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Botany. — JOH. H. VAN BURKOM: "*On the connection between phyllotaxis and the distribution of the rate of growth in the stem*". (Communicated by Professor WENT).

(Communicated in the meeting of November 30, 1912.)

Various investigators have studied the longitudinal growth of the stem. They have for the most part paid attention to the total increase in length of the stem and only a few investigated the distribution of the rate of growth in one or several internodes. Complete investigations on widely different plants with regard to the distribution of the rate of growth over the whole growing region have so far not appeared. There occur indeed in the literature two important utterances which are based on preliminary observations. The first is the opinion expressed by SACHS[1]) that the growth of stems with distinct nodes differs from those with indistinct nodes. If the stem is sharply articulated then according to SACHS each internode shows its own curve of rate of growth. This rate increases from the base of the stem towards the apex, reaches a maximum and decreases again towards the upper node. If the stem has indistinct nodes then the whole growing region yields a single curve of rate of growth of this type.

ROTHERT[2]) has further described this. He speaks of individualised internodes when each internode grows as a separate unit and passes through the great period of growth, whilst in other cases the whole stem passes through this growing-period as one internode. Notwithstanding that these two authors have clearly distinguished two methods of growth, the growth of the whole stem in one growing-period has had most attention paid to it, so that in most text books it is given chief consideration.

This is the circumstance which led me in 1907 to make measurements on various plants in the Botanic Gardens at Utrecht.

With regard to the results of this inquiry which will be shortly communicated in my Dissertation, I wish here to make a brief preliminary statement.

With the aid of a little stamp made for this purpose or of a brush and India ink, linear marks were made on the stem, so that it was divided into zones.

1) SACHS Jul. 1873. Ueber Wachsthum und Geotropismus aufrechter Stengel. Flora 56 Jahrgang. Regensburg.

2) ROTHERT W. 1896. Ueber Heliotropismus. COHN's Beiträge zur Biologie der Pflanzen Bd VII.

Immediately on the completion of intervals of time which were as far as possible equal, the length of the zones was measured accurately to $^1/_4$ m.m. I calculated from the increase in length the average rate of growth per m.m. during each separate space of time.

In making the measurements a great difficulty was the determination of the exact boundary of the zones, because the portion of the stem on which the mark had been placed, grew at the same time. I therefore tried to determine as far as possible the middle of the mark. In my later observations, I succeeded in avoiding the error due to this, by marking alternate zones with a lengthwise line. I then took the extremities of the longitudinal mark as the zone-boundary.

Rapid growth also caused this boundary to become indefinite and difficult to determine.

To gain an idea of the errors in my observation, I frequently also measured in the course of my observations the zones which had already been found to have grown out.

I thus obtained numerical data concerning the length of the same zone measured at different points of time.

The greater number of these data were identical, only a few deviated. Calculation showed that the average error was smaller than the expected degree of accuracy.

In *Asparagus officinalis* LINN., *Ginkgo biloba* LINN., *Hedera colchica* HOCH and *Linum usitatissimum* LINN., the whole region of growth formed a single curve of rate of growth, i. e. regularly increasing growth from below upwards and then decreasing growth above this.

Acer dasycarpun EHRL., *Acer platanoides* LINN., *Deutzia scabra* THBG., *Lonicera tatarica* LINN., *Syringa vulgaris* LINN., and *Viburnum Veitchi* C. H. WRIGHT showed a similar curve of rate of growth with this difference that the zones in which the nodes were situated showed less growth than the zones lying nearest to them.

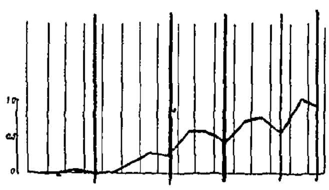

Fig. 1. *Deutzia Scabra* THBG. 13—17 Juli.

Fig. 1 shows the curve of rate of growth in *Deutzia Scabra* Thbg. from 13th to 17th July [1]).

1) On the abscissae axis the zones have been plotted at equal distances. The thin lines give the division-marks between the zones, the thick lines are the nodés.

As ordinates I have plotted the average rates of growth of each zone during a definite space of time.

The rate of growth of the lowest zone of the stem is given in the curve on the left, and that of the uppermost zone on the right.

In *Clematis alpina* MILLER, *Clematis recta* LINN., *Eucalyptus Globulus* LABILL., *Dahlia variabilis* DESS. *Polygonum cuspidatum* SIEB. et ZUCC, *Polygonum Sachalinense* F. SCHMIDT and *Sambucus niger* LINN. the zones lying below the node had moreover a distinctly slower growth than the others. (See fig. 2).

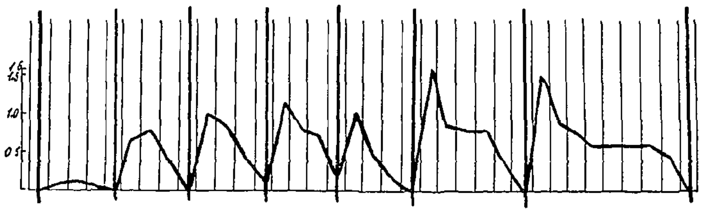

Fig. 2. *Polygonum Sachalinense* F. SCHMIDT 9—11 May.

In both groups of plants in the beginning the lowest part of each internode grew fastest whilst the rate of growth near the upper end decreased till in the "node-zone" it became very slight or zero (Polygonum).

Afterward the maximal rate of growth was displaced toward the apex and diminished in magnitude.

The zones in which the maximal rate of growth had lasted the longest time, during which period this maximum in the internode also reached its greatest value, increased much more than the uppermost zones in which the maximum lasted only for a shorter time and in which it was moreover much decreased in intensity.

The difference between the first group (Acer etc.) and the second group (Clematis etc.) lies in the rate at which the maximum of growth travels along each internode and the point of time at which it occurs.

In the first group the displacement of the maximum begins in a very early stage of development and the maximum is very quickly found below the node. On the other hand this movement is slow in the plants of the second group, so that for some time, often indeed for a considerable time, the uppermost zones of an internode show less growth than the inferior zones of the same internode.

Since the difference is confined to the moment of time in which and the velocity with which the maximum moves in the direction of the apex, the two groups are not sharply differentiated, and sometimes it is possible to obtain a curve of the rate of growth from plants in the one group which agrees with that from the other group.

I have not yet been able to determine from my observations what factors may influence the movement of the growth maximum. When the maximum chanced to occur just under the node and was therefore measured in the nodal zone, this zone showed the maximum growth.

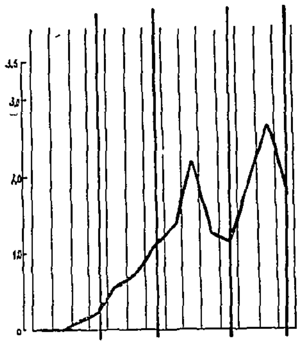

Fig. 3. *Sambucus niger* LINN. 11—16 Mei.

The ascent of the zone of maximal growth from the basal portion of the internode now continued in the lowest zone of the second internode up to the maximum rate of growth of this internode. In this case I found in both internodes one ascent of the rate of growth without diminution in or near the nodal zone (see fig. 3).

Humulus lupulus LINN. showed two different curves of the velocity of growth, namely, some had a regular course (one maximum for the whole growing zone) and some with a decrease at the upper end of some internodes. These divergent results can be brought into agreement by specially noting the movement of the maximum.

Its quick passage into the nodal zone, not only in the undermost growing internode but also in the second internodes, caused the curve of velocity of growth in these internodes to become a regularly ascending line. In the higher internodes the maximum occurred under the nodal zone.

If a sufficient number of growing internodes had been marked on the same stem, I was indeed able to observe this.

I think I have also observed that the movement of the growth maximum in an internode of *Humulus* takes place at about the same time as the maximum of the whole growing region is found in that internode.

I regarded the growth as intercalary, if there was either in the upper or in the lower portion of an internode a short zone which maintained its growth a long time, whilst the middle of the internode was already full grown.

I have observed intercalary growth in *Commelina nudiflora* LINN., *Equisetum limosum* LINN. and *Tradescantia repens* VAND.

In *Commelina* I saw this stage preceded by growth throughout the whole internode with the greatest rate of growth below. The maximal rate did not, however, move towards the upper end but remained situated in the basal portion, whilst in the upper part growth quickly diminished and wholly ceased.

In order to observe well the growth of stems with individualised internodes, external conditions must be favourable. I found that during the days on which the temperature was very low (an average of 10° C.) the curve of rate of growth was almost a horizontal line with scarcely any maxima, and this was also the case with plants which at a higher temperature had a strongly undulating curve.

All plants, which were found to have a lower rate of growth in or also under the nodal zone (to which class plants with intercalary growth also belong) possess complete nodes, that is to say, they show an external thickening round the stem at the point where a leaf is inserted. This *may* happen in plants with alternate leaves, but it *always* occurs in plants with opposite leaves.

On the other hand plants in which ill-defined nodes ("incomplete nodes") are found, show in the growing region a single curve of growth rate and the nodal zones are not differentiated by a smaller rate.

It is therefore seen from these observations that there is here a connection between phyllotaxis and the distribution of growth in the stem.

With regard to the structure of the stem three theories are chiefly put forward. Next to the view that the leaves spring from the stem as independent organs (Strobilus theory) stands the phyton theory, which declares that the stem is composed of the basal parts of the leaves (GOETHE, GAUDICHAUD). ČELAKOVSKY [1]) expressed this view in his caulome theory.

A third opinion regards the interior of the stem as an axis round which there is a layer of leaflike origin.

HOFMEISTER regarded this development as ontogenetic, whilst POTONIÉ [2]) thinks that it has taken place phylogenetically. The pith is according to POTONIÉ the primeval caulome, round which originally xylem and phloem have developed from "leaf feet" (phyllopodia).

ČELAKOVSKY's theory as also those of HOFMEISTER and POTONIÉ, holds that the surface of the stem is composed of parts which belong to the leaves lying above it. DELPINO [3]) has called these parts "leaf-feet" (phyllopodia).

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1) CELAKOVSKY L. T. 1901. Die Gliederung der Kaulome. Bot Zeitung 59er Jahrgang.

2) POTONIÉ H. 1912. Grundlinien der Pflanzen. Morphologie im Lichte der Palaeontologie. Jena.

3) DELPINO. Atti della reale Università di Genova. Vol IV, Parte II, 1883.

In plants with incomplete nodes there is found to the left and right of the point of attachment of the leaf an area which belongs to a leaf placed above, therefore there are two different phyllopodia.

When we now assume that in plants with alternate phyllotaxis (incomplete nodes) the phyllopodia themselves are subject to the same growth as is also to be seen in the node of the stems with complete nodes, then parts having a different rate of growth will be adjacent.

The question now arises, how in that case will the rate of growth be distributed over the whole area of growth, when according to this supposition each piece of the stem has the average rate of growth of its component parts.

In order to trace this I have made a calculation for which the known rate of growth of the stem of *Polygonum* was chosen as the startingpoint, because internodes of this plant are very markedly individualised.

I assumed that each leaf only surrounded a fifth part of the circumference of the stem and that the leave were displaced along the stem to the position $^2/_5$.

From the averages of the rates of growth of the five zones thus situated at the same height I obtained a regularly ascending curve with a short descending branch.

Its course agreed with the curve for plants with alternate phyllotaxis.

Although I do not see in this any proof of the theory that the stem may be composed of leaf vases or may be covered with them, yet it is clear in either case that the observed manner of growth is not inconsistent with this.

If this theory is accepted, there is moreover agreement between the growth of plants with complete nodes and those with incomplete ones.

Finally I should like to point out that I have observed in one plant, namely, *Ginkgo biloba* LINN. a difference in growth between three stems, which were in the light and three which grew in the shade.

The number of my observations is too small to warrant any certain conclusion, but nevertheless I consider I have observed that the greater increase in length of the shaded stem must only be attributed to a slight extent to the greater rate of growth, but was more especially due to a longer region of growth, that is to say, each zone grows during a longer period of time.