

ART. VI.—*Tendril Movements in Cucurbita maxima and C. Pepo*;
by D. P. PENHALLOW. With Plate V.

IN the summer of 1874, certain experiments were made with reference to the mechanical energy with which the organization of tissues is effected, as illustrated in the lifting power of the mammoth squash.* During the same and following years, as suggested not only by these experiments, but more particularly by Darwin's paper on Climbing Plants in the Journal of the Linnean Society for 1865, I undertook to study the movements of the squash tendrils and terminal bud, and trace the relation of these phenomena to meteorological and other conditions of growth, in order to determine if possible, a rational solution of a question at that time not at all well understood, except in its more external aspects, as studied by Sachs, De Vries and Darwin. At that time it was recognized that plants possess no nervous system, yet phenomena were continually observed which were wholly inexplicable upon any other ground than that the plant must possess something akin to nerves. At that time also, it was regarded as fully demonstrated that each protoplasmic mass of a cell is a unit within itself, its limitations being determined by the surrounding cell wall.

The observations which I then made upon tendril movement have never been published, though the results were fully worked out five years since. Publication was withheld in the hopes that at no distant day, the correct solution of certain phenomena, which could not then be satisfactorily accounted for, might be reached.

The very important discoveries of the past few years, touching the continuity of protoplasm, served to give a clue which has been followed up during the past summer with the results that the true explanation of the tendril movement in *Cucurbita* and possibly also in the whole family *Cucurbitaceæ*, appears to have been reached from histological research, and we now feel justified in presenting the facts obtained, more especially as they will doubtless tend to enlarge an already rapidly widening field for observation.

* Phenomena of Plant Life; Clark.

Darwin has shown in his several works, in a very careful and painstaking manner, how the movements of plants are produced or modified in certain organs by various mechanical influences, as well as by natural conditions to which plants are ordinarily subjected. He has also shown us what direction these movements take and the figures they describe, and to his first paper on Climbing Plants, in the Journal of the Linnæan Society for 1865, was due the suggestion that, if these movements are but normal manifestations of growth, dependent upon the perfect maintenance of the vital condition of the plant, they must necessarily be affected by whatever operates in any manner—whether to augment or diminish—the physiological changes in, and conditions of the plant as a whole; and, therefore, that they must afford a ready means of determining the effect of varying meteorological conditions upon growth, and those which are best adapted to its promotion. It was, therefore, with this idea in mind, that the experiments here recorded were undertaken. It was recognized as of prime importance that, to secure results which should be of the greatest value, the plants must be grown in the open air and under the varying conditions to which they would be naturally subjected. It was also thought desirable to select a plant of vigorous growth, in which movements were sufficiently pronounced and rapid to permit of frequent and accurate observation. The mammoth squash (*Cucurbita maxima*) was found to answer the requirements better than any other plant obtainable. With this, all the original experiments were obtained, but during the past summer, *C. pepo* was used for the purpose of confirmation and to gain information upon one or two additional points of minor importance. This was possible, since the structure of the tendrils and also their movements are the same in each case, so that our remarks may apply equally well to both species, and doubtless to a very large extent, to the entire family.

Seeds of the mammoth squash were planted in a carefully prepared lot, sufficiently removed from trees and buildings to prevent the plant being subject to any but the normal conditions of light, air, temperature and moisture. As soon as the vines were long enough, they were carefully trained from west to east, their branches being allowed to run in whatever direction they might choose. The tendrils, upon which observations were made, were in some cases selected as soon as they became straight and active, in other cases not until they had been moving for some hours or perhaps a day. The aim, however, was to record the movements for as many consecutive hours of night and day, during the entire period of growth, as possible. Through variation in movement of the tendrils and terminal bud, rate of growth in the vine and weight of the

squash, a knowledge of the conditions favorable and adverse to growth was sought. To accomplish this satisfactorily, observations were made through day and night for one week, at least once each hour, generally at much more frequent intervals, and every observation recorded was accompanied by record of local* temperature, humidity, cloud, condition of the plant, etc., etc.

The method of recording the tendril movements was as follows:—

A board made two feet square, was provided with two pointed legs by means of which—thrusting them into the ground—it could be securely fixed in a vertical position. Upon the board there were fastened several sheets of heavy white paper, so arranged that each could be removed in turn, without disturbing the position of the board, (fig. 1). The recording board thus prepared was then firmly fixed in a position at right angles to the horizontal tendril. To prevent any accidental movement of the latter from its proper position, a stake was driven by the side of the vine at the node from which the tendril arose, and the plant was then secured firmly to it. With the tip of the tendril only one-fourth of an inch from the surface of the paper, it was an easy matter to mark the position at any time with a pencil. The position was noted whenever, from the rate of movement and distance traveled, it was thought a change of direction was about to occur. In this way the observations were made at varying intervals, sometimes of one hour, sometimes of only one-half a minute, and many, originally taken, were finally eliminated from the results whenever they fell in the same straight line. The time was always carefully noted, as also all conditions of atmosphere and of the plant which might have a possible bearing upon the movement.

Tendrils.

The tendrils of the squash are modified leaves,† and are placed alternately opposite, an arrangement well adapted to bring the plant between secure but elastic supports on either side. They are composed of four or five long and slender filaments—wholly devoid of external appendages by means of which they can become attached to objects—borne upon a stout stalk or petiole of from 6 to 10^{cm} in length. The arms are of very unequal length. In vigorous vines the longest arm, which is the first to develop, often exceeds 30^{cm} in length. The extreme lengths of vigorously moving tendrils may gener-

*The temperatures were taken from a thermometer hung by the side of the plant, two feet above the ground.

† The exact morphological nature of the tendril in *Cucurbitaceæ* is still a matter of some doubt. It is variously regarded as a modified leaf, stipule or branch. Evidence favorable to each of these views may be adduced.

ally be taken at from 8^{cm} when they first emerge from the bud condition, to 35^{cm} when activity ceases.

At first rolled up compactly as they come from the bud, with the coils turned inward, the arms gradually extend to their full length, and, within two days, activity begins in the central arm while those which are lateral may yet be loosely coiled. After motion once commences, the order of activity is from the center outward, until all are involved. In this we see one of those curiously interesting provisions of nature for the accomplishment of her plans. If all the tendrill arms were of the same length, or, more important, became equally active at the same time, the express purpose for which they were provided, would fail of accomplishment in nine cases out of ten. As it is, their activity extends over a considerable period, and the first one in motion may have grasped an object, or, failing, have become hard and inactive, long before the last gets fairly in motion. It is the function of the tendrill to draw the vine to a secure and elastic support. By the succession of activity here exhibited, one arm after another is enabled to grasp the object of support and gradually draw the vine up to a secure position; whereas, by a simultaneous activity of all, a few only might gain hold, or, if all, only the last one or two would bear all the strain, and the vine would remain at a greater distance from the point of support.

Histology of the Tendril.

In its histological aspects, the tendrill of the squash vine presents a most interesting study, and throws much light upon the cause of the movement; indeed, it is to evidence of this character that we must chiefly look for a true solution of this question. We shall consider this part of our discussion under two heads: (*a.*) Structure and peculiarity of component tissues in their mutual relations, and (*b.*) Continuity of protoplasm.

(*a.*) Transverse sections of the tendrill display the form and general structure which is shown in fig. 3. From this it will be seen that within the fundamental structure there are seven fibro-vascular bundles, the largest of which are along the lower side of the section and therefore traverse the lower region of the tendrill arm through its entire length. A more detailed examination discloses several important facts. Directly beneath the continuous epidermis of one row of cells, there is a somewhat thick layer of collenchyma tissue (fig. 3 *a*), extending completely round the tendrill with the exception of three regions where its continuity is fully interrupted by parenchyma tissue (fig. 3 *b*). These areas of interruption are found to occupy the same relative positions in all squash tendrills;

one lies in the concavity of the upper surface, while the other two occupy lateral positions, being situated at the extremities of the major axis of the section. Within these areas (fig. 3 *b*, *b'*, *b''*), the tissue is found to be composed of rather large and rounded, somewhat thin-walled, parenchyma cells (fig. 5) containing protoplasm and a large amount of chlorophyll, while there are also inter-cellular spaces and corresponding stomata in the epidermis. Externally this tissue may easily be seen to extend the entire length of the tendril, forming three darker green bands alternating with the more whitish green bands of collenchyma tissue. The color distinction between them is most obvious, both externally and in transverse section. From the very prominent part which this tissue takes in the ordinary circumutations of the tendril and the frequency with which pointed reference must be made to it, we have deemed a descriptive term essential. We have therefore given it the name of *vibrogen*, or as signifying that the origin of the movement is to be found there. Immediately within the collenchyma layer is a zone of rather large and rounded parenchyma cells (*c*, fig. 3) consisting of three or four rows, the innermost cells being smaller. This tissue connects the three vibrogen bands through their inner portions. The cells are filled with protoplasm, chlorophyll and other granular matter, though the chlorophyll is conspicuously less than in the three bands of vibrogen which it unites with. It is this layer of cells, however, which imparts the green color to the tendril as a whole, modified as it is by the external layer of collenchyma. Directly interior to this zone is a narrow belt, within which the fundamental tissue becomes meristomatic at a very early period, and ultimately—usually very early in the growth of the tendril—gives rise to numerous rather small and thin-walled wood cells (fig. 3 *d*, *d'*, *d''*). In the earlier periods of growth, this wood tissue will be found forming a crescent along the lower side of the transverse section, as at *d*, but later, toward the left of the tendril, it arises opposite the two masses of collenchyma tissue near the upper side *d'*, *d''*, its interruption or want of continuity coinciding exactly with the want of continuity in the collenchyma, or with the position of the vibrogen tissues. Ultimately, however, these breaks may close up, and the woody zone then becomes more or less continuous around the entire tendril. So long as the tendril arm remains active, these wood cells are thin-walled (fig. 4 A), but as age advances and activity diminishes, the wood cells are found to become thicker and more resisting and finally assume the appearance of all highly lignified cells (fig. 4 B), thus ultimately defining the hard and woody nature so characteristic of these tendrils after they have been for some time coiled about a support.

Interior to the wood zone is the remaining portion of the fundamental tissue. In the outer portion of this, the vascular bundles already referred to arise, while the inner portion remains as a pith region and often shrinks away from the center, developing a lysigenetic air cavity, thus leaving the basal portion of the tendril arm like the petiole from which it arises, hollow.

That these various tissues bear an important relation to the movement of the tendril and its power to grasp an object or coil up without contact, is most certain, and what these relations are will be seen after we have considered the motions themselves.

We should also remark, in passing, that this structure is not peculiar to the tendril arm, since in all its essential features, i. e., collenchyma, vibrogen and woody tissue, the same structure is to be observed in the petioles of both tendrils and normal leaves, with this difference, however, that in these latter, the vibrogen is found in more than three bands, and these are arranged at tolerably regular intervals about the circumference of the petiole.

(b.) The recent developments concerning the continuity of protoplasm in vegetable tissues, at once served as a suggestion that in active tendrils this continuity should be found, if anywhere, and that it must doubtless furnish an important clue to the proper explanation of many phenomena connected with movement of the tendril itself.

Thin transverse sections of the tendril were treated upon a glass slide while yet quite fresh, with concentrated sulphuric acid for a period of two or three seconds, at the end of which time they were quickly immersed in water and thoroughly washed to remove all acid. Care must be taken not to allow the action of the acid to proceed too far, or both structure and protoplasm will be destroyed. If successful, the cell walls should be strongly swollen, but not broken.

After washing in water, the sections were stained in picric aniline blue,* being allowed to lie in the stain for ten minutes. At the end of this time they were thoroughly washed to remove all the picric acid, as is indicated by the failure to discharge any more yellow, and a change of color in the sections to a well-defined blue. The results are best when the alcohol washing succeeds in removing all the picric aniline from the cell walls, but leaves a maximum of aniline blue in the protoplasm. At the end of this treatment the sections were mounted in 25 per cent glycerine for examination.

* This is essentially the stain recommended by Gardiner (Phil. Trans., 1883, p. 817), and was prepared by saturating a 50 per cent solution of alcohol with picric acid. To this add BB blue until a dark greenish blue solution is produced.

For permanent preservation, the sections may be mounted directly in glycerine jelly, or they may be washed out in water, cleared up for a few seconds in concentrated carbolic acid* and then mounted in chloroform balsam. Either method gives very satisfactory preparations, though the former is preferable.

The results obtained by this process are most satisfactory, particularly in the collenchyma tissue (fig. 6). There the walls become strongly swollen, and the protoplasmic connections are sharply defined as blue threads running through the colorless walls (fig. 7). Salt solution does not give so satisfactory results, through its failure to properly swell the cell wall, which is essential, while on the other hand, the cellulose reaction developed in the collenchyma under the action of chlor-iodide of zinc, renders this process of little value in this particular case, as there is then too little distinction between the blue filaments and the blue cellulose of the cell wall.

It is thus clearly demonstrated that there is a distinct continuity of protoplasm through the living tissues of the tendril, particularly in the collenchyma (fig. 7), and this must have an important bearing upon the transmission of impulses, e. g., those produced by irritation, from one portion to another.

Externally, the form of the tendril arm is that of a long filament, well-rounded on the lower side, but flattened and even slightly channeled above. The extremity, for a distance of half or three-quarters of an inch, takes a more perfectly rounded form and turns slightly downward, the concave side of the curve being that which is always the more sensitive. The lower surface, which is almost entirely free from epidermal hairs, is always the most sensitive to contact, curvature being readily produced by contact of the finger with it, though the same effect is not produced upon irritating the upper side. A curve in one direction as the result of irritation, is removed only after the lapse of some little time, when, by continued growth, the opposite sides become equal in length. The lower side is the one which, in the majority of cases, first comes in contact with an object of support, and in any case, it is finally the side toward which the bending most strongly tends.

In one case, a tendril irritated on the lower side by the finger, coiled upon itself completely in one minute. The cause of irritation removed, the tendril straightens out again, provided it is not already too far advanced in age, or the irritation is not too long continued. Slight pressure such as would be caused by small loops of thread, also often exert a definite influence.

* Phenol used in this way gives most satisfactory results as a clearing reagent, and for a long time has with us, replaced turpentine entirely. Jour. Royal Mic. Soc., vol. iii, pp. 693 and 858.

Irritation on the upper side, near the tip, produces a curvature through the central region of the arm, with the concavity uppermost, showing in this, a distinct transmission of the impulse to somewhat remote parts. A sharp blow on the upper surface, as with a pencil, throws the arm into a series of long undulations. Whenever the irritation is quite local, the resulting flexure is abrupt, but the curve becomes longer in proportion as the irritating body is moved over a greater length, thus showing that the impulses of this character are not readily transmitted.

During the entire movement of the tendril, distinct torsions are developed, as may readily be seen by following one of the lines of vibrogen tissue. Oftentimes the torsion is developed to such a degree as to turn the tip fully one-half revolution, thus making it apparently bend upward instead of downward. This fact is one which has all the more significance from the statement of Sachs* that in *Cucurbitaceæ* "no torsion takes place." Repeated observations, however, have fully confirmed its correctness. That this torsion bears an important relation to the circumnutating cannot be doubted, and what its connection is, will be seen later.

When in its circumnutating, the tendril arm comes in contact with an object, it immediately twines about it and grasps it firmly, the basal portion at length forming a double, reversed spiral, which draws more and more closely, and thus secures the plant more firmly to its support. It then rapidly becomes more and more hard and woody. Frequently the tendrils coil about themselves or other tendrils, or catching upon the edge of a leaf, they bend it under into close rolls, which increase in size as the coiling of the tendril progresses. Failing to secure an object of support, the tendril at length coils up in an irregular, knotted spiral, drops downward and either decays or gradually dries up and becomes hard and woody.

The woody character, which the tendrils assume in the end, is by no means to be regarded as the result of contact or other mechanical influence, but it is a natural change which necessarily follows from the structural elements of the tendril, as will be seen later; therefore, this serves to supplement, and give additional force to, other changes relating more especially to the former.

The figure described by the nutating tip is approximately ellipsoidal, the major axis being horizontal, (fig. 2). This axis not infrequently reaches a length of 24 to 27^{cm}; that of the minor axis being from 13 to 22^{cm}. In *Echinocystis lobata*, the diameter of the figure, according to Darwin, is even larger than this, measuring from 38 to 41^{cm}.† While the tendril

* Text Book, p. 866.

† Climbing Plants, pp. 128-129.

describes a figure, the vertical plane of which is parallel with the axis of the plant, the space through which the tip moves is greatly augmented by a supplementary movement in the growing end of the vine, on which the tendril is found. This secondary movement causes the tendril tip to describe a double movement which increases the possibility of contact with surrounding objects.* It is of short duration, however, since the movement of the vine is confined to the few internodes at the end, and at any one node, continues for about two days only, after the tendrils are in motion; so that by the time the first arm of the latter has grasped a support, the movement of the vine at that particular node may have ceased entirely. So long as there is no contact with a suitable support, which must be of a size easily grasped by the coils, the tendril continues to revolve until a gradual increase of woody tissue arrests its activity. Toward the close of its movements, the tendril often falls to the ground and remains there for some time, or commences to coil upon itself, only to straighten out once more and resume its nutations. This may happen several times at decreasing intervals as the tendril grows older, until finally, the whole arm coils upon itself in a simple spiral with the coils turning outward, becomes hard and woody and its functions then cease entirely.†

When brought in contact with an object near the tip, the latter, at once affected by the irritation, coils about the support with a firm grasp. The effect of irritation does not immediately extend along the remainder of the tendril, as is shown by the fact that when the tip is brought into contact, the basal portion of the tendril continues its movement and passes by as a curve, the sensitive surface, thereby becoming convex instead of concave, as would occur if it felt the influence of contact. After a time, however, the effect of contact extends to all the cells of the basal portion, which then draws itself into a closer and closer spiral. When a tendril comes in contact with an object, it does not immediately lose its power of nutation, but retains it for a very considerable period, and this is largely dependent upon and influenced by the age of the organ, retention being longer in the young and vigorous than in the more aged. It becomes apparent, therefore, that when the tip is arrested,

* The fact that there is this double motion as a resultant of tendril vine action, shows that the true figure is to be obtained only when the tendril revolves about the inner surface of a glass globe and the changes of direction are recorded from the outside. This, however, was not practicable in our case, nor was it essential to the accuracy of the conclusions to be obtained, as will be seen later. For our purpose, the plane recording surface was amply sufficient.

† My observations upon this point confirm those of Darwin with regard to other members of *Cucurbitaceae*, that when a spiral is developed freely, it is always simple; that it only reverses when the tip is attached to a support.

the bands of growth still continue to act in the basal portion, and still tend to bow the tendril alternately in all directions. Their power to do so is necessarily modified by fixation of the tip, and the natural result would be for the base to pass by the support as a curve, with the sensitive side outermost, and then develop torsion. These changes we find to occur from the beginning. If the coiling were primarily due to irritation, then we should expect to find the coil first developed as the result of simple contraction on one side, and this would not immediately give rise to torsion. The spiral formed in one direction after a time reverses itself as a natural result of excessive torsion in one direction, as Darwin has already proved,* and there is thus completed a double spiral spring, which draws more and more closely, becomes hard and woody after a time, and holds the plant to a strong but elastic support. How useful this arrangement is, may be readily seen during a strong wind when, under its influence, the plant is forced this way and that, in danger of being torn and broken. The springs then yield just enough to relieve the strain and avoid the possibility of danger. It was frequently noticed that, while corn and other plants offering much resistance to strong winds, were torn badly, the squash always came out whole.

During its active period, the tendril arm elongates rapidly, and the cessation of movement and of growth in length are simultaneous. From a series of measurements made, the following data were obtained. An arm just uncoiled from the bud measured 12^{cm} in length. One day later it had increased to 14·8^{cm}, and on the following day to 18·3^{cm}, thus giving a total increase in length of 6·3^{cm}, or one-half its original length. August 8th, five tendrils but a short time in action, were carefully measured and marked. The Monday following, 10th, all except one were found to have coiled about themselves or other objects. The coils were drawn out as fully as possible and measurements taken, but even then, the full length could not be obtained. The measurements were as follows:

| | No. 1. | No. 2. | No. 3. | No. 4. | No. 5. |
|---------------------|------------------|--------|--------|--------|--------|
| August 8th,..... | 12 ^{cm} | 12·4 | 17·7 | 10·4 | 17·5 |
| August 10th,..... | 24·5 | 19·0 + | 25·0 + | 20·5 + | 33·0 + |
| Gain, | 12·5 | 6·6 | 7·3 | 10·1 | 15·5 |
| Add for coils,..... | ---- | 1·0 | 3·0 | 5·0 | 1·0 |
| Total gain, | 12·5 | 7·6 | 10·3 | 15·1 | 16·5 |

Thus we find the extreme range in elongation to be from one-half of to the same length as the tendril when it first

* Climbing Plants, p. 163.

emerges from the bud condition, and the mean ratio of increase (to original length) would be as 1:1.14, showing that the tendril practically doubles its length during the period of circumnutation. This, taken in connection with previous facts, has a striking significance.

The movement of the arm is not the only motion to be observed in the tendril as a whole. It does not require a very critical inspection to show that the same torsion which is developed in the arm, is also produced as conspicuously in the petiole from which it springs, and, as Miss G. E. Cooley* has demonstrated, the torsion is associated with a well-defined circumnutation of the petiole, independently of the movements of its arms.† By inserting a fine glass filament, with a blackened bead at its end, into the extremity of the petiole between the arms, she clearly showed that the resulting figure corresponds closely with that of an arm, when the two were in the same line of extension, but differed when the tendril arm turned off at right angles to its petiole.

From structural considerations, we felt also justified in concluding that the leaf tip must perform a circumnutation similar to that of the tendril itself. This Miss Cooley also demonstrated to be a fact. By placing a board, similar to that used for taking the motion of the tendrils, against a leaf having a diameter of 12^{cm} and a petiole 22^{cm} long, a figure of twenty-six changes of direction was obtained within the space of three hours. The movement was found to be much slower and the figure much smaller than in the case of the tendrils. This, however, would appear to be the case from theoretical considerations alone, when we compare the structural features of the two and also take into account the great difference in diameter. The figure described by the nutating tip of the leaf was quite regularly ellipsoidal, though the curve was retraced before the ellipse was fully completed, thus showing another point of similarity to the movement of the tendril. The figure obtained was 8^{cm} long by 5.5^{cm} wide, and the movement of the leaf appeared to be through the two ends and one side of the ellipse. Whether this would hold true in all cases or not, could only be determined from a greater number of observations. The important fact is demonstrated, however, that the leaves have a definite circumnutation, and that this depends upon the same causes which determine the movement of other organs in the same plant.

While experimenting with the tendrils, it was also deemed advisable to determine the movements of the growing extrem-

* Assistant Professor of Botany, Wellesly College. The facts collected by her were obtained during a course of Physiological Botany under my direction.

† This is in harmony with the observations of Sachs. Text-book, p. 870.

ity of the vine itself, since it was noticed that, usually directed upward, the tip described a movement which had a marked vertical and somewhat conspicuous lateral range. The method of securing the record was the same as for the tendrils, though owing to the constant advance of the terminal bud, the record paper was placed about six inches in advance, and the point of contact was then obtained by means of a rightangled triangle.

[To be continued.]

