VI. *Preliminary Note on the rate of Growth of the Female Flower-stalk of* Vallisneria spiralis, Linn. *By* ALFRED W. BENNETT, *M.A., B.Sc., F.L.S., Lecturer on Botany at St. Thomas's Hospital.*

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ALTHOUGH the extraordinary rapidity of growth of the peduncle of the female flower of *Vallisneria spiralis* (probably one of the most remarkable instances to be found in the vegetable kingdom) appears to be familiar to botanists, I have been unable to find any record of actual measurements. The present communication to the Society I prefer to call a "Preliminary Note," inasmuch as a much more extensive series of experiments than I have at present had the opportunity of making will be required before the subject can be considered exhausted.

The object of the great length attained by the female flower-stalk is well known. The flower is by this means brought to the surface of the water in which it grows, which I should infer, from the length it attains (though I do not recollect any exact record of this), to be from three to four feet. It is there fertilized by the pollen supplied by the male flower, which, growing submerged on a short peduncle, breaks off from it and rises to the surface, where it floats about until the pollen meets with a female flower, the latter after impregnation being again carried, by the spiral coiling of the peduncle, beneath the surface, where it ripens its seeds.

The first memoir, as far as I have been able to trace, of the structure of *Vallisneria* is by E. J. Quekett, "Observations connected with the Anatomy and Physiology of *Vallisneria spiralis*," in the first and only volume of the 'London Physiological Journal' for 1843. The mode of fertilization and the phenomena of rotation within the cells of the leaves are here described; and the description appears to be the basis of the ordinary accounts found in works on descriptive botany. A far more minute and accurate account of the structure of the plant is by Chatin, in his 'Mémoire sur le *Vallisneria spiralis*, Linn., considéré dans son organographie, sa végétation, son organogénie, son anatomie, sa tératologie, et sa physiologie,' 1855. The author of this memoir points out the singular error into which previous writers have fallen, in describing the peduncle of the female flower as originally coiled up spirally and unrolling towards the period of impregnation, an error repeated by Richard, Turpin, and even by Grenier and Godron in their 'Flore de France,' and by nearly all subsequent writers, whether scientific or popular, and forming the text of one of Erasmus Darwin's most poetical images in his 'Loves of the Flowers.' Chatin states, and with perfect correctness, that "la hampe des fleurs femelles, d'abord droite, ne se déroule jamais." Neither of these authors, however, gives any details on the special subject of this paper.

The first flower noticed on the plants growing in my aquarium, where the water is about 8 inches deep, was on July 19th of the present year, when the total length of the

peduncle was 26 in., lying in several long coils on the surface. I am almost certain that the whole of this growth, at all events in excess of the 8 in. which would have brought the flower-bud to the surface, had taken place within the preceding 48 hours. At 10 o'clock the next morning the peduncle was again measured, and had attained the extraordinary length of 38 in., or an increase of 12 in. in 24 hours. At 4 P.M. it measured 41 in.; at 9 A.M. on the 21st 42¼; and at 10 A.M on the 22nd it had attained its ultimate length of 43 inches. The window in which the aquarium was placed had a south-west aspect; but the climatal conditions were by no means favourable to rapid growth, the temperature being rather low, the sun scarcely visible during the whole time, and the rainfall excessive. Lest it should be thought that this is the result of an error of observation, I may mention that Mr. W. W. Reeves, the Secretary of the Microscopical Society, informs me in a note that he has observed an even greater rapidity of growth than this. I do not know whether any other instance is known of a single internode attaining a length of over 3½ feet. This flower was never fertilized (there being at that time no male plant in my aquarium), but remained open, and the stigmas in an apparently receptive condition, nine days longer, till July 31st, when I left home. During this time no actual recoiling of the peduncle had taken place, though it displayed a strongly marked waviness.

It did not occur to me, until the flower-stalk had nearly completed its growth, that it would be interesting, in accordance with the plan proposed by Prof. Sachs, to ascertain in which portion of the flower-stalk the main portion of this rapid increase took place, though a few measurements which I did make convinced me that the apical portion was that in which there was the greatest activity.

I was unable to renew my observations before the latter part of September, in which interval a large number of female flowers had appeared. The one on which the most complete series of observations was made was first observed on Sept. 21st, at 10 A.M., when the apex of the flower-bud was 5 in. below the surface of the water, or the flower-bud and peduncle measured together 3 in. In two days and a half, or by 4 P.M. on the 24th, the peduncle had reached the length of 10·7 inches, or, when straightened, the base of the unopened flower-bud was 2·7 inches above the water, the bud, enveloped in its spathe, being 0·5 in. in length. The following were the successive measurements:—

		inches.	Increase.
Peduncle and bud	Sept. 21st, 10 A.M.	3	
,,	22nd, 10 A.M.	4·75	1·75
,,	12 noon	5	·25
,,	2 P.M.	5·2	·2
,,	8 P.M.	5·5	·3
,,	10 P.M.	5·75	·25
,,	23rd, 9 A.M.	7·25	1·5
,,	12 noon	7·6	·35
,,	3 P.M.	8·0	·4
Peduncle only	Sept. 23rd, 6 P.M.	8·0	·5
,,	10 P.M.	8·4	·4
,,	24th, 8.30 A.M.	10·0	1·6
,,	4 P.M.	10·7	·7

During the three portions of days constituting this period, the growth was at the rate respectively of 1·75, 2·5, and 3·25 in. in twenty-four hours.

At this stage it seemed possible to measure the rate of growth of different zones of that portion of the flower-stalk which, when straightened, was exposed above the surface. As, however, neither of the "auxanometers," or instruments for measuring growth, described by Sachs in his 'Text-book' can be used for weak stems which do not naturally stand erect, the only available mode appeared to be to mark off at intervals of time measured lengths from the base of the flower-bud. This was done (but necessarily, from my engagements, at very unequal intervals) with black varnish, each length of one inch being marked off as it rose (when straightened) above the surface of the water, and indicated successively as A, B, C, &c., any fraction of an inch remaining over being added to the subaqueous portion. The following table exhibits the result, neither the final length attained nor the rapidity of growth being so great as in July, as, indeed, might have been expected.

	A	B	C	D	E	F	G	H	I	K	L	M	Subaq.	Total.	Incr.
Sept. 24th, 4 P.M.	1·0	1·0	..	..	..	..	..	..	..	..	..	..	8·7	10·7	
10 P.M.	1·0	1·0	1·0	..	..	..	..	..	..	..	..	..	8·0	11·0	·3
25th, 8 A.M.	1·1	1·1	1·1	1·0	..	..	..	..	..	..	..	..	8·1	12·4	1·4
27th, 10 A.M.	2·25	2·5	1·8	1·0	1·0	1·0	1·0	1·0	1·0	1·0	1·0	..	8·8	23·35	10·95
2.30 P.M.	2·6	2·75	1·9	1·15	1·15	1·1	1·05	1·05	1·0	1·0	1·0	1·0	8·1	24·85	1·5
10 P.M.	2·75	2·9	2·0	1·15	1·15	1·15	1·1	1·1	1·1	1·1	1·1	1·05	8·5	26·15	1·3
28th, 9 A.M.	2·9	3·0	2·1	1·15	1·15	1·15	1·15	1·1	1·1	1·1	1·1	1·1	8·75	26·85	·7
10 P.M.	3·1	3·1	2·15	1·15	1·15	1·15	1·15	1·15	1·15	1·15	1·15	1·15	8·75	27·45	·6
29th, 9 A.M.	3·25	3·23	2·15	1·15	1·15	1·15	1·15	1·15	1·15	1·15	1·15	1·15	8·8	27·75	·3
10 P.M.	3·25	3·25	2·15	1·15	1·15	1·15	1·15	1·15	1·15	1·15	1·15	1·15	8·8	27·75	·0

The general results arrived at are that between 4 P.M. on Sept. 24th and 9 A.M. on Sept. 29th the flower-stalk had increased in length from 10·7 to 27·75 in., the two zones immediately beneath the flower-bud from 2 in. to 6·5 in. This latter portion had increased during this period 225 per cent., the remainder of the flower-stalk 144 per cent. of its original length.

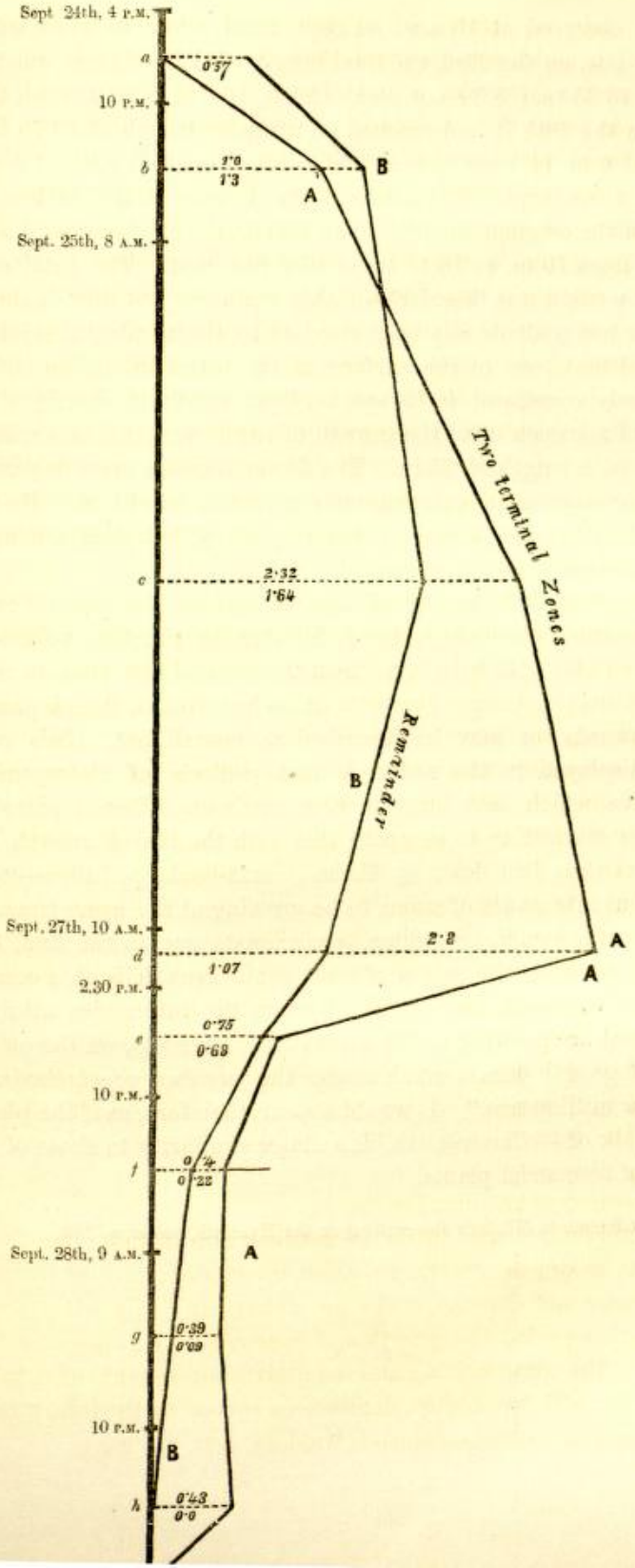
The term "Energy of Growth" of any particular part or zone of a plant is defined by Sachs ('Text-book,' p. 741) as "the power of that particular zone to attain a definite length." In the case of the stem of a plant consisting of a number of internodes, the measurements of Sachs, Pfeffer, and others show that the greatest energy of growth is generally displayed by an internode situated at some distance from the terminal bud, the energy of growth decreasing in the successive internodes, both towards the apex and towards the base of the stem. Similar careful measurements do not appear to have been made of the relative energy of growth of different portions of the same internode. In the case of the greatly elongated internode of *Vallisneria*, the maximum energy would appear to be very near the apex, the total energy of growth of the two terminal zones being to that of the remaining portion as 225 to 144, or nearly as 3 to 2. The energy would appear also, as far as any conclusion can be drawn from my few measurements, to decrease towards the base. For, dividing the portion of the flower-stalk excluding the

two terminal zones again into two parts, the uppermost of these (C–L) increased between 10 A.M. on Sept. 27th and 9 A.M. on Sept. 29th, from 9·8 to 11·35 in., or 15·8; the lowermost of them from 8·8 to 9·95 in., or only 13 per cent of its original length.

In calculating what Sachs terms the "Grand Curve of Growth" of the plant *, I have pursued a somewhat different plan to that adopted by this high authority. In his 'Text-book' (p. 737) he gives the following instructions for the construction of such a curve:—"If the increments of growth during successive equal times are drawn as ordinates, with the intervals of time as abscissæ, a curve will be obtained which, starting from the axis of abscissæ, reaches a maximum of elevation and returns again to the axis." In constructing these curves, it appeared to me that results of greater value would be obtained if, instead of the actual increment for any given time, the proportionate increase in relation to the length at the commencement of the interval were taken as the ordinate. By this means it seems to me that the energy of growth of each particular portion of the stem at any particular time will be represented by the altitude of the curve. Thus, supposing a stem increases during two successive equal intervals of time from 4 to 5 and from 5 to 6 inches, the energy of growth will not be equal to the two intervals, but will be less in the latter interval in the proportion of 4 to 5; inasmuch as it will have increased during the former interval 25 per cent., during the latter interval only 20 per cent. of its length at the commencement of that interval. It will be evident that though my grand curves of growth will agree with Prof. Sachs's in their general features, they will differ in minor particulars, and will in general be less abrupt. In constructing the curves from the data already given, I have first of all divided the increment during each interval of time by the length at the commencement of the interval, in order to get the proportionate increase as above indicated, and then the result by the number of hours in the interval, in order to reduce the times to a uniformity, the length of the intervals between the observations varying greatly, owing to my engagements. It is obviously, then, indifferent on what scale the curve is constructed, *i. e.* what is taken as the unit of measurement. In the diagram which accompanies this (p. 137), each unit of 1 inch on the ordinates represents an increase of 1 per cent. per hour; while an inch on the line of abscissæ represents a period of 12 hours. In accordance with Prof. Sachs's plan I have placed each ordinate in the centre of the abscissa to which it belongs. The two accompanying curves have thus been obtained, one exhibiting the variation of the energy of growth for the two terminal portions, the other for the remainder of the flower-stalk. The general result is seen to be that the terminal portion exhibits a considerably greater energy during the whole of the time with the exception of the first few hours.

A second series of observations was made on another flower-stalk; but I have not thought it worth while to record the results in detail, in consequence of an accidental injury (to which the slender and delicate stems are extremely liable when undergoing measurement), which both retarded the growth and caused it to be somewhat irregular. The curves constructed in the same manner showed a striking resemblance to those in the previous instances, but with two abrupt depressions caused by the injury referred to.

* See 'Arbeiten des botanischen Instituts in Würzburg,' 1873, Heft 2, t. i.



Curves of Growth of the two terminal zones and the remaining portion of the female flower-stalk of *Vallisneria spiralis*, Linn.

A. Grand curve of growth of the two terminal zones; B. Grand curve of growth of the remaining portion of flower-stalk. On the line of abscissæ every inch represents a period of 12 hours; on the ordinates every inch represents a growth at the rate of 1 per cent. per hour. The figures above each ordinate express the growth of curve A, those below the ordinate the growth of curve B on this notation. The ordinates are erected from the centres of the several periods of time, *a*, *b*, *c*, &c.

This flower-bud was first observed at 10 A.M. on Sept. 22nd, when its apex was 1 inch below the surface. By 9 A.M. on the 23rd, the total length of the peduncle was 9·75 in.; at 8.30 A.M. on the 24th, 13·95 in.; 8.30 A.M. on the 25th, 16·6 in.; 10 A.M. on the 27th, 19·0 in.; and at 9 A.M. on the 28th it had reached its ultimate length of 19·75 in. Two terminal zones, together 1·6 in. in length, were first marked off at 6 P.M. on Sept. 23rd, and had finally, at 9 A.M. on Sept. 28th, attained the length of 3·6 inches, or had increased 125 per cent. on the original length. The remainder of the stem had during the same time increased from 10 in. to 16·15 in. or 61·5 per cent. The total energy of growth of the terminal portion was therefore in this instance just double that of the remainder; but the latter had undoubtedly been checked by the accidental injury.

The flower-bud, when it first rose to the surface of the water in the aquarium, was ·5 in. in length, and closely enveloped in its spathe, from which it shortly afterwards gradually emerged, but did not open until the growth of the flower-stalk was nearly completed, when it had attained a length of ·75 in. The flower remains open floating on the surface for weeks, with the stigmas in an apparently receptive condition. By the time its growth is completed the flower-stalk has become very wavy, but does not coil up in shallow water when the flowers are unimpregnated.

The only record I have been able to find of observations on the rate of growth of different portions of the same internode is by J. Münter, in the first volume of the 'Botanische Zeitung' for 1843. He here lays down the general law that in the internodes of dicotyledonous plants the energy of growth, or, as he terms it, the *vis procreativa*, increases from below upwards, or may be described as centrifugal. This result he found most strikingly displayed in the peduncle and pedicels of *Pelargonium*, the only observations, I believe, which have hitherto been made on different parts of individual internodes *. It is interesting to compare this with the law of growth of stems taken as a whole, which is thus laid down by Sachs ('Text-book,' p. 740) :—"As it is usual for several contiguous internodes of stems to be growing at the same time, and the maximum rapidity of growth occurs, according to circumstances, in the 2nd, 3rd, 4th, or 5th internode beneath the bud, the region of most rapid growth is at a considerable distance from the apex of the stem, and especially when the internodes attain a considerable length and several are growing at the same time. In roots, on the other hand, the maximum rapidity of growth occurs much nearer the *punctum vegetationis*, usually at a distance of only a few millimetres." It would appear, therefore, as if the phenomena of growth in the flower-stalk of *Vallisneria* exhibit a closer similarity to those of the roots than of the aerial stems of terrestrial plants.

* See also the reference to Münter's observations on the Hyacinth, *postea*, p. 143.