# OBSERVATIONS ON THE GROWTH OF WATER PLANTS.

## II

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1) The growth of the female flower stalk of Vallisneria spiralis ;
2) The influence of the oxygen content of water on the growth of water plants ;
3) The influence of hetero-auxin on the growth of waterplants ;
4) Longitudinal growth, length of cells and dry weight ;
5) Summary ;
6) Literature.

### 1) The growth of the female flower stalk of Vallisneria spiralis.

The petioles of most water plants grow, in their natural habitat, till the leaf blades have reached the surface and then stop growing or go on doing so a little more, so that the leaves may form a mosaic. When they are put into deeper water they start growing anew till the blades have reached the surface again. *Limnanthemum nymphaeoides* forms an exception in so far that, when growing in water, the temperature of which is higher than this species is used to, the petioles mostly grow « too long », so e. g. in a depth of 15 c.M. they may reach an average length of about 30 c.M. Outdoors, however, I never observed this and we may say that, as a rule, there is a more or less strict relation between the depth of the water and the length of the petiole.

The female flower stalk of *Vallisneria spiralis* does not keep to this rule. I observed it growing in one of the basins in the hothouse, where the depth is 27 c.M. and I planted it in aquaria which are 45 c.M. deep. In both circumstances the stalk grows up to lengths of 80, 100, 120 c.M. and more, the greater part of it floating on the surface in long coils.



In table 1 a-b-c-d are recorded part of the observations which may give an idea of the rate of growth.

**Table 1. — Growth of the female flower stalk of Vallisneria spiralis ; in c.M.**

| Date and hour | | Number of hours | Plant N° I | II | III | IV | V |
|---|---|---|---|---|---|---|---|
| table 1a) aquaria | | | | | | | |
| 6/6 | 12.— | 0 | 52 | 13 | 29 | 14 | |
| | 18.— | 6 | 60 | 17 | 36 | 18 | |
| | 23.— | 11 | 62 | 20 | 37 | 19 | |
| 7/6 | 9.— | 21 | 62 | 26 | 40 | 20 | 32 |
| | 16.— | 28 | 62 | 41 | 52 | 24 | 38 |
| | 22.— | 34 | 62 | 47 | 66 | 29 | 45 |
| 8/6 | 10.— | 46 | 62 | 55 | 85 | 54 | 60 |
| | 15.— | 51 | 62 | 55 | 86 | 60 | 60 |
| | 22.— | 58 | 62 | 56 | 87 | 62 | 60 |
| 9/6 | 10.— | 70 | 62 | 57 | 87 | 65 | 60 |
| table 1b) aquaria | | | | | | | |
| 14/6 | 21.— | 0 | 33 | | | | |
| 15/6 | 14.— | 17 | 58 | 31 | | | |
| | 18.— | 21 | 67 | 34 | | | |
| | 21.— | 24 | 68 | 41 | | | |
| 16/6 | 8.— | 35 | 71 | 48 | | | |
| | 15.— | 42 | 78 | 50 | | | |
| | 23.— | 50 | 83 | 63 | | | |
| 17/6 | 10.— | 61 | 83 | 66 | 27 | 24 | |
| | 16.— | 67 | 83 | 69 | 33 | 33 | |
| 18/6 | 11.— | 86 | | 69 | 47 | 48 | |
| 20/6 | 10.— | 133 | | | 114 | 86 | |

| Date and hour | | Number of hours | Plant No 1 | II | III | IV | V |
|---|---|---|---|---|---|---|---|
| table 1c) aquaria | | | | | | | |
| 20/6 | 15.— | 0 | 45 | 45 | 45 | | |
| 21/6 | 15.— | 24 | 45 | 71 | 91 | | |
| 22/6 | 10.— | 43 | 45 | 71 | 92 | | |
| table 1d) hothouse | | | | | | | |
| 7/6 | 9.— | 0 | 4 | 23 | 37 | | |
| | 16.— | 7 | 5 | 27 | 47 | | |
| 8/6 | 10.— | 25 | 7 | 42 | 48 | | |
| | 15.— | 30 | 7 | 42 | 50 | | |
| 9/6 | 10.— | 49 | 10 | 49 | 64 | | |
| | 16.— | 55 | 12 | 54 | 74 | | |
| 10/6 | 11.— | 74 | 18 | 66 | 77 | | |
| | 16.— | 79 | 20 | 71 | 80 | | |
| 11/6 | 10.— | 97 | 23 | 83 | 80 | | |
| | 17.— | 104 | 28 | 86 | 81 | | |
| 14/6 | 21.— | 180 | 60 | 89 | 82 | | |
| 15/6 | 11.— | 192 | 60 | 93 | | | |

Some facts are very striking ; one of them is that growth may be accomplished at an amazing pace. I have drawn lines round the data of the most marked examples ; 46 c.M. in 24 hours, 15 c.M. in 7 hours, 25 c.M. in 12 hours, etc. may be called uncommon and I would not assure that these are the greatest rapidities which may be reached. Stalks which grow as long as 140 and 160 c.M. most certainly have periods of at least this pace if not more ; unfortunately these rather rare samples escaped my attention until I found them full grown.



It is to be wondered at, that no more attention has been paid to this organism. The only author who did so was, as far as I know, BENNETT (1,2) who describes a small number of observations in which he at least cites one case in which growth was of the same rate as was measured by me. In describing a stalk of 7 inches (1), he says : « After an interval of 93 hours it had reached the astonishing length of 43 in. » ; this means an increase of 90 c.M. in 93 hours which tallies well with my observations. In the second note BENNETT observes an increase of 12 in. in 24 hours. GOEBEL (7) says : « Das Wachstum ist ein rasches. », which certainly is rather laconically expressed and I doubt whether this author has ever observed the growth of *Vallisneria* himself.

It is also a remarkable fact that this very rapid growth sometimes stops suddenly or at least slows down very considerably ; see e. g. table 1a, Nº III, 1d, Nº III. In the beginning growth is slow ; see table 1d, Nº 1. I have confirmed this observation by an auxanographical record ; the growth of the first 15 c.M. took three days, then gradually it speeded up to 8 à 9 m.M. an hour, somewhat later it was more than 10 m.M. an hour till the surface was reached and as the stalk cannot be lifted out of the water it was impossible to record the further growth with the auxanometer ; which was a pity because I observed the curious phenomenon that the highest rate occurs in most cases when the surface of the water has already been reached ; see e.g. table 1 a, Nº III, 1 b, Nº II and III, 1 c, Nº III. Amongst the longest stalks observed I mention those of 121, 138, 144 and 164 c M.

There are marked individual diffrences between the stalks in the same aquarium, growing on plants which are of the same age and apparently developed under equal conditions ; see e. g. table 1 c. When the water column was made extra high by means of an inverted glass cylinder, it had not the least influence. I put some plants with stalks in a basin which was 90 c.M. deep ; one stalk was 24 c.M. at the beginning and needed 5 days to grow up to 85 c.M ; the tother was 12 c.M. and needed 7 days to reach the surface ; growth stopped in both stalks after that. It is clear that for some reason every flower stalk can reach a determined length regardless of the depth of the waterlayer.

There is also an individual difference in the behaviour of stalks when the longitudinal growth has been accomplished. As no fertilisation occurred, no actual coiling took place; yet in some of the stalks a very distinct waviness is to be seen, in others nothing of the kind. (GOEBEL and BENNETT rightly contest the opinion of older authors, that the female flower stalk develops as a spiral which unrolls to enable the flower to reach the surface and which, after fertilisation, recoils to the bottom. Indeed, the young stalk is perfectly straight; spiraling only begins after fertilisation. In some handbooks, a. o. J. P. LOTSY, « Vorträge über organische Stammesgeschichte », 1911, R. VON WETTSTEIN, « Handbuch der systematischen Botanik », 1911, A. ENGLER, « Syllabus der Pflanzenfamilien », 1912, G. HEGI, « Illustrierte Flora Mittel-Europas », 1935, I found figures of *Vallisneria spiralis* with coiling flowerstalks, merely indicated as « female plants », but it is nowhere said that such is the situation after fertilisation; it is possible, therefore, that the old, erroneous idea is still alive.)

In the hothouse the stalks were of a light green colour, in the aquaria they were white or light rosa. This difference may probably be ascribed to external conditions; e. g. in the place where the aquaria stood the light was much stronger than in the hothouse basin; the leaves in this place also developed anthocyan very strongly and remained short; they grew no longer than about 30 c.M., whereas in the basin they reached lengths of 60, 70 c.M. and more, so that they floated for the greater part on the surface. The two sets of plants made a strikingly different impression, but apparently the growth of the flowerstalks was not influenced by it.

In table 2 are recorded the cell measurements and the determinations of the dry weight.

It appears that cell elongation is the chief means by which the longitudinal growth is accomplished; there are many irregularities, probably owing to individual differences; I could not detect any essential distinction between stalks from the hothouse basin and those from the aquaria.



**Table 2. — Celllenghts and dry weight in the female flower stalk of Vallisneria spiralis ; a means above, 1/4 : at 1/4 from the top, m : in the middle, 3/4 : at 3/4 from the top, b : below.**

| length of stalk in c. M. | epidermis (in micra) | | | | | subepidermis | | | | | dry weight per c. M. in m. Gr. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | a | 1/4 | m | 3/4 | b | a | 1/4 | m | 3/4 | b | |
| 7 ½ | 54 | | 38 | | 17 | 65 | | 73 | | 21 | 0.19 |
| 11 | 63 | 62 | 68 | 84 | 90 | 138 | 105 | 107 | 97 | 138 | 0.18 |
| 16 | 73 | | 50 | | 74 | 102 | | 85 | | 104 | 0.25 |
| 27 | 62 | 79 | 123 | 162 | 210 | 102 | 88 | 183 | 243 | 305 | 0.18 |
| 46 | 76 | 265 | 210 | 140 | 100 | 91 | 245 | 280 | 285 | 240 | 0.11 |
| 47 | 149 | 200 | 230 | 275 | 240 | 390 | 370 | 475 | 385 | 355 | 0.16 |
| 60 | 132 | 186 | 252 | 268 | 340 | 174 | 237 | 400 | 395 | 330 | 0.15 |
| 62 | 104 | 200 | 360 | 200 | 330 | 150 | 385 | 380 | 425 | 480 | 0.10 |
| *72* | *129* | *290* | *390* | *285* | *205* | *285* | *360* | *500* | *430* | *230* | *0.10* |
| 87 | 58 | 310 | 410 | 435 | 160 | 120 | 325 | 415 | 405 | 160 | 0.16 |
| 96 | | | | | | | | | | | 0.18 |
| 106 | 180 | 320 | 400 | 275 | 235 | 330 | 410 | 640 | 425 | 370 | 0.13 |
| 107 | | | | | | | | | | | 0.15 |
| 110 | 225 | 475 | 425 | 370 | 425 | 285 | 410 | 360 | 400 | 475 | 0.12 |
| 115 | 350 | 425 | 250 | 305 | 385 | 485 | 700 | 440 | 355 | 360 | 0.10 |
| 134 | 215 | 400 | 610 | 400 | 355 | 340 | 730 | 760 | 680 | 500 | 0.11 |
| 136 | 365 | 540 | 590 | 475 | 335 | 440 | 700 | 600 | 620 | 340 | 0.07 |
| 138 | 174 | 340 | 670 | 565 | 440 | 390 | 605 | 800 | 600 | 510 | 0.12 |
| 164 | 460 | 630 | 370 | 550 | 520 | ? | ? | ? | ? | ? | 0.07 |
| 13 st. between *44 and 54 c. M.* | | | | | | | | | | | 0.17 |
| 6 st. between 55 and 91 c. M. | | | | | | | | | | | 0.14 |
| 6 st. between 63 and 86 c. M. | | | | | | | | | | | 0.16 |
| 18 st. between 61 and 102 c. M. | | | | | | | | | | | 0.15 |
| 6 st. between 83 and 101 c. M. | | | | | | | | | | | 0.22 |

### 2) The influence of the oxygen content of water on the growth of waterplants.

In our paper of 1937 (6) we stated that there does not exist a strictly quantitative relation between the length of the petiole and its dry weight per c.M., which ought to be the case if water intake, and consequently cell elongation, were the only cause of growth in deep water. We put the question, in how far respiration may play a part in the growing process, especially to what degree it influences the dry weight during the rapid elongation of the petioles.

In order to solve this question I grew two sets of *Limnanthemum nymphaeoïdes* in aquaria; the surface of one aquarium was covered with a layer of parafin oil and through the other aquarium a constant stream of air was led by means of an airpump.

There was a marked difference in development; it was always much stronger in the not-aerated water. The first experiment lasted from 18 to 27 April; on the last day the petioles were measured: av. length in aërated water 37.9 c.M., under the oil 56.4 c.M.; on 30 April the remaining leaves were measured: av. length in aërated water 27.5 c.M., under oil 58.0 c.M. The air stream was then stopped and the oil removed, so that both sets of plants were in the same conditions again; on 4 May a strong development of new leaves had taken place in the formerly oil-covered aquarium and no growth could be observed in the other one; a strong dose of oxygen apparently hinders the development of young leaves.

This result was confirmed by repeating the experiment twice; the oil could be easily left out, it did not change the response of the plant.

Cell measurements and a great number of determinations of dry weight gave no conclusive data; they are all of the same order as those published in our last paper and therefore it is not worth while giving them here. The important fact is that they by no means gave a distinct indication of the reason of the very different development with and without, or rather with much and with little oxygen. Determination of the pH did not give ony explanation either; the hydrogen ion concentration appeared to be the same in both conditions.



The same experiment was done with *Sagittaria sagittifolia*; here too, in three successive experiments, growth was stronger in the water where oxygen was lacking; as an indication of development I took the number of the aerial leaves which were formed and the average length of their petioles:

| | | | |
|---|---|---|---|
| from 2 — 9 May | | | |
| without oxygen | 13 | aerial leaves, average length | 53.1 c.M. |
| with » | 8 | » » , » » | 45.2 » |
| from 10 — 24 May | | | |
| without oxygen | 11 | aerial leaves, average length | 59.5 c.M. |
| with » | 10 | » » , » » | 48.9 » |
| from 24 May — 3 June | | | |
| without oxygen | 9 | aerial leaves, average length | 66.9 c.M. |
| with » | 12 | » » , » » | 61.0 » |

When the air stream and the oil were removed, it appeared that the aftergrowth in the aquarium, formerly covered with oil, was the strongest.

Experiments with *Nymphaea alba* and *N. odorata* gave contradictory results.

The oxygen content of the water had no influence on *Vallisneria spiralis*, neither on the development of the leaves, nor on that of the flower stalks.

### 3) The influence of hetero-auxin on the growth of waterplants.

Vegis (12) observed that adding hetero-auxin to the water speeded up the development of the turiones of *Stratiotes aloides*, provided he kept the concentrations between certain limits; above these the hetero-auxin acted as a poison. 7½ and 3 parts per million are among the concentrations which he found furthering growth and I tried these to see how they would act upon several species of water plants. Our aquaria contain 20 L. so that 150 or 60 m.Gr. of hetero-auxin were added to them.

Young plants of *Limnanthemum nymphaeoïdes*, the petioles of which had an average length of about 15 c.M., were planted in aquaria in which the water was 45 c.M. high. In the hetero-auxin solution (7½ per million) the petioles remained somewhat shorter than in the controls; after 4 days I noted: av. length in hetero-auxin solution 45.6 c.M., in control 53.6 c.M. (pH in hetero-auxin solution 7.55, in control 7.50) ; the measured leaves were taken away ; 4 days later new ones had developed which measured in hetero-auxin solution 43.5 c.M., in control 51.0 c.M.

A second experiment was done with 3 per million ; the result was the same ; after 9 days the av. length in hetero-auxin solution was 38.7 c.M., in the control 50.4 c.M. ; 6 days later ten new leaves had reached the surface in the control and only three in the test aquarium.

A third experiment (3 per million) gave an opposite result : after 9 days av. length in hetero-auxin solution 66.5 c.M., in control 47.3 c.M.

Determinations of celllengths and of dry weight, although numerous, gave no indication of a distinct difference as to these aspects between the plants treated with hetero-auxin and the controls ; the data, moreover, are similar to those of last year and therefore I need not publish them here.

There were some other phenomena which are worth while mentioning. In the first place the leafblades, which have not yet reached the surface of the water, roll up hyponastically at a certain moment after adding hetero-auxin. Cell measurements indicate that this is done by slightly stronger cell stretching on the lower side. The blades were spread at the beginning of the experiment because, as usually, I took « mature » plants with floating blades from shallow water. When they reach the surface again they do not spread any more, but remain floating as stiff rolls. A moving picture (for technical details see this issue of the Biologisch Jaarboek : B. Hubert, « A simple apparatus ... ») of *Limnanthemum* growing in a hetero-auxin solution disclosed the fact that the rolling up takes place simultaneously and very rapidly ; in this case the leaves rolled up epinastically, in the opposite direction as is usual ; whether this must be ascribed to the continuous light, which was needed for taking the film, could not yet be made out.

The petioles themselves also show abnormalities ; they often are strongly coiled with here and there sharp twists ; see fig. 1. I measured the cells at the spots marked with a cross and saw something peculiar : at those spots celles were considerably shorter than elsewhere in the petiole and in those spots only ; they are also characterised by their nucleus which is strikingly



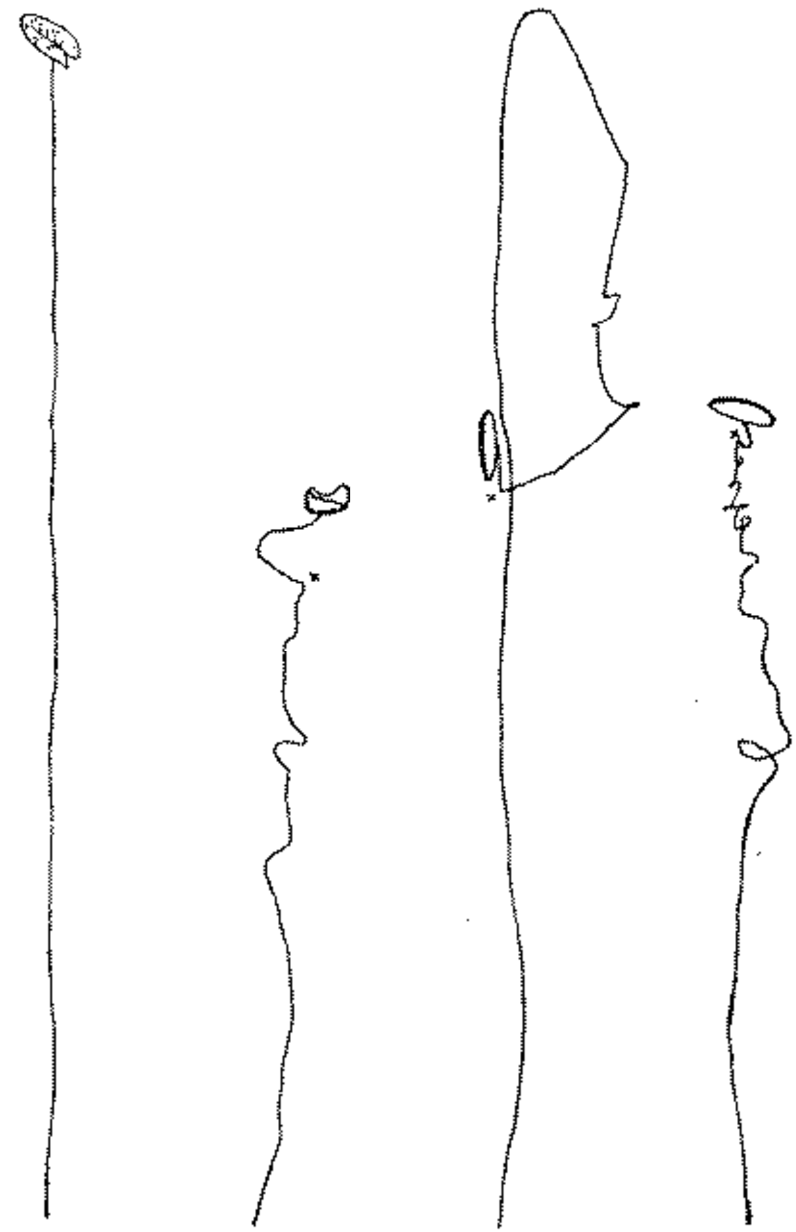

Fig. 1. Leaves of Limnanthemum nymphaeoides in 3 per million heteroauxin ; control on the left.

big and granular. Part of the measurements are recorded in table 3.

**Table 3. — Celllenghts in twisted parts of petioles of Limnanthemum nymphaeoides.**

| petiole No. | | epidermis (in micra) | subepidermis (in micra) |
|---|---|---|---|
| 1 | 1 c.M. above 1st twist | 160 | 135 |
| | 1st twist upper side | 47 | 59 |
| | 1 c.M. below 1st twist | 161 | 132 |
| | 1 c.M. above 2d twist | 165 | 177 |
| | 2d twist upper side | 66 | 82 |
| | 1 c.M. below 2d twist | 159 | 171 |
| 2 | 1 c.M. above twist | 183 | 132 |
| | 2 m.M. above twist | 89 | 72 |
| | twist upper side | 52 | 64 |
| | twist lower side | 64 | 66 |
| | 1 c.M. below twist | 179 | 142 |
| 3 | 1st twist upper side | 33 | 45 |
| | 1 c.M. below 1st twist | 119 | 95 |
| | 2d twist upper side | 40 | 60 |
| | 2d twist lower side | 38 | 42 |
| | 1 c.M. below 2d twist | 138 | 114 |
| | 3d twist upper side | 35 | 48 |
| | 1 c.M. below 3d twist | 144 | 126 |

On certain spots hetero-auxin apparently causes cell division; why this division is locally limited to a few spots only, must remain unexplained for the moment. In other spots, where the twists are less sharp, I saw groups of short cells among the normal ones.

*Sagittaria sagittifolia*, when treated with 3 per million hetero-auxin, shows something similar: hyponastical rolling up of the leafblades and irregular coilings in the petioles; see fig. 2 and 3.

Petioles do not grow shorter owing to the addition of hetero-auxin, as was sometimes the case in *Limnanthemum*; cell measurements on the strongest curved parts showed no difference worth mentioning when compared with the straight parts of the petioles. The rolling up of the blades appeared to be due to a slightly stronger cell stretching on the lower side.



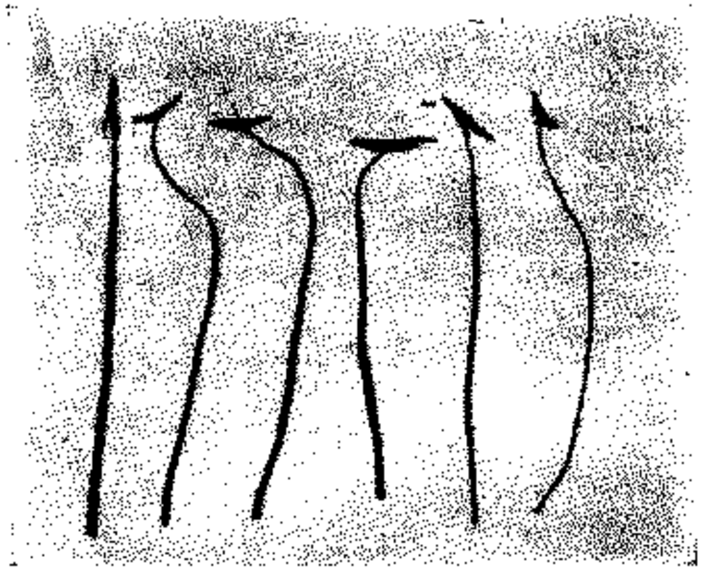

Fig. 2. Leaves of Sagittaria sagittifolia in 3 per million hetero-auxin.

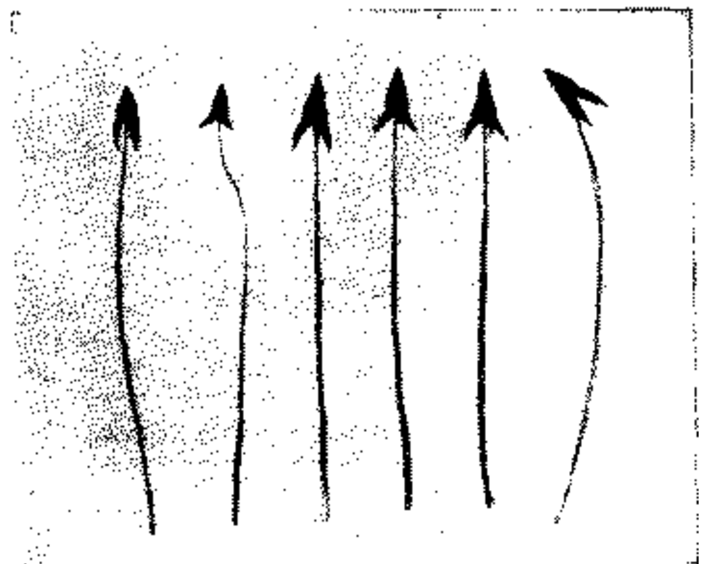

Fig. 3. Leaves of Sagittaria sagittifolia: controls.

One experiment only was done with *Nymphaea alba* and *N. odorata*; 24 hours after adding the hetero-auxin (3 per million) the characteristic coilings were to be seen in part of the petioles and also in a flower stalk; part of the leaves showed a distinct beginning of hyponastic growth. In other cases it takes 2 till 4 days before one sees the response of the plant; here the

Fig. 4. Female flower stalk of Vallisneria spiralis since three days in 3 per million hetero-auxin; 9.— a.m.

reaction was very rapid, contrary to what I expected, because the rigid petioles and blades, to say nothing of the young flower stalk, which was only 6 c.M. long, could be supposed not to take



in the hetero-auxin so easily, in any case to be more resistent against it; nevertheless they apparently took in the hetero-auxin very rapidly, but after that reaction they straightened and no further response was to be seen; the plants grew as normally as the control ones. Yet, the hetero-auxin could not have disappeared altogether from the water because its after-effect, which will be described below, took place just as in other experiments.

Fig. 5. The same as in fig. 4; 5.— p. m.

The effect of 3 per million hetero-auxin on *Vallisneria spiralis* consisted in a postfloral phenomenon, viz. a more or less regular rolling up of the female flower stalks; it began 24 hours after applying the growth substance and proceeded for 3 or 4 days. Figures 4 and 5 show the finest example I observed. The stalk was 85 c.M. long, floating for the greater part on the surface without any indication of waviness; the hetero-auxin was added

Fig. 6. Flower stalk of Vallisneria spiralis in 3 per million hetero-auxin; irregular coiling.

on 3 July; on 4 July the total length could no more be measured because of the winding; on 5 July the flower was pulled below the surface of the water and then the coiling proceeded till, on 6 July, it was complete; fig. 4 shows the situation on that day at 9. — a. m., fig. 5 at 5. — p. m.; the total height of the coil was



not more than 3 c.M. I ascertained that neither the length of the stalk nor of its cells were changed after the coiling.

In other cases the coiling was less perfect, an example is to be seen in fig. 6; this stalk was strongly and irregularly rolled in the upper part, the lower remained in the condition shown on the photo. Others were still less coiled, but in any case much more so than in water to which no hetero-auxin had been added. Those stalks only which developed in the test aquarium some weeks later showed no indication of coiling; apparently the hetero-auxin had disappeared by that time.

In hetero-auxin solution the ovaries grew in length, but not in thickness; their length varied between 20 and 25 m.M., whilst in the non-treated plants it was between 11 and 17 m.M. (in one case 20 m.M.); the diameter is the same, between 1100 and 1500 micra. It can hardly be said that parthenocarpy has been induced by applying the hetero-auxin (compare 8, 9, 10); agar blocks with hetero-auxin placed upon the pistils had no effect whatever. I had no time to continue the researches in this direction.

In most cases the addition of hetero-auxin to the water has a peculiar after-effect which, al though not bearing on the growth of waterplants, is worth while mentioning here. It consists in a cloudiness of the water, a white or grey colour, which at first is slight but which may become very dense later on. Still later it may clear up and especially in this case it appeared that the phenomenon is caused by bacteria; the clearing up occured because those bacteria settle down in a thick film on the petioles and other parts of the plants or on the bottom of the aquarium. Under the microscope they yield the impression that they produce some slimy substance which keeps the film together.

In other cases the water remained clear for a longer time but took on a black colour; when this happened the bottom always was dark black as is mud in which a strong sulfate reduction takes place. Sometimes I observed the white opaqueness first and after a few days it made place for the darkening.

It may be easily understood that all sorts of things may happen to the hetero-auxin when it is mixed with the many substances present in aquaria, in which there is earth and sand and a number of waterplants. This is a problem in itself and a very complicated one, which I cannot deal with here. The remarkable fact is that the addition of 3 per million of some substance can cause such a very strong, explosive development of bacteria ; we need not think hat this substance acts as a food ; its concentration in this respect is of no importance ; it is more probable that its addition neutralises some factor which is inhibitive to the development of the bacteria ; this is the more likely as the development did not always begin directly after the adding of the hetero-auxin ; sometimes it took several days, sometimes even weeks before the effects became visible. So e. g. in the case of *Nymphaea* ; as I have said above, the plants reacted almost immediately to the growth substance and afterwards recovered and grew on ; a slight cloudiness was to be seen which suddenly, but several days later, became very strong, water and bottom being dark black. The plants themselves grew on and seemingly were not hindered by it.

In the aquaria with *Vallisneria* not the slightest opaqueness was ever to be seen.

As hetero-auxin is not soluble in water, it is dissolved in 2 à 3 c.c. alcohol ; when this quantity of alcohol without growth substance is added to an aquarium it appears that the plants are not influenced by it, but a white opaqueness was quite visible and later on a strong darkening !

### 4) Longitudinal growth, length of cells and dry weight.

The determinations of the dry weight of the petioles in *Limnanthemum*, begun in 1937, have been continued on a much larger scale. In table 4 part of the data are recorded.



**Table 4. — Petioles of Limnanthemum nymphaeoides ; length of cells and dry weight**

| date | number of pot. | average length in c. M. | particulars | extreme dimensions of cells in micra: epidermis | extreme dimensions of cells in micra: subepidermis | dry weight in m. Gr. |
|---|---|---|---|---|---|---|
| 16/3 | 2 | 12.5 | outdoors, shallow water ; nat. hab. | 37 — 61 | 37 — 55 | 3.10 |
| 25/3 | 8 | 10.7 | | | | 3.00 |
| 2/4 | 6 | 16.2 | » | | | 1.37 |
| 8/4 | 5 | 13.9 | » | | | 1.64 |
| 27/4 | 5 | 12.8 | » | | | 2.02 |
| 4/5 | 5 | 13.7 | » | | | 2.26 |
| 14/5 | 5 | 13.4 | » | | | 2.10 |
| 23/5 | 5 | 14.6 | » | | | 2.81 |
| 3/6 | 5 | 14.2 | » | | | 3.03 |
| 16/6 | 4 | 13.2 | » | | | 3.97 |
| 25/6 | 4 | 11.3 | » | 22 — 62 | 30 — 58 | 2.62 |
| 3/7 | 4 | 13.0 | » | 22 — 71 | 26 — 70 | 2.90 |
| 11/7 | 4 | 14.9 | » | | | 3.49 |
| 18/7 | 4 | 12.7 | » | | | 4.04 |
| 26/7 | 4 | 14.2 | » | | | 3.77 |
| 2/8 | 4 | 14.1 | » | | | 3.80 |
| 9/8 | 4 | 16.4 | » | | | 3.42 |
| 16/8 | 4 | 17.2 | » | | | 3.12 |
| 23/8 | 4 | 17.9 | » | | | 3.26 |
| 30/8 | 4 | 16.3 | » | | | 3.30 |
| 4/6 | 5 | 70.2 | outdoors, deep basin | 25 — 73 | 30 — 67 | 0.83 |
| 16/3 | 1 | 7.5 | aqu., planted 12/3 | | | 0.67 |
| | 1 | 8.5 | » | | | 0.41 |
| 2/4 | 7 | 10.2 | aqu., planted 25/3 | | | 0.89 |
| 8/4 | 5 | 14.7 | » | | | 0.86 |
| 27/4 | 4 | 20.0 | » | | | 0.86 |
| 5/6 | 3 | 13.8 | aqu., planted 4/6 | 22 — 56 | 26 — 59 | 3.20 |
| 7/6 | 3 | 17.3 | » | 21 — 46 | 23 — 52 | 1.70 |
| 10/6 | 9 | 59.3 | aqu. filled 8/6 | 51 — 141 | 58 — 105 | 0.46 |
| 10/6 | 3 | 19.2 | aqu., planted 4/6 | | | 1.72 |
| 15/6 | 10 | 68.7 | aqu. filled 13/6 | | | 0.34 |
| 25/6 | 4 | 17.0 | aqu., planted 20/6 | 26 — 61 | 32 — 62 | 2.18 |
| 3/7 | 4 | 29.7 | » | 38 — 68 | 51 — 73 | 0.94 |
| 11/7 | 4 | 33.5 | » | 48 — 67 | 67 — 80 | 0.80 |
| 18/7 | 4 | 25.8 | » | | | 1.06 |
| 22/7 | 4 | 38.2 | » | | | 0.72 |
| 26/7 | 4 | 52.0 | aqu. filled 22/7 | 30 — 111 | 40 — 96 | 0.61 |

We see that the longer the petiole, the smaller is the dry weight per c.M. ; but small figures for the dry weight also occur in short-petioles when they have been taken from their natural habitat and placed in aquaria ; within a few days the dry weight sinks to half of what it was before and even to less. When the petioles grow longer, the cells usually undergo a stretching ; but it cannot be taken as a rule that the longer the cells, the smaller is the dry weight.

We see striking examples of long petioles with short cells, which have a very low relative dry weight ; see e. g. the specimens of 4 June.

A peculiar case is recorded in table 5. We see that in deep water

**Table 5. — Petioles of Limnanthemum nymphaeoides; length of cells and dry weight.**

| | length in c. M. | epidermis | | | subepidermis | | | dry weight per c. M. in m. Gr. |
|---|---|---|---|---|---|---|---|---|
| | | in micra | | | | | | |
| | | above | middle | below | above | middle | below | |
| shallow, 24/2 | 24 | 30 | 49 | 52 | 37 | 47 | 44 | 0.27 |
| | 19 | 35 | 64 | 55 | 42 | 58 | 55 | 0.21 |
| | 24 | 40 | 76 | 49 | 43 | 61 | 50 | 0.27 |
| 28/2 | 24.5 | 37 | 68 | 67 | 59 | 60 | 70 | 0.24 |
| | 20 | 30 | 60 | 71 | 36 | 55 | 67 | 0.30 |
| | 20.5 | 25 | 58 | 59 | 35 | 62 | 47 | 0.37 |
| average | 22.0 | 32.8 | 62.5 | 58.8 | 42.0 | 57.2 | 55.5 | 0.28 |
| deep, 28/2 | 48.5 | 44 | 65 | 56 | 52 | 80 | 62 | 0.33 |
| | 48 | 31 | 58 | 63 | 41 | 54 | 58 | 0.29 |
| | 52 | 32 | 93 | 51 | 34 | 71 | 43 | 0.25 |
| average | 49.5 | 35.6 | 72.0 | 56.6 | 42.3 | 68.3 | 54.3 | 0.29 |
| average shallow/deep | 2.25 | 1.08 | 1.15 | 0.96 | 1.01 | 1.19 | 0.98 | 1.04 |



the average length is 2.25 × the average in shallow water ; the relation of the celllengths is practically 1.0 and equally so the relation of dry weight per c.M. These data allow the conclusion that in this case the longitudinal growth was due to cell division only ; but we know that in other cases cell stretching acts a part too in the elongation of the petioles. The data of this year, however, although much more numerous than those of 1937, do not yet allow any definite conclusion.

A single observation about *Alisma Plantago* also means a warning not to draw conclusions too rapidly. A petiole of 90 c.M., which had grown in one of the deep outdoor basins, was measured ; I give the celllengths, compared with those of 1937, in table 6.

**Table 6. — Petioles of Alisma Plantago.**

| length in c.M. | particulars | epidermis | | | | | subepidermis | | | | | dry weight per c.M. in m.Gr. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | in micra | | | | | | | | | | |
| | | a | 1/4 | m | 3/4 | b | a | 1/4 | m | 3/4 | b | |
| 37 | 1937; shallow water | 104 | | 142 | | 100 | 132 | | 131 | | 88 | 7.11 |
| 81 | 1937 ; deep water | 292 | 187 | 156 | | 130 | 251 | 186 | 145 | | 131 | 2.23 |
| 90 | 1938 ; deep water | 103 | 133 | 96 | 108 | 144 | 117 | 162 | 135 | 138 | 162 | 2.13 |

We see that the petiole of this year equals the long one of 1937 in total length and relative dry weight, but its cells are about of the same length as those in the short sample of 1937 ; this case strikingly resembles that of the petioles of *Limnanthemum* of 4 June.

When we look at the data for the female flower stalks of *Vallisneria spiralis* (see table 2) we see again that there is no relation between celllenghts and dry weight. The lowest dry weights, it is true, occur in the longest stalks, but on the whole it must be said that there is such little difference between dry weight of stalks of widely varying lengths, that here too we may not assume any close and simple relation between cell elongation and the amount of dry matter.

What we have said above, which is supported by observations on other plant species, proves that water intake, cell elongation, and consequently dry matter per unit of petiole length are by no means so closely connected as one might be inclined to expect; respiration may act a part here, although my experiments with aerated and non-aerated water gave no indication in this direction; assimilation, thickening of the cell walls, storage of food (especially very conspicuous in the stalks of *Vallisneria*) and other life processes are likely to prove of influence here.

## 5) Summary.


1) The growth of the female flower stalk of *Vallisneria spiralis* is an extraordinarily rapid one; slow in the beginning, it may reach a pace of more than 2 c.M. an hour, which pace may be kept on for a whole day; the depth of the waterlayer is of no influence. This growth is mainly accomplished by cell stretching.

2) Oxygen content: in *Limnanthemum nymphaeoides* and *Sagittaria sagittifolia* it appears that an overdose of oxygen in the water slackens the growth of the existing petioles and the formation of new ones.

3) Hetero-auxin, added to the water in a concentration of 7 ½ or 3 per million, hardly ever stimulates the longitudinal growth, on the contrary, it mostly slackens it. Leafblades of *Limnanthemum nymphaeoides* and *Sagittaria sagittifolia* roll up hyponastically; the petioles show more or less marked twisting; this was especially the case in *Limnanthemum* where the sharpest twists were accompanied by cell division. The same phenomena, but only transitory, occurred in *Nymphaea alba* and *N. odorata*.

In *Vallisneria spiralis* the hetero-auxin caused a rolling up of the flower stalks; this post-floral phenomenon was followed by a slight indication towards parthenocarpy.

The addition of hetero-auxin stimulated in most experiments the development of a tremendous lot of bacteria.

4) Numerous determinations of dry weight and celllength showed that longitudinal growth can hardly ever be explained by water intake and cell stretching; respiration, assimilation, thickening of the cell walls, food storage and other processes are probably involved in it.


Ghent, Botanical Institute. September 1938.



## 6) LITERATURE.


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