SCIENCE

VOL. LXXII

FRIDAY, SEPTEMBER 5, 1930

No. 1862

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SIZE AND FORM IN PLANTS¹

By Dr. F. O. BOWER

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Two years have passed since the association last met in Britain. Events have happened in that interval which mark the close of the Darwinian Epoch. Down House, in which Darwin lived and worked, has been bought, restored and endowed by Mr. Buckston Browne and presented by him to the association, who hold it in custody for the nation. The house is now open as a shrine to those who treasure Darwin's memory. They may enter the study where the "Origin of Species" was penned, or wander out to the Sand Walk, and draw such inspiration as those spots may yet afford to those who are face to face with problems cognate to his own. These years have also severed personal links with Darwin himself. Sir William Thiselton-Dyer, who died in December, 1928, had been

¹Address of the president of the British Association for the Advancement of Science, Bristol, September 3, 1930. his frequent correspondent. It was he who, more than any other, carried the evolutionary stimulus forward into the botanical schools of Britain. Sir Edwin Ray Lankester, whose portrait by Orpen was a poignant feature of last year's academy, died in August, 1929. Not only was he the leading zoologist of his time, but he has left a deep impress on general morphology, for he was the first to analyze from the evolutionary aspect the degrees of "sameness" of parts, whether in animals or in plants. These two octogenarians were among the latest links between Darwin himself and living men of science. And so this last meeting of the association before its centenary next year falls at a nodal point in the personal history of evolution.

Morphology, or the study of form, was closely interwoven with the life work of Darwin, and--to use his own words—"it is one of the most interesting departments of natural history, and may almost be said to be its very soul." Since the association has seen fit to choose as this year's president a botanist whose work has dealt specially with form in plants, the occasion seems apt for considering certain morphological questions that present themselves in this eighth decade since the "Origin of Species" was published.

The word morphology was applied by Goethe in 1817, in a general sense, to the study of form. Though a pre-Darwinian, he showed rare foresight in insisting that the living form is only momentarily stable, never permanent. But years elapsed before that instability of form of living things, which he clearly saw, became the very focus of evolutionary theory. Even Goethe's prophetic gaze was blurred by the hazy imaginings of idealistic philosophy. The clarifying mind of Schleiden resolved that mist by resort to naked fact. In 1845 he stoutly asserted that the history of development is the true foundation for all insight into living form. This opened the way for a host of workers, who patiently observed and compared the facts of individual development, particularly in plants of low organization. By them the field was prepared for the magic touch of Darwin, and in the enthusiastic words of Sachs, "the theory of descent had only to accept what genetic morphology had actually brought to view."

The effect of that theory should have been to sweep aside all idealistic morphology based on the higher forms, and to rivet attention upon organisms low in the scale. It was the habit of starting comparison from the highest state of organization that was the fundamental error of the idealistic nature philosophers; even now traces of it still persist. An illuminating alternative was presented by that noble passage with which the "Origin of Species" ends. Speaking of his theory, Darwin wrote: "There is a grandeur in this view of life, with its several powers, having been originally breathed by the Creator into a few forms, or into one; and that-from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved." He forecast from the application of his theory that "our classifications will come to be, as far as they can be so made, genealogies; and they will then truly give what may be called the plan of creation."

Whether there was only one original form of life or many is still an open question. Nevertheless, among the welter of organisms rightly held as primitive, the Flagellata may with some degree of reason be named as combining in their motile and sedentary stages respectively the animal and vegetable characters. They suggest a sort of starting-point from which the two kingdoms might have diverged. The probability of their common origin is strong; but the divergence must have been early, each taking its own independent course, with increasing size and complexity of the individual. In tracing this I would ask your special attention this evening to the kingdom of plants.

The first of the laws laid down by Lamarck² in his "Histoire Naturelle" as fundamental in the evolution of animals and plants ran thus: "Life by its intrinsic forces tends to increase the volume of every living body, and to enlarge its parts up to a limit which it determines itself." When in unicellular organisms, following this law, a certain size has been reached. fission follows, and the equal halves separate as new individuals. In pluricellular bodies, however, the products of cell-division do not separate, but continue a communal life; and the individual may increase, with further division of its cells, to large size and complexity. We may picture how, based upon the mobile stage of a flagellate, the aggregate might form an animal body with motility as a leading feature; on the other hand, based upon the sedentary stage, an immobile plant-body would result. The animal. adopting a predatory habit and colorless, might progress along lines of dependent nutrition, finding and ingesting food already organized; the sedentary green plant might evolve along lines of physiological independence, constructing its own organic supplies. Whether or not this be a true picture, the whole organization of the two kingdoms diverged on the basis of nutrition. Herbert Spencer contrasted them physiologically, showing how animals are expenders, while plants are accumulators; that the former are limited in their growth by the balance of expenditure against nutrition; in the latter growth is not so limited. Thus the problems that follow on increasing size may be expected to work out differently in view of the animal kingdom comprising organisms of high expenditure and not self-nourishing, while plants are self-nourishing accumulators.

The result of this difference may be illustrated by contrasting some of the highest examples of either kingdom; for instance, the elephant with the trees of the forest through which he roams. On the one hand, the relative fewness of the mobile elephants, their less stature and compact form, their columnar legs needed to support the barrel-like body, the receptacle for ingested food, the economy of external surface and the highly developed internal surfaces. On the other hand, the height, immobility and large number of the trees, with their massive stems and

² Lamarck died in 1829, and the association has contributed to a fund being raised for a memorial by the Linnean Society of Northern France.

highly complex shoots and roots, so necessary for acquiring food directly from the air and soil. We may further contrast the genesis of the individual in either case. In the mammal the parts are formed once for all, its embryology being an incident closed early in the individual life; but in the tree embryology may be continued for centuries, and is theoretically unlimited, except by death; during life it has the power of producing leaves and branches from every distal bud. The fact is that, though certain underlying principles are the same for both kingdoms, the working out has been distinct from the first. Hence the morphology of plants must stand on its own feet; indeed it has been said with some degree of truth that whenever botanists have borrowed their morphological outlook from the sister science they have gone wrong.

The normal development of a multicellular plant starts from the fertilized egg, and elaboration both external and internal follows on increasing size. Polarity, that is, the distinction of apex and base, is defined in most plants of high organization by the first cell-cleavage. The apex adopts at once the continued development that is its characteristic. Branching of various types follows in all but the simplest, to constitute the complex shoot, while correlative basal branching gives the root system that fixes the nonmotile body in the soil. The scheme of growth and branching thus started is theoretically open to unlimited increase, and the initiation of new parts is in point of number on a geometrical scale. This is suitable enough for organisms able to accumulate material, as plants do; indeed, the elaboration of the vegetative system will enhance its powers of selfnutrition, so far as the parts become functional; but this is never fully realized beyond the earlier steps.

The focus of all such development is the growing point, respectively, of root or shoot. Any one who carefully dissects a suitable bud, peeling off the successively smaller leaves, may finally see with the naked eye or with a simple lens a pearly cone of semi-transparent tissue at the tip of the stem. This is the growing point itself, which possesses theoretically unlimited formative power. It is like a permanent sector of the original embryo that is fed continually from the mature tissues below, and as continually forms fresh tissues at the tip. But as the tip advances, lateral swellings of the surface appear in due order, which are new leaves and buds. Various attempts have been made to link the genesis of these outgrowths of the radial shoot with the outer world as regards their position and number. But we have it as the latest authoritative statement on this point that such a relation does not exist. "This much is proved," says Professor von Goebel, that, "so far as we can see, the question relates to conditions of growth and symmetry that arise in the growing point. . . All theories as to leaf position that allotted a passive rôle to the growing point were mistaken, however acute the reasoning that was brought to bear thereon."³ This is von Goebel's summing up for external parts. On the other hand, within the growing point, and often, though not always, related to the external parts, there is a progressive formation of internal conducting tracts, continuous from the adult region upwards to the tip. A like reference of the origin and disposition of these vascular tracts to the growing point itself appears to be equally justified. In fact the tip possesses the initiative for both.

The complex shoot that results from such initiation is exposed as it matures to external conditions which modify its form. Their effect is very obvious in the young shoot of the higher plants. As the shoot elongates its young tissues are soft and plastic. While in this state its form may be influenced by gravity, the incidence of light, mechanical contact and other causes which produce reactions of form called "tropisms." All these promote the well-being of the whole. The net result becomes fixed as the part matures, and its constituent tissues harden. Thus the adult form is the consequence of the primary initiation at the growing point, modified by the conditions to which the plant may have been exposed during the plastic period. This is a commonplace of the text-books. But amid all the careful analysis and experiment that has been devoted to the influences which thus affect form, one factor, insistent and unavoidable, has been habitually left out, viz., the influence of size. Reference is occasionally made in text-books to the effect of surface tension in determining the simple form in minute organisms, such as unicellular algae and bacteria, and to the deviations from that simple form as the size increases and the influence of surface tension ceases to be dominant. At the other end of the scale of size mathematicians have calculated the extreme stature mechanically possible for a tree-trunk constructed after the ordinary plan, and of materials of known strength. The result is about 300 feet, and this coincides approximately with the limit of height of the canopy of a tropical forest. But in point of size practically the whole of the vegetable kingdom lies between the microbe and the forest tree. Unfortunately the study of these middle terms, from the point of view of change of form as the size increases, has not been pursued by botanists with the same perception as zoologists have shown in the study of animals.

At the back of all problems raised by increasingsize stands the well-known principle of similarity,

³ "Organographie," third edition, Part I, pp. 299-300.

which applies to all structures, inorganic as well as organic. It involves among other consequences that where form remains unaltered bulk increases as the cube, but surface only as the square of the linear dimensions. But in living organisms it is through the limiting surfaces, or "presentation surfaces," as they are called, that physiological interchange is effected. Provided a surface be continuous and its character uniform, it may be assumed that such interchange will be proportional to the area of surface involved. If, then, the form of the growing organism or tissue were retained as at first-for instance, a simple sphere, oval or cylinder-its surfaces of transit would increase at a lower ratio than the bulk which they enclose. There would be with increase in size a constantly decreasing proportion of surface to bulk, and as constantly an approach to a point of physiological inefficiency. But any change from a simpler to a more complex form would tend to uphold the proportion of presentation surface. Thus the success of a growing organism might be promoted by elaboration of form. Naturally other factors than that of size cooperate in determining form. Nevertheless the recognition of such elaborations of form, whether external or internal, as do tend in point of fact to maintain a due proportion of surface to bulk as growth proceeds should help to make morphology a rational study. The diffuse form habitual for plants, even the origin of leaves themselves, becomes intelligible from this point of view.

In the construction of any ordinary vascular plant there are three of these presentation surfaces, or limiting surfaces of transit, that are of prime importance: (1) the outer contour by which it faces the surrounding medium; (2) the sheath of endodermis which envelops the primary conducting tracts, and (3) that collective surface by which the dead woody elements face upon the living cells that embed them, through which water and solutes pass in or out. Each of these may vary independently of the others, and each would be a fitting subject for observation as bearing on this problem of size. But as a test case of the relation between size and form, it is the collective surface where dead wood faces on living cells that will meet our requirements best, for its study can be pursued among fossils almost as well as in living plants. The problem is one not merely of current physiology of the higher plants; it is one of adaptive progress. Accordingly measurements must be made of the wood of fossils as well as of living plants. and of young sporelings as well as of the adult.

We have seen that plants are essentially accumulators of material. A natural consequence of this is that primitive types, endowed with apical growth but

with no secondary cambium, will enlarge from the base upwards. Any sporeling fern shows this. The leaves themselves increase in number; each successive leaf is as a rule larger than the one that came before, and the stem that bears them also expands upwards. In fact it takes the form of an inverted cone. To grasp the size-problem for primitive plants the mind must be rid of the idea of the forest tree, with its stem tapering upwards, for that is a state of highly advanced organization. The primitive form of stem is that of an inverted cone, enlarging upwards, with a solid core of wood within. A cone standing upon its tip is obviously unpractical. Not only is it mechanically unstable, but if the original structure be maintained so that the larger region above is structurally a mere magnified image of the smaller below, a constantly diminishing proportion of presentation area to bulk must needs follow, in respect of all the limiting surfaces. Such stems would all tend to become physiologically insufficient. Our immediate problem is with the woody column. How can that due proportion of presentation surface of the dead wood to the living cells, which physiologists hold to be essential, be maintained in the expanding stem, so as to meet the increasing requirements of transit and distribution of the sap?

This is not the place for a recital of the details of elaboration of the wood which have been observed and measured. It must suffice to state in general terms how primitive woody plants have met the difficulty in the absence of cambial thickening. The starting-point is a minute cylindrical strand composed of dead tracheids only. Some primitive types show nothing more than a conical enlargement of this upwards, with the cells more numerous than before. The approach of a locomotive at speed along a straight track may visually suggest such increase in size without change of form; successive photographs of it might be compared with successive sections of those simple stems enlarging upwards without change of plan. The largest examples of this are found in some of the early club mosses and ferns, in which there is an enlarging solid woody core. But for want of resources in this and other features they have paid the penalty of death. Most plants having this crude structure are known only as fossils, and no really large vascular plant lives to-day which shows Under present conditions it is only where the it. size is small that a simple mass of dead tracheids seems to be effective for water transit. Thus we see that simple enlargement without change of form does not suffice.

In more resourceful plants a remedy is found in elaboration of the form and constitution of the primary wood. The changes which actually appear in it, as the size of the individual or of the race increases, are very various, but they all tend towards making the wood a living whole. The most efficient state would be that in which each dead woody cell or element faces upon one or more living cells, and this structure is approached in modern types of wood. In tracing the steps which have led towards it, whether in the fossil story or in the individual life of plants, we follow up an evolutionary history of high functional import. Actual measurements and calculations have shown in living plants the advantage that follows. It has been found that changes in the elaboration of form and structure of the primary woody column have saved, in specific instances, about 50 per cent. of the contingent loss in that proportion of presentation surface to living tissue which would have followed if a simple cylindrical core had been retained. The structural changes do not, it is true, maintain the full original ratio of surface to bulk, but it may well be that saving even half of the contingent loss would bridge the acute risk and lead to survival.

The molding and subdivision of the primary conducting tracts as a whole, or of the woody masses which they contain, present the most varied features. Their contours often appear arbitrary and even irrational, so long as no underlying principle is apprehended. They have presented a standing problem to anatomists. But when it is realized that as the size increases there is a physiological advantage in any elaboration of form whatsoever, a rational explanation is at hand. The variety of the forms assumed suggests the common principle underlying them all, which is that thereby a due proportion of presentation surface tends to be maintained.

One of the simplest and most frequent examples of such elaboration of form is that of the fluted column, which in transverse section gives the familiar stellate figure characteristic of roots. It is also seen in many stems, and is described as "radial." Where the part is small the woody strand is roughly cylindrical, but where larger it often becomes fluted, with varying number and depth of the flanges. In many instances the ratio of their number to the diameter of the whole tract is approximately constant. The structure is in fact adjusted to the size. This is so in roots generally, in leafy stems and in leafless rhizomes-and a similar size relation is even found in the fluted chloroplasts of certain algae. In all these an obvious risk following an increase in size tends to be eliminated. viz., an undue loss of proportion of surface to bulk.

The somewhat technical facts thus briefly described may be taken as examples of a relation of form to size which is very general. They suggest the existence of a size factor, which is effective in determining form. The susceptibility to its influence resides in the part that shows the results. The internal contours are defined ab initio, instead of coming into existence during the course of development, as is the case with the convolutions of the mammalian brain. In the stem and roots of vascular plants the fully matured conducting tracts may be traced upwards, with their outlines already defined, through successive stages of youth towards the growing point, which has been their source. Their form may be seen already outlined in its young tissue closely short of the extreme tip. This fact suggests that the susceptibility to the size factor resides in the growing point itself, for immediately below it those tracts possess that form which will aid their function when they are fully developed.

Of all the factors that contribute to the determination of form in growing organisms there is none so constant and inevitable in its incidence as this size relation. Its operation becomes manifest with the very first signs of differentiation of the embryonic tissues. The effects of other factors that influence form, such as gravity, light, temperature, contact and the rest, appear later in point of time. Their influence is liable to diminish as the organism reacts to them by curvature or otherwise, and to vanish when the reaction is completed. Under experiment they may be controlled or even inhibited. But the operation of the size factor is insistent; it can not be avoided either under conditions of nature or by experiment, though the size itself may be varied under conditions of nutrition and the permeability of the presentation surfaces may not be constant, with results as yet unknown. When we reflect that all acquisition of nourishment and transit of material in plants of primary construction is carried out through limiting surfaces, the essential importance of the size factor is evident, for upon its influence the proportion of each presentation surface itself depends.

The evidence that size itself is, among other factors, a determinant of form rests upon the constancy with which, in an enlarging organism, changes of primary form tend to maintain a due area of presentation surface such as active transit demands. That evidence has been derived chiefly from the conducting tracts of primary individuals as they enlarge conically upwards, and from parts belonging to distinct categories, also from comparison of different individuals not necessarily of close alliance. Very cogent evidence lies in the variety of the changes of form by which the same end is attained. Finally the converse facts bring conviction when, as often happens, a distal diminution of size in stem or leaf is accom-

life.

panied by simplification along lines roughly the converse of those that follow increase. All this shows that a real relation exists between size and primary form. The term size factor has been used to connote that influence which affects form in relation to size, but without defining it except by its results. Nevertheless, we have seen that its action may be located in near proximity to the growing point, or in the embryo itself. It has not, however, been found possible to assign to that effect an immediate cause. The attitude thus adopted towards an undoubted factor seems justified by the broad logic of science and by the practice of its highest votaries. When Newton put together his great physical synthesis he pointed out at the close of the "Principia" that the cause of gravitational force was unknown. "Hitherto I have not been able to discover," he said, "the cause of these properties of gravity from phænomena, and I frame no hypotheses." Likewise, in its own more restricted field of botanical phenomena, the size factor may be recognized as effective in development, though the

immediate cause of its effectiveness is still unknown. The position thus adopted assumes the shoot to be a unit, not a congeries of "phytons." The elaboration of its form, whether external or internal, would be a function of the increase in size of that unit, and the result would tend to maintain the adequacy of the presentation surfaces. This conception of the shoot and of its parts would accord with the views of General Smuts, as stated in his remarkable work on "Holism," published in 1926. Many present here to-day will have heard his address in Cape Town last year, when opening the discussion on "The Nature of Life." All will value this masterly statement in brief of his theory. I suggest that the operation of the size factor, whether in relation to external leaf development or in the elaboration of internal conducting tracts, illustrates that "measure of self-direction" ascribed by him to every living organism.⁴

The discussion of the problem of size and form in plants, which has occupied our attention thus far this evening, raises questions of profound significance in the sphere of pure botany. There is, however, another interest inherent in the study of plants beyond that of pure science. I mean botany as applied to the needs of man. To-day this touches human life more closely than ever before. Every meal we eat, many of the clothes we wear, timber, rubber—a whole volume in itself—the drugs, narcotics, dyes and scents, and most of that vast tale of accessories that ameliorate life, depend for their supply, quality and often for their existence upon the skilled work of the botanical expert. He is trained in our schools and univer-

4 "Holism," p. 98.

sities. His experience there is perfected by work on farms and plantations, in forests and in factories, often by adventurous life abroad. It would be superfluous for me to enter into detail on such matters, for happily the director of Kew presides over the botanical section, and he can speak with the fullest knowledge on the application of botanical science to modern

Government departments are now linked more closely than ever with universities and technical colleges by the golden chain of grants. The botanical institutes that have sprung from this joint source are mostly focused at such centers as Kew and South Kensington, Cambridge and Oxford, Harpenden and Merton, Long Ashton and Corstorphine, Plymouth and Millport, with important outliers such as Dehra Dun in India, the Imperial College of Tropical Agriculture in Trinidad and the Research Station at Amani, East Africa, while similar stations are to be found in Canada, at the Cape, in Australia and New Zealand. Their activities are as diverse as their positions. Agriculture, forestry, plant breeding and distribution, seed-testing, mycology and plant pathology -these are but a few of the headings under which applied botany is now pursued; and a duly qualified staff is required for each. Kew itself, thanks to the foresight of the Empire Marketing Board, is developing ever more and more as a coordinating center for the whole empire. Highly specialized study such as this has sprung into existence in the last half century. As regards Britain, its origin may be traced to the biological laboratory of the old Normal School of Science at South Kensington, where biological research was revived under Huxley and Thiselton-Dyer.

The first botanist there trained in pure science who turned the newly acquired vision to practical account in the interests of the empire was Marshall Ward. For two years he investigated the coffee disease that had half ruined Ceylon. It is a long step from this individual effort in the East to the firmly established and efficient Mycological Bureau, recently housed at Kew in a new building devoted to the world-wide study of the fungal diseases of plants. Such advance along a single line of applied botany may be taken as an index of the progress from simple beginnings in pure botany to that wide-spread attack now being made upon the economic problems that face imperial agriculture. The history of it thus briefly suggested may be read as a parable, showing how natural is the progression from the study of pure science to its practical application. For there is no real distinction between pure and applied science. As Huxley told us long ago, "What people call applied science is nothing but the application of pure science to particular problems."

At the moment there is an unprecedented demand for botanical specialists to fill investigational and advisory posts at home and abroad, and there is a shortage of applicants. The realization of this will doubtless be transmitted through the universities and colleges to the schools of the country and lead to an increased supply. On the other hand, it lies with the government to react as other markets do in taking steps to equalize supply and demand. A condition of the success of a specialist will always be a thorough foundation upon pure science, and this will be fully realized in the selection of candidates. Government, whether at home or in the wider imperial field, can make no better investment than by the engagement of the best scientific experts available. In respect of botany this has been attested by many well-known instances.

Some reference will naturally be expected here to the remarkable address given by Sir William Crookes in 1898, when the association last met in Bristol. He then forecast that, in view of the increase in unit consumption since 1871 and the low average of acre-yield, "wheat can not long retain its dominant position among the foodstuffs of the civilized world. Should all the wheat-growing countries add to their area to the utmost capacity, on the most careful calculation the yield would give us only just enough to supply the increase of population among bread-eaters till the year 1931. The details of the impending catastrophe," he remarked, "no one can predict, but its general direction is obvious enough." The problem is one of applied botany, with a setting of world economics and a core of physical chemistry. After raising the specter of wheat shortage before the eyes of his audience of 1898, Crookes laid it again by the comforting words:

The future can take care of itself. The artificial production of nitrate is clearly within view, and by its aid the land devoted to wheat can be brought up to the 30 bushels per acre standard.

We who are living within a few months of the fateful year of 1931 are unaware of any wheat shortage. Sir William Crookes' forecast of 1898 as to the advance in the production of combined nitrogen has been fully realized. Artificial fertilizers are not in view only, but at hand and in mass. Moreover, the northern limit of successful wheat culture has been greatly extended by the production of new strains with ever-shortening period between sowing and reaping, while the establishment of new varieties is extending the productive area in South and West Australia into regions where the rainfall is of short duration and restricted in amount. The future, since 1898, has indeed taken care of itself; so that, notwithstanding the warning of so great a man as Sir William Crookes, the wheat-eating public is still able to sleep well at night so far as the wheat shortage is con-What better example than this could we cerned. desire, not only of the importance of applied botany, but as showing also how its advance follows on research independently pursued? For the production of synthetic nitrogen, which has now become a commercial proposition, and the improvement of the strains of wheat by selective breeding along Mendelian lines, are both involved in solving this crucial question of food-supply. And both owe their origin to advances in pure science.

In conclusion, we shall all be conscious of the fact that a most distinguished former president of the association has lately passed away, one who more than any man has influenced the policy of government in relation to science. I mean Lord Balfour. We recall how in 1904 he, so thoroughly imbued with the spirit of his alma mater, presided over the meeting in Cambridge. He was distinguished as a philosopher, great as a statesman, and particularly so under the stress of war. He it was who, after peace returned, used his rare influence in transforming the war-time experiment of a committee of the Privy Council for scientific and industrial research into a permanent and essential part of modern government. But this was not all. His critical, constructive and experienced mind was led to formulate a still wider plan. A Cabinet Committee for Civil Research was to be established on the lines of the Imperial Defence Committee. He designed it so as to bring the whole national administration within the range of scientific influence. The Department of Scientific and Industrial Research, so wisely kept in being after 1919, now forms part of that larger scheme. This department is responsible for making recommendations as to the expenditure of funds voted by Parliament for research, especially in relation to industry. Thus science is welcomed into the inner circle of imperial administration. This the state owes to Lord Balfour.

And so in this hundredth year of its existence the British Association sees research recognized and fostered in the service of the state in a way never dreamed of in 1831, when a small body of enthusiasts met at York for the advancement of science. But though the individual seeker after truth may thus be involved in official harness, as of old an inner voice will yet speak to him. He will himself be as near to nature to-day as he was in the simpler days that are gone.