted showed the tobacco mosaic virus to consist of rod-shaped molecular aggregates of ribosenucleoprotein. Here was a chemical entity capable of causing an infectious plant disease, requiring suitable living host cells for its reproduction or duplication, something non-living when isolated, living when introduced into the cytoplasm. In some of their properties viruses were organisms, in others large molecules.

The nature of plant physiology

Here we have raised in an acute form the question of the transition from a chemical to a biological level of organization. A spate of questions is thrust upon us: what is the chemical nature of protoplasm? how is protoplasm built up? how is its unique organization preserved? how is its pattern transmitted? why in all organisms above the unicellular level does the body of the organism eventually die? From consideration of such questions there emerges the concept of life as a dynamic system, a system characterized by change, a system of happenings, of processes proceeding. The development of this concept demanded the study of life as a material system in unstable and therefore changing equilibrium with its surroundings—demanded the emergence of the sciences of plant and animal physiology. The material nature of the system being studied, life being treated as a unique state of matter, implied that here we employ the techniques of experimental science, particularly those developed by chemistry and physics. Here also we must attempt to extend the concepts of the physical sciences to aid in the interpretation of a higher level of organization.

Plant physiology in the eighteenth and the nineteenth century

While eighteenth-century botany was preoccupied with the discovery, naming, description, and classification of new plants, physiology was mainly a speculative occupation of physicians. However, standing out from these by his independence of thought was the figure of the Reverend Stephen Hales. Educated in physical science at Cambridge, he was won over to the study of plants by walking the surrounding countryside with John Ray's *Flora of Cambridge* to guide him. In his vicarage garden at Teddington, Hales sought by experiments to explain

the action of living plants on the basis of known physical forces. In 1727 he published, under the title *Vegetable Staticks*, a lucid description of these experiments—experiments some of which are still repeated in University courses, often, I may add, with less skill than by their originator. These eighteenth-century experiments laid the foundations of our knowledge of the water relations of plants.

By the second half of the eighteenth century chemists and engineers and clerics were elucidating the nature of air and of the effects of plant and animal life on its composition. In Joseph Pristley's *Experiments and Observations on Different Kinds of Air* (1774), in J. Ingen-Housz's *Experiments upon Vegetables discovering their Great Power of Purifying the Common Air in Sunshine and Injuring it in the Shade of Night* (1779), and in Nicholas Théodore de Saussure's *Recherches chimiques sur la Végétation* (1804) are described well conducted experiments demonstrating that at all times plants and animals are absorbing oxygen and exhaling carbon dioxide, are carrying out the process of breathing or *respiration*; that in addition green plants have the unique power in sunlight to effect a process, termed *photosynthesis*. In this process the plant takes up carbon dioxide and evolves oxygen; in this and other respects it is the reverse of respiration. In 1799 Ingen-Housz, in his book *Food of Plants and Renovation of the Soil*, summarized the evidence that in photosynthesis the uptake of carbon dioxide leads to the synthesis of organic matter, and in 1845 Mayer, author of the *Law of the Conservation of Energy*, clearly set forth the view that in photosynthesis the radiant energy of the sun is converted into chemical energy stored in the molecules of the synthesized organic matter.

These and other pioneer researches on respiration and photosynthesis were set forth with great clarity in the

Physiology of Plants, published in 1865 by Julius Sachs, Professor of Botany at Wurzburg and perhaps the most influential teacher of his subject in the nineteenth century. Here we find summarized evidence that respiration effects a continuous liberation of energy by the oxidation of the organic food reserves of the cell and the concept that this constant supply of energy is essential for the maintenance and growth of the organized structure of protoplasm. Here, in an account illuminated by his own researches, Sachs informs us that the centres of photosynthesis within plant cells are discrete bodies containing a pigment complex chlorophyll; that the chlorophyll functions as the essential catalyst; that the first visible product of photosynthesis is starch appearing, in the cells, as minute grains; and that this starch is a complex organic compound, utilizable either as the fuel for respiration or as the starting-point for the synthesis of the other forms of organic matter needed for plant growth.

In this lecture it is my main purpose to show how the scientific study of plants has contributed to our understanding of life. I do, however, wish to stress that almost every aspect of this study is of great practical importance. Consider for a moment the process of photosynthesis whose general nature was so well understood by Sachs almost 100 years ago. This process is the greatest synthetic industry on earth. It is powered by the atomic energy of the sun. It is responsible for the presence in the earth's atmosphere of oxygen. Its activity in past ages fixed the energy now being released from coal, peat, and oil. It is the sole basis of the food supply of all animals, including man. It is the source of natural products like timber and fibres. Its output is of the order of some 200,000 million tons per annum of organic matter. It is no exaggeration to say that the material progress of mankind in the immediate future will depend just as much on the wise utilization of the

properties of the green cells of plants as on the proper application of the new sources of power made available by atomic physics.

But to continue my main thesis: Sachs in 1865 was able to cover a wider range of knowledge of the physiology of plants than I have so far indicated. Dumas's method of estimating nitrogen, described in 1830, made it possible to demonstrate the universal occurrence of significant amounts of this element in all plant tissues and to study its origin in nature. The forceful writings of Justus Liebig, particularly the publication in 1840 of his book *Chemistry in its Application to Agriculture and Physiology*, had led to a wide acceptance of the inorganic theory of plant nutrition; that the essential nutrients required by plants are obtained either from the soil or from the air in inorganic form. Liebig had incorporated an ammonium salt into his patent fertilizer and shown it to act as an effective source of nitrogen. The French chemist and engineer Boussingault, in 1838, had similarly demonstrated the manurial properties of Chilean nitrate, first introduced into Europe in 1820.

Boussingault, in his experiments, had used washed sand as a growth medium to replace soil. By 1860 Sachs and Knop had developed the method of water-culture (hydroponics). These techniques made it possible to identify the elements essential for plant growth, to create a rational basis for fertilizer practice, and ultimately to recognize and treat effectively important deficiency diseases of crops.

Cell metabolism and the discovery of enzymes

The plant physiologist in his study of nutrition is, however, not only concerned to define what nutrients are essential but seeks to trace the chemical changes which these nutrients undergo in the sum total of chemical reactions proceeding in living cells; to trace, that is, their role in cell *metabolism*. To study not only nitrogen nutrition but the cellular reactions whereby nitrate is used to synthesize protein; to study not only the uptake of carbon dioxide in photosynthesis but the chemical steps which, in that process, result in the synthesis of starch and sugars. At first, studies of this kind could only be approached by quite indirect means, knowledge of cellular mechanisms had to be purely circumstantial. However, in 1897 E. Buchner had performed an experiment which was to make possible a new approach to cell metabolism; an experiment which can be regarded as initiating the science of Biochemistry.

Buchner destroyed the structure of yeast cells by grinding them with silica and then submitted the gritty paste to a pressure of more than 200 atmospheres in an hydraulic press. The clear juice so obtained was capable of degrading sugar to alcohol; of effecting yeast fermentation. The biological and chemical theories of fermentation so keenly argued by Pasteur and Liebig thirty years earlier had both been vindicated. Here was a soluble ferment, true derived from a living organism, but itself a clear aqueous solution, capable of effecting a natural fermentation. The yeast press-juice of Buchner was subsequently shown to contain a mixture of soluble ferments or *enzymes*, each responsible for promoting (or catalysing) one of the sequence of linked reactions involved in sugar fermentation. When these enzymes were separated from one another and purified, they were found to be either proteins or protein more or less closely associated with units of smaller molecular weight termed co-enzymes (some of these co-enzymes were later shown to be identical with the vitamins).

The purification of enzymes also revealed that they are catalysts of high specificity. The enzyme urease catalyses the hydrolysis of urea but has no action on any of the

substituted ureas or upon any other compound. With the progress of biochemical studies it became apparent that enzymes are present in cells only in minute amounts, that they are extremely active, specific, and in many cases unstable catalysts, and that all, or almost all, of the chemical changes proceeding in living cells are under enzyme control. Protoplasm clearly contained several kinds of proteins; reserve proteins, structural proteins responsible for its molecular framework, and unique colloidal properties, and, in addition, minute amounts of a large number (at a conservative estimate several hundred) of specific enzyme proteins whose properties and concentration determined the rate and nature of cell metabolism.

Nucleoproteins

Now we must turn our attention in another direction to describe the discovery of a further kind of protein and to discuss briefly its special role in living cells. This I hope will illustrate how plant physiology is making possible a still deeper understanding of the major discoveries outlined earlier. Though, as I think my lecture emphasizes, botanists must in their researches be increasingly specialized, their work has in the modern period created a greater depth and unity in their science.

Friedrich Miescher, working in the laboratory of Hoppe–Seyler at Tübingen, isolated in 1868 the nuclei from pus cells which he collected from discarded bandages. In these nuclei he demonstrated the presence of an unusual phosphorous compound which he termed nuclein. This was a new kind of protein, a *nucleoprotein*, we should say today that it was desoxyribosenucleoprotein—a compound formed by combination between a basic protein and desoxyribosenucleic acid (now naturally always referred to by those in the business as DNA).

Using the modern tools of analytical chemistry and new specific cell reagents it has been possible to study quantitatively the distribution of nucleic acids within cells and to show the universal presence not only of DNA but of a second kind of nucleic acid, ribosenucleic acid (RNA) itself also associated with basic protein.

From such studies we know that DNA-protein is concentrated in the chromosomes, its distribution coinciding with the chromatin granules of the cytologists. Nuclei also contain RNA-protein, but this is concentrated in separate nuclear regions and seems to be implemented in the synthesis of the chromosome nucleo-protein—the DNA-protein.

Nucleic acids were, as their name indicates, at first regarded as strictly nuclear constituents. Recent work has, however, shown that the cytoplasm contains minute inclusions, cytoplasmic particles, reproducing by fission and rich in nucleoprotein of the RNA-type. Isolation of these cytoplasmic particles, by high-speed centrifuging, has shown that they are uniquely rich in enzymes—they are the highly active centres of cell metabolism.

These studies enable us to pose two questions of great importance. First, what is the chemical nature of the genes? Second, how do genes exert their control on cell development and through this on the characters of the organism?

The chemistry of genes and viruses

Cytoplasm, although the site of protoplasmic synthesis, cannot persist in the absence of the nucleus; nor are isolated nuclei capable of self-perpetuation. The two are interdependent. This suggests that the nucleus is dependent upon cytoplasm for organic and inorganic nutrients; and that the nucleus controls cytoplasmic activity by sending out into it 'messengers' or organizing agents. Recently

geneticists have made observations which suggest that some of these 'gene messengers' are involved in the formation of units able to persist and even duplicate themselves in the egg cytoplasm. Such units have been termed *plasmagenes* and they seem to be intimately associated with the cytoplasmic particles, themselves capable of duplication by fission.

The chromatin granules, carriers of the nuclear genes, the cytoplasmic particles apparently carriers of the plasmagenes and of other and less stable 'gene products', and the viruses are all units capable of self-duplication, a self-duplication without loss of their specific properties. They are all either nucleoproteins or are rich in nucleoprotein. The nuclear genes and viruses both show the phenomenon of mutation.

Letting our footsteps be guided by a growing body of evidence, by ever clearer indications, we may venture to speculate. We can suggest that viruses have, and probably still are, arising by the complete escape of plasmagenes from nuclear control. Such plasmagenes if able to persist and multiply in a foreign cytoplasm—the cytoplasm of the host cells—would there cause pathological disturbance of its metabolism and induce disease. We can also suggest, with considerable confidence, that nucleoproteins have the unique property, when in living cells, of exactly replicating their molecules and that it is the nucleoproteins which confer upon genes, plasmagenes, and virus not only their ability to replicate themselves but their specific properties. From this follows the hypothesis that the massive molecules of nucleoprotein can exist in, at least, as many specific configurations as there are individual genes, plasmagenes, and viruses, that gene and virus mutations arise from sudden and stabilized changes in molecular configuration, that evolution therefore depends upon the structural variations achieved in these special molecules.

The mechanism of gene action

We have just given a provisional answer to the question: what is the chemical nature of the gene? How then do genes control development? To this we can answer, again provisionally, that each nuclear gene sends into the cytoplasm a separate specific 'gene messenger' similar in nature to itself which in the cytoplasm, probably in the cytoplasmic particles, is involved in the control of development through the medium of cell metabolism. The RNA-protein of the nucleus seemed to be concerned with the synthesis of chromosome protein; may not the RNA-proteins of the cytoplasm, concentrated in the cytoplasmic particles, be responsible, under nuclear control, for the synthesis of enzyme proteins.

Now gene mutation can be experimentally induced by various radiations, and if genes act through their influence on cell metabolism we would expect that many mutations would be expressed in breakdowns or derangements in the delicately adjusted reaction chains of cell metabolism. This is the thesis behind the work initiated by G. W. Beadle and E. L. Tatum at Stanford University in 1940, and subsequently developed in many laboratories. X-ray-induced mutants of fungi and bacteria have been isolated which have more elaborate nutritive requirements than the parent 'wild' strains from which they arose and the exact nature of their additional nutritive requirements has been defined. Using appropriate X-ray dosage many of the mutants obtained differ from the 'wild' strain in having a requirement for a single additional organic compound; a compound essential in their metabolism and readily synthesized by the 'wild' strain. The special nutritive requirement of the mutant arises from its inability to effect a particular and identifiable reaction in cell metabolism. Further, in a number of cases, the enzyme controlling the

critical step is known and the mutant can be shown to differ from the 'wild' strain in lacking the operative enzyme.

Now if the micro-organism shows a sexual method of reproduction, we can use the mutant in breeding experiments. When we have been able to do this, it has been found that the mutants differing from the 'wild' strain in lacking a single enzyme are single gene mutations. The individual nuclear gene concerned therefore acts by controlling, probably in some cases through the intermediary of a nucleoprotein plasmagene, the synthesis of a single specific enzyme.

Plant physiology and biochemistry have in many directions deepened our understanding. To illustrate this we have had to choose a single though important example—the carrying forward of our understanding of inheritance and variability to a new level by exposing their chemical basis and by showing that, at least some, genes act by controlling the activity in the cytoplasm of single specific enzyme proteins. There is increasing evidence that gene control of metabolism in this way can ultimately result in the physiological and the visible morphological characters whose inheritance is the concern of the practical plant-breeder.

The Unity of Science

Botanists first achieving accurate descriptions of plants and provisionally systematizing their knowledge, later extending their observations to a new level by employing compound microscopes, and finally studying the mathematics of inheritance and the chemical and physical attributes of living plants, have not only made great contributions to the material welfare of mankind but to our understanding of the nature of life. They have also raised questions the answers to which will, no, actually *are*, enlivening and taxing the whole of science.

In a University we are apparently presented with a unique opportunity to effect cross-fertilization between different branches of learning. I have given some hints of the exciting borderlands between the biological sciences, of Botany, Zoology, Medicine, and Agriculture and between these sciences and Chemistry. Equally fertile are the borderlands between biological science and Mathematics and Physics, and between biological science and the social sciences. Development of these 'no-man's' lands is going to bring a new unity to science and make possible profound advances in understanding. Listen for instance to the concluding sentence from Sir Alexander Todd's Presidential Address to the Chemistry Section of the British Association this September. 'The further study of these fascinating substances (he is referring to the nucleic acids) and of their behaviour jointly by the chemist, biochemist, biophysicist and biologist may open new chapters in our knowledge of life and heredity and in the conquest of disease.' This refers to just one of the major problems raised by biology. Here clearly is a unique challenge, which if accepted will enrich our University teaching and research. In the past many of the most important discoveries arising from the scientific study of plants have been made quite outside and unconnected with Universities. This need not be the case, botanists working in a true University atmosphere and provided with adequate facilities, appropriate to their science as it now is, are going to be in the forefront of scientific advance.

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