BUD VARIATION.

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THE reproduction of plants is effected in one of two ways, either by the contact of one elementary organism with another of a different kind, in consequence of which a spore or an embryo is formed, which ultimately developes into a perfect plant, or by the production of buds.

The word bud is here used in a broad sense to express any separable portion of a plant, not produced by sexual agency, and which when separated has the power of growing into an organism like the parent plant. The process of bud-formation then, reduced to its simplest expression, is a process of segmentation, or subdivision. Illustrations are to be found throughout the whole vegetable kingdom, but in no family are they more frequent, or do they play a more important part, than in the great group of the Fungi, among which are the moulds and blights so destructive to the higher plants on which they grow. One of the most remarkable circumstances about these plants is the varied manner in which they are reproduced. Spores, or reproductive bodies of four, five, or more shapes are met with at different times on the same plant, and, inasmuch as they are often formed at various times and under diverse conditions, it is no matter for surprise that they should have been assigned, not to the same plant, but to different ones, and hence each one has had the misfortune of being separately named.* Now. thanks to the labours of those who have, with infinite skill and patience, succeeded in unravelling the life-history of these plants, all these varied forms are known to be different states of the same plant. Of these spores some are true reproductive bodies in the sense already explained, while others are buds extending and multiplying the plant, but not reproducing it.

We do not know in all cases, indeed we only know in a few.

* See a paper on the subject of Polymorphism in Fungi, in "Popular Science Review," Jan. 1871, y Mr. M. C. Cooke. the complete life history of these plants and the particular office the bud-like formations fulfil. For our present purpose, however, it will suffice to say that they vary in size, form, and apparently in the conditions under which they are produced. In spite of these diversities, we know that they develop into organisms precisely like those from which they sprung.

Among the sea-weeds the same state of affairs exists; there are true spores and bud-spores, and these bud-spores vary in character on the same plant at different times and in different seasons.

In the Lichens we have a similar formation of true spores and bud-spores, but so far as is at present known, there is not the same diversity in the bud-spores, or "gonidia," of Lichens that there is in the other groups. There is, however, this difference; the bud-spore of the lower plants consists of a single cell, whereas in the Lichens it is made up of several cells : it is an aggregate, not a unit.

In Hepaticæ and Mosses the bud-spores are like those of Lichens, but more highly-organised. In the case of the Ferns and Equiseta there are buds very nearly like those of flowering plants, consisting of a number of minute scales, the outer of which remain scaly, and ultimately perish; the inner gradually develop into leaves, while the central pimple of cellular tissue from which these scales emerge lengthens into a shoot, that shoot into a branch, and so on.

Moreover, that bud, if separated and placed under proper conditions, will form a new plant.

In this way the gardener prepares his cuttings. He takes a "slip" with a bud attached, places it in moist earth, covers it with a bell-glass to prevent undue evaporation, and places it in a sufficiently warm locality. After a time the cutting "strikes," as it is termed; that is, it forms roots, which roots absorb nourishment. The cutting is thus truly a chip of the old block. That which the gardener does by art Nature herself often does unassisted. Many Begonias form buds from almost any portion of their surface, and in prodigious numbers, recalling the way in which similar buds are formed on the Mosses, but in even greater profusion. Other illustrations may be seen in the little bulbs which beset the stalk of the tiger-lily, or protrude from the margin of the leaf in Bryophyllum. This process of bud formation occurs also, to some extent, in the animal kingdom, as among the hydras, but is by no means of such general occurrence as in plants.

Under ordinary circumstances all the buds on any particular plant are in all material points alike, and the shoots resulting from those buds are also alike. There are differences in size and vigour and what not, for no two are precisely alike any more than any two sheep in a flock, or any two peas in a pod, are precisely alike; still, for general purposes, we may say that all the buds and all the shoots from those buds are alike. To such an extent is this true that it is the general practice amongst gardeners to propagate, by means of cuttings or grafts, any particular variety they may be desirous of perpetuating, because reproduction by seed does not offer the same certainty of reproducing the particular quality required as propagation by buds does. But it now and then happens that one or more buds on a particular plant, and one or more shoots, are not like the rest, and then we have what in garden phraseology is termed a "sport," but which is more correctly styled a budvariation.

We propose to cite sundry selected illustrations of this phenomenon, with a view to show how wide the range of variation may be, and in what different ways it may manifest itself. The simplest case, because it involves no appreciable change of form, is that in which a single bud, or a collection of buds in one particular part of a plant, is more precocious in its development than the others on the same tree. Instances of this kind are not uncommon. The buds on one particular branch may be each year considerably in advance in point of development of their neighbours, and this without there being any appreciable reason, such as more perfect protection or shelter on one side than on another. Thus we have seen two shoots of red currants taken from the same branch : on the one spray the flowers were ten days earlier in point of expansion, the new shoots being as much as 6 in. in length, while on the other spray the buds were only just expanding. With reference to this point, it may be remarked that the same phenomenon occurs in the case of seedling varieties. There are certain horse-chestnuts-some of which have almost historical fame, such as the Marronnier du Vingt-Mars in the Tuileries Gardens -which are year by year several days in advance of their kind in their development. But the circumstance of the whole organism exhibiting this precocity is not so striking as is the early development of one particular branch or set of branches, as compared with the rest.

In point of size, whether increased or diminished, there is often great difference in the different branches of the same tree. For some reason or other—what, no one knows—the shoots on a particular branch, instead of lengthening as the rest do, remain stunted and dwarfed. Several curious garden varieties of firs, such as the Clanbrasilian fir, have originated in this way, and are reproduced or propagated by cuttings or grafts at the will of the gardener. The birch affords frequently illustrations of this phenomenon, in the form of those tufted agglomerations of contracted shoots so strikingly resembling birds' nests. A similar occurrence is not uncommon in the wild cherry; and a correspondent—Mr. Webster, of the gardens, Gordon Castle informs us that he has observed similar growths in the common laburnum, in the Wych elm, and in the Scotch fir. Sometimes the determining cause may be discovered in the shape of an insect or fungus, but in this case the unusual condition ceases with the destruction of the impeding cause, whatever it may be, and the condition cannot then be perpetuated by the art of the gardener.

Variation in the colour of certain leaves or flowers is an equally common occurrence, and is perhaps more easily understood. Each individual cell, to a large extent, lives independently of its neighbours, and the secretions it forms and deposits are very often different from those of adjoining cells. Colouring materials, especially fluid ones, are notoriously liable to be formed in isolated cells. Again, variations in colour sooften depend on the mere superposition of cells containing material of different tints, that the changes met with, though striking to the eye, do not seem to indicate so complete a change as in the case of alterations of form or size. Very many of the variegated Pelargoniums, so fashionable now-a-days, have originated as "sports" from some previously existing variety. The intrinsic change between some of these varieties, even where apparently very considerable differences exist, is, in some instances, very slight.

A marked difference in the amount and quality of the pubescence is not unfrequently manifested in some of these cases of bud variation. A plant which ordinarily has its leaves and its younger branches invested with a coating of hairs (epidermal appendages), all on a sudden produces a shoot on which the leaves are destitute of such clothing, or *vice versá*. Some of the moss roses have originated from plain-leaved varieties in the manner just indicated.

But of all these cases the most striking are those which involve a change of form. We see, for instance, not unfrequently a particular branch bearing leaves very different from those on the rest of the tree, so different that but for their production on one and the same tree, the observer might readily take them to belong to different species. Many trees now cultivated for ornamental purposes have originated in this manner, such as the cut-leaved beech, the oak-leaved laburnum, and very many more, commonly to be found in plantations. Very often the whole "habit" or aspect of the tree is altered by these variations: thus many of the so-called "weeping trees" have sprung from a solitary branch of a tree which presented a pendulous character. Some trees, it may be remarked, naturally produce leaves of very different forms: especially notable in this respect is the Euphrates Poplar, *Populus euphratica*, supposed with reason to be the willow mentioned in the Psalms. Occasionally the variation is confined to one half of the leaves. A remarkable instance of this kind has been noted by A. Braun in a species of *Irina*, where one half of the leaf was undivided, the other deeply gashed into narrow segments.

The history of these variations is pretty much the same in all cases. All on a sudden a tree, which heretofore has produced shoots and leaves of the usual character, emits shoots with leaves of a totally different form. If they be such as the cultivator thinks likely to serve his purpose, he takes care to propagate them by means of grafts or cuttings. Sometimes variations of this character may be reproduced by seed, but there is little certainty as to this. The same kind of variation occurs in flowers and fruits. In the former it is usually associated with distinctly recognisable alterations in the phenomena of reproduction, as in what are spoken of as dimorphic or trimorphic flowers, some instances of which have been so carefully investigated by Mr. Darwin. To this latter class of bud variation we shall do no more than make passing allusion, but there are other cases which have apparently no relation to variations in the phenomena of fertilisation or reproduction, and which are strictly analogous to those already mentioned as occurring in the leaves. Every now and then, for instance, two roses of different forms and colours will be met with on the same stalk, such as a white moss rose in association with a pink one of a different form and destitute of mossy appendages. We have in a former paper in this Journal referred to some of these cases and to the famous Cytisus Adami-a laburnum bearing yellow and purple flowers as well as leaves of different character-and have also alluded to the alleged causes of these strange phenomena, on which account it is not necessary now to do more than refer to them. What is a rare occurrence in the rose, and is only known in one or two species of laburnum, is comparatively common in the chrysanthemum. There are indeed particular varieties of this favourite autumn flower which are specially liable to produce flowers of different characters on the same branch. Generally speaking, but by no means always, the change is confined to the colour of the flower only, and colour, as we have seen, is proverbially fickle in flowers. Among commonly cultivated plants azaleas and camellias are peculiarly liable to "sport." In the former plants indeed one may often witness much variation in the shape and colour of individual blossoms, and very frequently parti-coloured flowers and others intermediate between extreme forms. In the case of the fruit similar variations occur-peaches and nectarines on the same bough; black and white grapes in the same bunch; gooseberries of different kinds on the same bush; pears, apples, or cherries, of different shapes, colour, and flavour, on the same bough. All these are, though of course rare, yet familiar occurrences to those on the look-out for such phenomena. It is necessary in some of these cases to investigate closely to see whether or no grafting of different sorts on one stock has not taken place. No doubt some of these cases, recorded by lovers of the marvellous, were simply cases of adhesion or inoculation, but, allowing for these, there still remains a large number which cannot be explained by any such process.

The above-cited illustrations might be largely added to were it necessary to do so. Mr. Darwin's work on "Animals and Plants" contains allusions to many others, and includes many references to the literature of the subject. The horticultural journals, British as well as foreign, contain very numerous records of such cases; * but we have cited enough for our present purpose, and may now pass on to the discussion of some of the alleged causes of the phenomena in question.

It must first of all be premised that these bud variations are not necessarily to be considered as malformations. Their organisation is often perfect, they are not distorted, they are simply variations; and next, they occur not exclusively in plants that have been long subjected to cultivation, but also in wild plants. Now plants that have been long in cultivation have for the most part been hybridised or "crossed" over and over again. Thus in the case of the pelargonium, it is supposed that all the immense number of different kinds now in cultivation have originated from two or three species. These have been hybridised or crossed, their offspring has been crossed in the same way, and so in the pelargonium of the present day we have a plant which has, so to speak, a great deal of very confusedly mixed blood in it.

Bud variation is very often only a reversion—a harking tack—to the characters possessed by the parent; it is the result, as the phrase goes, of a *dissociation of hybrid characters*, the consequence of a sort of filtration by which the constituent elements become separated from their previous admixture.[†] This reversion may be proximate, just as you may see in a family of children that, while most of them resemble both

* A list of many such instances may also be found in M. Carrière's "Production et Fixation des Variétés."

+ The papers of Naudin, Braun, Rejuvenescence (Cytisus Adami), and Duchartre, Note sur le Chasselas Panaché, in the "Journal de la Société impériale et centrale d'Horticulture," 1865, should be read in reference to this part of our subject. parents, some are like the one or the other, while some again present little likeness to either parent, but reproduce the lineament of some remote ancestor. A singular illustration of this phenomenon was brought under the writer's notice by Mr. Wills, and in which two plants of pelargonium showed the characters of three separate ancestors; the exact lineage of one was not fully known, but the history of the other was definitely recorded. The plant in question presented, after the fifth generation by seed (and not till then), various branches bearing leaves undistinguishable from those of the varieties known as "Unique," "Beauty of Oulton," and "Italia Unita"—three very distinct varieties, each of which were known to have been at some time or another ancestors of the plant in question, either as furnishing pollen or as the seed-parent.

Another plant of mixed origin, after retaining its characters for three years, suddenly produced branches some of which had leaves of the form and colouration of those of "Beauty of Oulton," the original seed-parent, while the remainder were bedecked with leaves in all respects similar to those of "Lucy Grieve," the ancestral pollen or male parent. The two varieties in question are widely different. In the cases just alluded to there was not a mere change of colour—an affair of comparatively minor importance—but there was a change of configuration and substance. Other cases of a similar nature have been recorded by various observers, amongst others by Mr. Grieve, the raiser of the popular "Mrs. Pollock" pelargonium.

Of course any plant produced from seed requiring for its development the contact of the pollen tube with the ovule or the germinal vesicle must be held to have mixed characters, and more markedly so in the case of unisexual flowers, either monœcious or dicecious. From this point of view a case lately recorded by Mr. Meehan becomes very significant. That gentleman relates that he obtained cuttings from *Cuphea leiantha*, a diœcious plant, producing its male and female flowers on different individuals. It is not stated whether the cuttings were taken from a male or a female plant, but it is stated that some of these cuttings produced male, others female, plants, and yet all were taken from a plant of one sex only. So, too, it is well known that certain unisexual trees will in some seasons produce male flowers only, in other seasons female flowers only, and vice versâ.

To enter into questions relating to the sexuality of plants would, however, lead us too far. We merely now indicate the facts, as proofs of the composite character of the plant.

But dissociation of mixed characters will not account for all the cases of bud variation. Very often we have no evidence at all of previous hybridisation or crossing; or, even where such has existed, the form produced is not like that of either of the supposed progenitors.

Such cases as the fern-leaved beech do not seem explicable by either hypothesis. The sugar-cane, which rarely if ever flowers, and hence offers no opportunity for hybridisation, nevertheless produces new varieties by means of bud variation. Potato tubers, again, vary greatly often on the same plant, but these may be the result of former crossing. A case related by Mr. Meehan, in the sweet potato (*Convolvulus Batatas*), is, however, not open to this objection. The plant in question, it appears, never flowers in the Northern States of America, and yet it has been known to produce tubers of two distinct varieties—the "Red Bermuda" and the "White Brazilian"—on the same root.

Reversion to an ancestral condition is a still more hypothetical cause than dissociation of mixed characters, as we have scarcely ever any means of knowing what the assumed condition was. We have, therefore, to look to other causes. We shall not advance matters much by attributing the changes in question to an innate tendency to vary possessed by buds as well as by seedling plants, which are, in so many respects, analogous with buds. Doubtless there is such a tendency, but we want to get at the "why and wherefore" of the proclivity. The following illustrations may in some slight degree furnish a clue to the attainment of the desired end. In the first place we must not overlook the circumstance that, under ordinary conditions, the several organs of plants often vary according to the part of the plant upon which they grow. Botanists recognise this when they give different names to the root-leaves, stem-leaves, floral-leaves, bracts, &c. Again, there are such cases as the seedless barberry. This plant can be propagated by cuttings, and its seedless condition can be thus perpetuated : but if the plant be multiplied by suckers or shoots thrown up from the underground stem, the fruits produced have seeds as usual. This is an evidence of a difference in the internal organisation of different parts of the same plant. Another illustration of a similar character lately came under observation, in which a sucker from the root of the tree of heaven. Ailanthus glandulosa, produced egg-shaped leaves and a dense cluster of flowers while only a foot or so in height (see fig. 1), the ordinary habit of the tree being to grow for several years before flowering, to form a lofty stem, and to produce large compound pinnate leaves like those of the common ash. This, in gardening phrase, would be a "sport," but it is clear it had nothing to do with hybridisation, the form produced being unlike that of any other allied plant. Moreover, there is no

evidence to render the occurrence of hybridisation in this particular case at all probable. We can only attribute it to a



difference in the organising force manifested in certain parts of the plant as contrasted with others.

Of a similar character are the observations made by practical gardeners as to the difficulty, and in some cases impossibility, of perpetuating a variegated condition of the leaves by dividing the root; plants so produced having green leaves. A French nurseryman, M. Lemoine, notes this in the case of variegated pelargoniums, and in certain forms of Symphytum and Phloz, and his experience tallies with that of English cultivators. Again, in the common practice of budding roses, if the bud be taken from a long rampant "gross" shoot, with a great tendency to form leaves and little tendency to produce flowers, the bud, transferred to its new home, will reproduce the undesirable characters of the parent shoot: hence the care requisite in budding to take buds from short-jointed flower-bearing shoots. A similar precaution is exercised by gardeners in the case of fruit-tree grafts.

The different forms which plants assume at different stages of their existence under normal circumstances must also be taken into consideration in speculating on the origin of bud variation. A large number of plants do not immediately assume their wonted habit, they pass through an intermediate stage or stages. This is particularly observable in the case of Conifers, the juvenile state of which is often very different from the appearance presented in the adult state. It now and then happens that, after a plant has lost its youthful characters and assumed its full-grown developement, sundry branches, for some unknown reason, revert to the infantile form. In the common ivy we have a familiar illustration of a similar phenomenon. When the plant is about to produce flowers it assumes an erect bushy habit, its leaves alter in form, indeed its whole aspect becomes changed. If now such branches be taken off and propagated, the characteristic form remains as in what are called tree ivies. If the life history of such a plant were not known, the bud variation just mentioned would appear even more inexplicable than it now does. Again, the leaves and flowers produced on the same plant at different seasons are often naturally different. Dr. Balfour has lately called attention to a remarkable instance of this phenomenon in a species of hawkweed, Hieracium, which presents three distinct forms according to the season at which it flowers. Occasionally even a casual observer is struck by the appearance of a second or even a third crop of flowers on laburnums, or pear-trees, Wistarias, and others. In such instances it will generally be found on examination that the adventitious flowers spring from buds which under ordinary circumstances never produce flowers, but only leaves, or that they are placed on portions of the tree usually devoted solely to the production of leaves. How much the aspect of the tree is altered in such cases may readily be surmised : the casual spectator cannot fail to notice it, but the explanation of the phenomenon rarely strikes him.

As might have been anticipated, a change in the external conditions under which a plant lives will often cause very considerable variation in its form: thus a species of fig, *Ficus stipulata*, is commonly grown on the walls of hot-houses, to which it clings ivy-fashion. The same plant grown as a standard in a pot has a totally different appearance. On the wall it has small thin leaves, and it clings to its surface like a large moss or a miniature ivy. Planted out it forms a stout bushy shrub with large coarse leathery leaves, so different from those formed when the plant is growing against a wall that no botanist unacquainted with the history of the plant would hesitate for a moment in ranking it as a distinct species. Some of the Marcgraavias present similar phenomena. In both the plants just named the writer has seen on plants growing against a wall shoots produced of the character of those formed by the plant when growing unsupported. The inference from these facts is that what we call "sports" or bud variations are often only exceptional illustrations of a normal tendency exceptional in so far that they are manifested at unusual times and places and under unusual conditions.

The individuality or comparative independence of buds-a circumstance often noticed-is also brought prominently into view by such facts as we have recorded. An interesting question arises as to whether there are differences in the plant originating from bud variation as compared with one the produce of variation from seed. It is a matter of every-day experience with gardeners that seedling plants vary greatly-even though the produce of the same seed-vessel, and even though not the offspring of hybridized or cross-fertilised parents. Is there any perceptible difference between a seedling variety obtained as just explained and a bud variety? In other words, are there any means of distinguishing, in the case of a cultivated plant of unknown history, a "sport" from a "seedling"? We have tried in vain to find any such difference. The experience of the most able cultivators furnishes no data on this head. But although this is so, there is an equally prevalent impression that while a variety cannot always be perpetuated "true" from seed, it can be propagated unchanged by cuttings or grafts. The best varieties of apples or pears-to cite only one instance -are propagated by grafts, because there is no certainty at all that the pips will reproduce the desired variety; far more commonly they produce something else. There is, then, a difference between seed variation and bud variation, in the greater degree of permanence of the latter. That this difference is not absolute is shown by the following case recorded by M. Rafarin in a French horticultural journal.

"In 1866, at La Muette, a pelargonium with pale rose-coloured flowers was observed to bear a branch, all the flowers on which were of a deep red colour. Cuttings were taken from this 'sport,' from which 20 plants were raised, which flowered in 1867, when it was found that scarcely two were alike. Thus while some bore rose-coloured flowers like those of the original plant, others had red flowers, like those of the 'sport'; others again had red and rose-coloured blossoms on the same plant and even in the same truss. Nay more, even the petals partook of the parti-coloured nature, for in the same flower were petals of a rose, or a red colour, or of a blended hue. Unfortunately neither the name of the variety nor its genealogy are given, so that we are unable to say positively whether this was a case of reversion or no."

It may perhaps be said that seedling variations such as happen in the apple or the pear are the necessary outcome of the crossfertilisation to which the plants in question have been subjected for ages, just as the bud variations in the case of the pelargonium are. This may be true in some cases, but can hardly be so in all: for instance, in a bed of seedling conifers, such as Lawson's cypress or deodars, raised from imported seeds taken from wild plants, often from the same cone, the number of seedling varieties is often large. In the case of cultivated plants as of domestic animals, Mr. Darwin has shown how the variations that arise are directly connected with the objects for which the particular plant or animal is cultivated. A plant, for instance, grown for the sake of its fruit is apt to vary in its fruit characters more than in its leaf characters. But although this may and no doubt does apply to a considerable extent in the case of seminal variations, it seems less applicable in the case of bud variations, as will be judged from the illustrations before given, as also from the negative evidence afforded by a plant like the Jerusalem artichoke, which is propagated exclusively by its tubers, and indeed never ripens its seed in this country, and which has produced no variation by "sport" or dimorphism, although so largely grown and for so long a period.

Mr. Darwin attempts to explain the phenomena of bud variation, as of inheritance and reproduction generally, by his hypothesis of pangenesis. This hypothesis proceeds on the assumption that every cell of a living organism gives origin to an innumerable host of "gemmules" in minuteness as in number transcending conception. These gemmules divide and multiply, or they lie dormant possibly for ages. They circulate throughout the organism or they become aggregated together, and so form embryos or buds, and they are transmitted from one generation to another. There is nothing improbable in the assumption of the existence of these gemmules; and, if we take their presence for granted, it is easy to see how they afford an explanation of the phenomenon of reversion to an ancestral condition, such as bud variation so frequently presents. Gemmules derived from a plant's remote progenitors are, according to the hypothesis, circulating in the present generation, and it only requires the occurrence of favourable conditions to determine the revivification of these now dormant gemmules to reproduce the ancestral form. There still remains the difficulty of ascertaining what the favourable conditions are which determine this change. The reason for the prolonged dormancy of the gemmules is also not obvious. But, supposing we admit the gemmule hypothesis as sufficient

to account for reversion by bud variation, there yet remain that larger class of bud variations wherein there is no suspicion of reversion.

This latter category, so far as we see, can only be explained by Mr. Darwin's assertion that, in "cases in which the organisation has been modified by changed conditions, the increased use or disuse of parts or any other cause, the gemmules cast off from the modified units of the body will be themselves modified, and, when sufficiently multiplied, will be developed into new and changed structures."

But before we can, with propriety, avail ourselves of this latter explanation, we have to be satisfied that a change of conditions has really been in operation. And this is too often beyond our ken. The majority of bud variations not distinctly referable to reversion, appear suddenly, without any obvious change of external condition, we know not why or wherefore. Suppose we admit, on the ground of intrinsic probability, the operation of changed conditions, even though we may have no direct evidence on the point, we have yet to explain how and why one particular shoot on one particular part of a plant should be acted on in this way, when there is no appreciable reason why it should be influenced more than the rest.

There is still another way of explaining the phenomena on the gemmule hypothesis, and that is, by supposing changes in the number, arrangement, or position of the gemmules; and this supposition, though plausible, is yet based on a number of mere assumptions, and, moreover, it leaves the cause of the altered condition of the gemmules entirely unexplained.

To sum up, then, we may say that there is no absolute difference between bud variation and seed variation. The changes manifest themselves in the same manner and in the same organs in the case of buds or seedlings respectively. The conditions, so far as we know, that produce variation in the one are the same that are effectual in the other. Lastly, apart from the different mode of origin, there is no essential difference between a bud formed as the result of fertilisation, *i.e.*, an embryo, and one formed without the direct agency of the two sexes, *i.e.*, a bud.