Art. XVII.—*Tendril Movements in Cucurbita maxima and C. Pepo;* by D. P. Penhallow.

(Continued from page 114.)

Conclusion.

With these facts before us, we may now proceed to discuss the various phenomena and draw such conclusions from them as appear justified.

Temperature.—The observations here recorded appear to be in harmony with the views generally received, that within certain limits, and with the conditions otherwise favorable, higher temperatures are promotive of the most rapid growth. According to the experiments of Sachs* upon the germinating seeds of *Cucurbita*, the most rapid growth was found to take place under the influence of a temperature of 33·7° C.; but we have to observe that the growing embryo was doubtless placed under conditions which permitted the normal tension of the parts upon which observations were made to be fully preserved. In our own observations, the greatest growth, or greatest tendril movement, was made under a temperature of 24·4° C., while the most rapid growth of the vine occurred when the temperature ranged from 29° to 36·6° C. It is important, however, not to lose sight of the fact that in these cases, we have to deal with modifying influences which affect growth through the tension of the tissues, a disturbance of which frequently occurs as a result of high temperature. Thus, if we compare an even number of hours of growth when the temperature is above 30° C., with the same number when

* Text-Book, p. 647, etc.

the thermal range is from 25° to 30° C., we shall find the growth in the latter case to be greater as the following show, where six observations covering the same hours of day are compared.

No. of obs.	Aver. temp.	Total growth.	Aver. growth per hour.	Rel. hum.
6	27·0° C	2·0 in.	0·333 in.	high.
6	34·9	1·6 "	0·266 "	low.

These figures show that there is a well defined limit to the temperature which is most beneficial to plant growth; and, furthermore, that this limit is not fixed, but is variable according to the attendant conditions. Certain exceptions to the general law seem at times to appear, as when the most rapid growth coincides with the maximum temperature, but these instances are really conformable, and are capable of explanation upon the ground that (1) the maximum temperature was in reality not very high, and (2) that if high, the conditions of humidity were at the same time most favorable, or (3) that these very rapid growths were only extreme fluctuations in a very variable wave, and this will appear from a careful inspection of the figures given. The same will be found to hold true with reference to all the observations here recorded.

The relative humidity of the atmosphere, or the degree of saturation as dependent upon temperature, exerts a direct influence upon the condition of tension in growing tissues, and consequently upon the growth itself, by inducing more or less rapid transpiration of moisture from the leaves. While, therefore, increasing temperature directly promotes growth on the one hand, it indirectly retards it on the other. Again, taking the figures already given, and comparing the atmospheric humidity with the results there shown, it will be seen that the greatest growth was obtained under conditions of greater moisture, therefore when transpiration was reduced to the minimum. On the other hand, the least growth was made under conditions of less humidity, and therefore when transpiration was active. Doubtless, also, the humidity of the soil exerted an important influence upon the processes of growth as observed, but, unfortunately, no record of this was kept, and the relations which it bore to growth cannot now be brought out as they should be.

Alternations of day and night cause a marked influence upon, and variation in, the phenomena of growth. Light generally exerts a retarding influence,* and other conditions being equal, we should naturally expect to find the greatest elonga-

* Sachs, Text Book, p. 755. Arbeiten das Bot. Inst. in Wurzburg, 1871. Bot. Zeit., 1865.

tion of the axis, greatest increase in the weight of the squash, and most rapid movement of the motile parts, during the hours between sunset and sunrise.

From the experiments now under consideration, we find that the growth during hours of darkness was in reality less than that during daylight, since we obtained in the case of tendrils, a movement of $1359{\cdot}90^{cm}$ for the day, against $536{\cdot}90^{cm}$ for the night; and in the growth of the vine, $44{\cdot}44^{cm}$ for the day against $34{\cdot}28^{cm}$ for the night. Rauwenhoff found that the growth in *Cucurbita pepo* for twelve hours of day, was 56·9 per cent of the whole, thus leaving only 43 per cent for the same number of hours of night, or a ratio of 1 : 1·32 in favor of the former. Our own results are in striking confirmation of this, since as already seen, our ratio is as 1 : 1·29 in favor of daylight. In the case of the tendrils, the superior influence of conditions during the day, becomes much more manifest.

The movements of the tendrils are found to occur in well-defined waves of greater and less activity, which, usually longer and of slower movement at the outset, are of decreasing length and greater activity with advancing age up to a certain period. This, however, is soon reached, and beyond this point the movements become somewhat longer, but more especially slower, with greater maturity.

It is also important to note that the motion of the tendril is always most rapid when accomplishing its grand sweeps through the central region of the figure it describes, but that it becomes slower and more intermittent when it reaches its extreme lateral position on either side. This is often very manifest in the figure obtained, but may be seen more clearly when the waves of growth are plotted. This fact was noted by Darwin* as occurring in the *Cucurbitaceæ*, especially in *Echinocystis*, but he does not appear to have gained a solution of its cause. Nevertheless, there is every reason to believe that it originates directly in the unequal torsion of the tendril arm, which would of course be greatest at the extreme lateral range, and produce the most variable action, while it would be least and give rise to the most uniform and regular movement, when the tip reaches the central region of its course.

So long as all the tissues remain soft and in an actively growing condition, the waves of growth will succeed one another in accordance with the controlling influences already spoken of, but as there is an advance in age with general hardening of the tissues and large formation of wood, a noticeable and general lengthening of the waves ensues. The tip may even drop toward the ground as if exhausted and not resume its nutations for one or even two hours. When it does, it is generally with a more sluggish action.

* Climbing Plants, p. 129–30.

From our previous considerations, it is clear that the movement of the tendril is but a normal manifestation of growth, which is subject to the same influences as other vital phenomena. It now concerns us to determine how this motion is produced. This we shall discuss under the following headings:—

(1) Growth in length.
(2) Torsion.
(3) Effect of irritation.
(4) Circumnutation.
(5) Spasmodic movement at the end of activity.
(6) Coiling about a support.
(7) Free coiling.

Growth in length.—We have already seen that the tendril arm begins to revolve as soon as it has unrolled from the bud and becomes straight. At this time it is in a state of rapid elongation through its entire length, and while the full length ultimately reached must necessarily be largely determined by the time at which it comes in contact with an object of support, the arms generally attain a length which is nearly or quite twice that which they have when first unrolled from the bud. It is therefore obvious that most rapid extension is simultaneous with the greatest activity, and the two are directly correlated throughout the entire period of movement. It is therefore, to this very rapid elongation that we must look in the first instance, for a true explanation of the movement, while secondarily, we must consider the differentiation of the component tissues, particularly in their relations of mutual tension.

The structure of the tendril, presenting as it does a diversity of tissues, at once shows that this rapid elongation cannot be partaken of by all the tissues in equal degrees. The fibro-vascular bundles and the zone of wood cells are those elements in which the least extension can occur, of all the tissues present. With reference to all the other tissues, therefore, these elements must be brought into a state of positive tension, which increases in strenth as age advances and the component cells become more strongly modified by the formation of secondary layers, thus making them more resisting.

The collenchyma tissue is also a structure which, while it may be capable of greater extension than the elements previously considered, is capable of comparatively little elongation after it is once fully formed. It may exert a positive tension on the wood cells and thus bring themselves into a state of negative tension, but with reference to all tissues in a more active state of growth, it is constantly in a condition of very strong, positive tension. This may be at once seen on making sections. Transverse sections are found to quickly bulge out in the center, with a strong, marginal contraction, which is found to be developed in the collenchyma itself. Longitudinal sections show a strong curvature with the concavity on the side along which the collenchyma runs, clearly demonstrating the strong tension of this tissue. We are also inclined to believe that the cutting, as all other irritation, causes a certain loss of water from the tissue within the area of irritation, and thus through condensation, a contraction and further increase of tension. This is essentially the view adopted by Sachs,* and it certainly appears justified. We must therefore not only regard the collenchyma as influencing all the movements dependent upon growth, but it must also be considered as that tissue which chiefly determines all movements caused by mechanical irritation, a view which is amply supported by its presence in the tendrils of *Vitis*, *Sicyos*, *Ampelopsis* and other vines, and the relation which it there bears to the movements of these tendrils.

The unmodified fundamental tissue, of large, rounded cells filled with protoplasm, is that in which the most rapid and continued increase takes place. As the central or pith region early loses its vigor and often shrinks away radially, that part lying externally to the wood zone and internally to the collenchyma is obviously the general region of this tissue which serves to retain the power of growth for the longest period, and of this, we find the vibrogen bands to not only represent the most active growth from the outset, but they retain it up to the latest period. Even after the tendril has become well fixed in a permanent spiral, the vibrogen will be found to contain an abundance of chlorophyll and protoplasm, and thus to essentially retain its power of extension, although then held in abeyance by the permanant character of the fibrous tissues. We must then conclude that the negative tension is most strongly developed in the parenchyma as a whole, and in the vibrogen in particular, while the positive tension is developed in all the fibrous elements, particularly in the collenchyma during the earlier periods of activity, and in the wood cells towards the close of the active period.

The collenchyma also bears an important relation to the other tissues in its hygroscopic powers. It is a tissue which is capable of the greatest variation of density through absorption and liberation of water, and whenever such a change is induced by any means, this tissue must become of primary importance in determining secondary movements in the tendril to which it belongs. From the information we have collected, not only with reference to this but to other tendrils as well, we feel tolerably safe in the view, that, in all cases of sensitive tendrils, the

* Text Book, p. 869.

collenchyma tissue is that in which the modification of tension is first determined.

Torsion.—We have seen in a previous paragraph, that when the tendril arm becomes straight from the bud and begins its circumnutations, the tip is turned slightly downward, or toward the rounded side of the arm. Soon after movement has commenced, it will be observed that the plane which the tip makes with the basal portion of the arm, does not maintain the same relative position, but that it continually changes. Thus the tip may point up, or down, or even sideways. If we follow any one of the collenchyma or vibrogen bands, throughout its entire length, we shall also find it to assume a variably spiral form, conforming to the direction of the tip. There is thus produced in the tendril, incident to its most rapid elongation, a distinct torsion which frequently turns the tip through 180°, and sometimes through 270°. Moreover, it will be found that the petiole of the tendrils develop a similar and strong torsion, as is clearly defined by the longitudinal bands.

The explanation of this torsion is simple when we remember the character of the tissues composing the tendril, and the very great difference of tension which is developed between them; while from our previous considerations, it must be clear that, in both tendril arms and petiole, the torsion is but the natural result of excessive growth in the vibrogen, exerting a strong positive tension upon the collenchyma and wood tissues.

Irritation.—Of the two sides of the tendril arm, that which is uppermost and slightly channeled is the least sensitive, while the power to respond to mechanical influences appears to be centered in the lower portion of the arm where the collenchyma is most abundant, and this leads us to infer that it is this tissue which is chiefly concerned in such changes. If the vibrogen were the chief factor in such cases, then the change of direction must follow one of three planes, to the right, the left, or upward, and also the effect of irritation would be most conspicuous when the vibrogen was touched. On the other hand, however, since the bending is almost always toward the lower side, at least never lateral, and since the collenchyma is particularly sensitive, we have strong proof pointing to the view that the bending is produced by a full maintenance of tension in the vibrogen, while that of the collenchyma on the side irritated is increased, and the growth of this tissue ceases for the time owing to contraction of the protoplasm from the cell walls, according to the well known influence of irritation upon living protoplasm.* The power of the tendril to respond to irritation, therefore, is correlated to the hygroscopic power

* Weiss, Allgemeine Botanik, pp. 81 and 82. Darwin, Insectivorous Plants, p. 38, &c. Häckel, Quart. Journal Mic. Sci., April, 1869.

of the tissues themselves, through which variable tension is most readily produced. We are thus led to the conclusion that the collenchyma is the most important tissue of the entire structure for the production of bending under the influence of mechanical stimuli.

A tendril subjected to local irritation for about thirty seconds develops an abrupt curvature at that point within one or two minutes, and not only continues to bend so long as the irritating body is present, but even for a few seconds after its removal. Puncture with a pin, or the action of a loop of thread, produces the same effect. Irritation over considerable length causes a longer curve for the same distance. There is in all such results no evidence that the impulse has been conveyed to portions lying on either side of the irritated parts, and very soon after the cause is removed the tendril straightens out and resumes its circumnutations as before. A blow, however, produces a different effect. When given on any part of the arm, the latter receives an impulse which extends through its entire length, and instead of developing one long curve or a single abrupt turn, it is thrown into a series of long waves. Also, irritation at the tip produces the effect of a long curve passing through the whole central region. These facts distinctly show that the terminal portion is much more sensitive than any other part of the tendril, and that irritation given there, or imparted to other portions by percussion, is directly transmitted through the entire length. That this transmission is accomplished through the protoplasm, which thus serves as the nerve material, can no longer be doubted in view of the continuity which we have shown to exist, coupled with the well known sensitive nature of this substance.

Circumnutation.—Our attention is first of all to be directed to the fact pointed out by Darwin* and confirmed by our own observations, that the "tendrils revolve by the curvature of their entire length, excepting the sensitive tip and the base, which parts do not move, or move but little." This clearly shows that whatever force is in operation, acts uniformly through the entire length of the whole motile organ, and that the movement does not have a local origin at or near the base. We must therefore conceive, as both Darwin† and Sachs‡ explain, that there is a longitudinal band of tissue, or rather that a line of cells extends from base to tip of the tendril, and that this band, or these cells are in a more active state of growth than those in other parts of the tendril, thus bending the latter toward the opposite side. So far, our observations are in strict harmony with these views; but they do not accord with the opinions of these eminent authorities when they state that

* Climbing Plants, p. 170. † Ibid. ‡ Text Book, p. 866.

these bands of growth "travel round the tendril and successively bow each part to the opposite side," and in this lies the essential part of the true explanation of the movement.

As already indicated, the figure described is not one of regular progression through successive points of an ellipse or other figure, but the tendril tip may change its direction very abruptly, often exactly retracing the path just passed over, or the change of direction may be less abrupt (fig. 2). This indicates in the first place, that the band of growth does not pass regularly through successive points in the circumference of the tendril, but that it changes its position without regard to order of succession. But it also appears from the figure obtained, that while revolving in this irregular manner, the total dextrorse and sinistrorse movements are practically equal.

An examination of the histological elements of the tendril as exhibited in cross section, together with the well defined relation of the different tissues with reference to tension, suggested that the true explanation of the movement was to be found in the vibrogenic tissue. But it appears (fig. 3) that these bands are three in number, two being lateral and one superior, the latter passing along the upper side of the tendril. If, therefore, they were the true source of the movement as described in fig. 2, then the lines traced must be developed as follows:

We must conceive that, while the parenchyma tissue grows most rapidly, and therefore exerts a determining influence in the circumnutation, the collenchyma and wood tissues of slower growth must also produce a secondary influence which will modify the direction determined by the vibrogen, and thus produce a resultant motion. Thus, line 1–2 (fig. 2) would result from excess of growth in b' or in collenchyma a, a' (fig. 3). But at 2, the direction of movement is reversed, and back to 3 it must be the resultant of excess of growth in b'', plus a weaker growth in collenchyma a''. From 3–4, vibrogen b' exerts a superior influence, while from 4–5, b has again the ascendancy over all the other tissue and the motion is therefore directly lateral. And so on for the other lines traversed, each change of direction being the direct expression of superior energy in one of the vibrogenic bundles, or the resultant of growth in both vibrogen and collenchyma, the excess of growth always being in *one* of the vibrogen bundles. But this result might be produced without the energy being specially localized at b, b', b''. The band of growth might pass through various points of the parenchyma tissue at c, c', c'', and thus cause the tendril to bow in various directions as explained by Sachs and Darwin. If, however, the vibrogen tissue exerts a preponderating influence, then, since two bands are lateral and one superior, the figure described must show that the total latitudes (assuming the three bands to be of equal size and strength, which they are, approximately) are one-half the total departures of movement. The following table exhibits the latitudes and departures for the thirteen tendrils experimented upon.

TENDRIL MOVEMENTS.

Total Latitudes and Departures.

No.	Lat.	Dep.
1	124·30	249·70
2	53·25	116·60
3	123·35	269·40
4	21·00	60·83
5 c	43·37	91·10
5 b–c	241·80	398·55
6 a–b	141·75	266·55
7 a	87·75	192·80
7 b	47·75	69·30
8 a	106·30	264·70
8 b	67·65	203·03
8 c	53·20	144·50
9	122·40	118·15
Totals	1193·87	2445·21
Means	91·84	188·09
Ratio	1 :	2·05

From this it will be seen that the total mean fully confirms our theoretical considerations, giving in round numbers, latitudes 91 and departures 188, or a ratio of 1 : 2·05. An inspection of the figures for each tendril, shows that in many, this ratio is fully preserved ; in others, the excess is in favor of the latitudes, but we have already shown that the lateral range is greatest in the most active tendrils, and that the motions became more irregular and in latitude, greater, as the tendril becomes older. Since it has already been explained, that the vibrogen tissue induces torsion of the tendril, it is clear that this latter is intimately associated with the circumnutation, since both have a common origin.

Spasmodic Movement.—It has already been noted that the movement of the tendril becomes somewhat spasmodic toward the close of its active period. Periods of rest, or of actual cessation of motion not only occur, but there is often greater irregularity of movement, and a failure to make those grand sweeps, often so conspicuous a feature of the rapid circumnutations. If we bear in mind the gradual modification of the tissues during the period of movement, and more particularly toward the end of activity, the proper explanation will be easily reached

While the vibrogen tissue constantly maintains its full tension, the wood cells are becoming continually thicker, therefore more permanent, less capable of extension and hence constantly developing a greater resistance to the general elongation of the organ as a whole. So long as this mutual tension remains constant, i. e., so long as the tension of the woody structure is released by continued growth in proportion to the development of the vibrogen, for just such time will the motions of the tendril be comparatively regular. With increasing positive tension, however, its normal release will necessarily become more intermittent on account of the modified character of the cells in which it occurs, and the resultant motion of the whole tendril arm must show corresponding irregularity.

Coiling about a Support.—The coiling about an object of support with which the tendril comes in contact, results from a combination of causes already discussed. We have already seen that at the period of contact, the tip first of all twines closely about the object, while the basal portion actually passes by, through continuation of the movement, until excess of torsion draws it up into a double spiral. The coiling of the tip is the direct result of irritation as already shown by Sachs and Darwin, and as the latter explains,* it is developed by a shortening of the side in contact with the object, the same change, i. e. condensation of structure through cessation of growth and loss of water, operating here as in the previous cases, and with Darwin, we can hardly agree with Sachs† that the coiling is in any way promoted by *accelerated* growth in the unirritated side.

When once the growth in length is arrested, as it appears to be soon after coiling, the maturity of the tissue is the predominating feature. Each tendril must be regarded as having a normal period within which all the changes of structure are to be accomplished. This may be, and undoubtedly is, shortened by mechanical influences which are sufficiently long continued, so that the maturity of a young tendril is much more rapid after having grasped a support than would otherwise have been the case. This has already been pointed out by Darwin. On the other hand, it is difficult to conceive that the normal period is at all prolonged for the purpose of enabling the tendril to find a support. Unless a tendril comes in contact with an object before its tissues reach a certain stage of development, it cannot grasp a support at all. This is well shown by the fact that old tendrils which are near the end of their activity, often catch hold but imperfectly, or if they secure a hold, fail to properly perfect their double spiral.

Free Coiling.—The changes incident to the free coiling of the

* Climbing Plants, p. 181. † Text Book, p. 859.

tendril have already been discussed incidentally, and it is only necessary to repeat in concise form, that coiling of this nature is simply due to increasing disproportion of tension in the various tissues, through maturity and cessation of growth in the wood cells.

It only remains for us to now call attention to the fact that the motions of leaves, petioles and tendrils are all due to one and the same cause, and that the much greater activity and range of movement manifested in the latter, finds ample explanation upon histological grounds: (1) in the much greater disproportion between length and diameter, (2) in the more strict localization of the vibrogen tissue, (3) in its greater flexibility through being comparatively solid, and (4) the greater effect of unequal tension when exerted longitudinally through a more filamentous structure.

In the nutation of the terminal bud of the squash vine, we have to deal with some conditions which do not generally obtain in vines, i. e. the horizontal position of the plant. The growing extremity for a distance of two or three feet from the tip, under the influence of negative geotropism, has a strong tendency to an upright position, which results in a gradual curve and the elevation of the terminal bud from twelve to eighteen inches above ground. As growth continues, the tip constantly ascends until that portion of the vine unsupported by the earth, has attained such length that it can no longer overcome the direct action of gravitation upon its mass. The bud is then seen to be rapidly depressed, but this downward movement is succeeded by an upward growth as before. These vertical oscillations continue as long as growth of the vine, and constitute the chief movements of the extremity.

A second class of movements is found in the irregularly ellipsoidal nutations of the bud. This may be directly referred to unequal growth on opposite sides of the stem. While in the bud, the internodes are very nearly in a straight line with one another. Later, however, when the development of leaf, flower and tendril proceeds at a much more rapid rate than the growth of the stem at the same node, the excessive formation of tissue on the side where these organs are inserted, causes a bending of the stem in the opposite direction. This must, therefore, throw the tip of the vine to one side of its former position. As this condition of unequal growth occurs at every node within the section of growth, the tendency is to throw the extremity first to one side and then to the other, and the final direction of movement is controlled by the excess of growth upon one side, over that on the opposite side. This conclusion was reached by me independently in the summer of 1875, and it was gratifying to notice somewhat later, that Sachs had been led to similar conclusions, though at a somewhat earlier date.

From the facts here presented, we feel justified in the following conclusions:

1. Growth is promoted by an increase of temperature and humidity.

2. Growth may be retarded by an increase of temperature when other conditions are not favorable.

3. The conditions favorable to growth, arising from temperature and humidity, may cause greater growth during the day, in opposition to the retarding influence of light.

4. Growth is retarded by excessive transpiration.

5. The conditions to which the plant is subjected being variable, there is a corresponding periodicity in the vital phenomena.

6. Movements of tendrils and terminal buds, being phenomena of growth, are modified by whatever variations of condition affect growth.

With reference to the circumnutations of the tendrils, the following appear justified:

1. Movements of the tendril and petiole are due to unequal growth by producing unequal tension of tissues.

2. The unequal growth is chiefly defined in the vibrogen tissue, which may therefore be regarded as the seat of movement.

3. The band of unequal growth does not arise at successive points of the circumference.

4. The vibrogen tissue consists of three longitudinal bands, each of which becomes more active in turn, without regular order.

5. Bending under the influence of irritation results from cessation of growth and condensation of structure.

6. The collenchyma tissue is that which is chiefly concerned in variations of tension under mechanical stimuli.

7. Coiling results (by contact) from cessation of growth and condensation of structure or (free coiling) from increased inequality of tension due to continued growth.

8. Transmission of impulses is effected through continuity of protoplasm in the active tissues.