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# Growth Distribution and Cell Arrangement in Apical Meristems

*Rozmieszczenie wzrostu i układ komórek w merystemach wierzchołkowych*

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The anatomic feature most characteristic for apical meristems is the pattern of cell arrangements. In some parts of the apex the cells may be arranged in layers, in others in filamentous series, or the cell arrangements may be irregular and show no definite design. The pattern of cell arrangements in the apex of a shoot or a root may vary greatly. What is then the cause that different cell arrangements are to be found in various cases?

The reason why cells are arranged into some definite pattern is to be looked for among such factors connected with the growth of the cell as the direction of growth and growth rate in the different directions, and factors connected with cell partition of which the most important is the plane of division. Or, briefly, the arrangement of meristematic cells depends on the mode of growth and on the manner in which the cells divide.

It is a well known fact that the mode of growth and the manner in which cells divide are interdependent. It is not difficult to observe that to one mode of cell growth there is a corresponding manner of division. For instance, meristematic cells from some one apex region always have more or less the same shape and size. A cell growing in one direction only must divide perpendicularly to that direction to counteract the change in its shape.

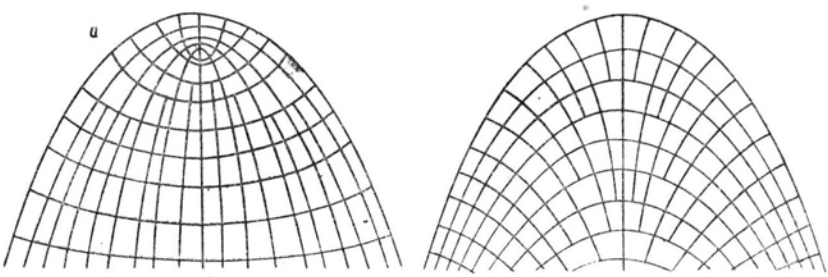
In the case of meristematic cells which are all alike, from the many factors regulating the manner of cell division, only the mode of cell growth is, indeed, changeable. It follows that in such conditions the manner of cell division is conditioned by the mode of its growth, and therefore the arrangement of undifferentiated meristematic cells depends, in the first place, on the mode of cell growth.

These considerations refer to individual meristematic cells. However, as the cells are the constituent parts of the apex their growth is dependent on the growth of the apex as a whole (H o f m e i s t e r 1867 page 129). Hence the cell arrangement in the apex is regulated by the growth pattern of the apex. Consequently, two grades in the inside relations of the apex may be distinguished: first the pattern of the cell arrangements in the apex is conditioned by the way these cells grow, and this in turn depends on the growth of the apex. The latter dependence is essential for understanding the patterns of cell arrangements.

Some idea of the influence which the growth of the apex as a whole has on the cell arrangements may be obtained by comparing the net formed by cell walls in the plane of the apical axis with the net drawn on the surface of a growing leaf. The growth of the whole produces changes in the arrangement of the cell walls in the apex, determining at the same time the direction and the positions in which the new walls will be formed, similarly as it conditions changes in the passive leaf net.

The dependence between the cell pattern and the manner in which the apex grows has long been known, but the reports published on the subject are very incomplete.

J. S a c h s (1878) describes the results produced by the mode of the apex growth which become apparent from the directions in which cell walls are arranged, i. e. from the anticlines and periclines. According to him the coaxial type of anticlines and periclines (Fig. 1b) is formed when



a b

Fig. 1. Confocal — *a*, and coaxial — *b* types of orthogonal trajectories (after Sachs 1878).

the maximum growth rate is at the tip. When at the tip the growth rate is least the anticlines and periclines (the ortogonal trajectories) form the confocal pattern (Fig. I a).

In B e r t h o l d' s (1886) opinion cell division confirms to the postulate of the minimal area of the partition wall dividing the cell into two co--equal parts. However, the way in which the growth of the whole takes place conditions the cell arrangement. A similar view is expressed by T h o m p s o n (1917, page 634 sqq.).

Some information on the relation between the mode of growth and the cell arrangement pattern are given by R e i n k e (1880) who states that the "growth curves" (Zuwachskurven) of the convexal type, which corresponds to the coaxial periclines, are connected with growth at the tip of the apex. This corroborates the previously quoted supposition of Sachs.

Some decades have passed since those reports had been published and during this time numerous workers have investigated the apex. The reports which have appeared on the cell arrangement patterns have been numerous, nevertheless, the elucidation of the relation here discussed has not advanced much. It seems that the responsibility for the present status lies chiefly with the atomic approach to the apex, most common in all investigations. With such an approach, based on the cell theory, the study of the mechanism involved in the formation of some cell pattern cannot reach further than the first grade of the aforecited relationship. Much descriptive information has been assembled on the cell arrangement patterns, the mode of cell growth, and the directions of cell divisions, but the understanding of the essential motives underlying some specified cell pattern or, otherwise, the understanding of growth pattern of the apex as a whole has been neglected. It may be argued that if the growth of all the apical parts is described an understanding of the growth of the apex as a whole will be gained, but this is a tedious and doubtful way.

Much more promising prospects for advancement in the problem under discussion open when the apex is considered as a whole which is indicated, for instance, by the attempts made by Sachs. In such an approach both grades in the relation are accounted for and the cells are considered as parts of the apex. The apex as a whole is then the starting point for further considerations, which makes possible to begin them by defining theoretically all the various possible modes of apical growth and the relations between the mode of growth and the cell pattern arrangements, leaving the descriptive study of existing apices till this is accomplished. It is possible to start by delineating the growth models for apices and the corresponding models of inner structures. Indeed, such is the object of the present paper.

When the modes of growth of the apex as a whole and of the cells as parts composing the apex are analysed the following properties must be kept in mind:

(*i*) the shape and the size of the apex do not change,

(*ii*) the difference in the growth of the parts composing an apex is compensative in character. If to maintain the apex shape a growth quantity "a" is needed, then the growth of the parts taking part in this process will add up to "a". Thus, if one of the parts grows more, then the corresponding part must grow relatively less.

(*iii*) The distribution of growth is not a mosaic where each part grows separately, it may be characterized in space as a growth field, and along an axis as a growth gradient [1]. As Weiss puts it: "A field is an entity, a pattern, not a mosaic" (quoted after Needham, 1950, where also a detailed definition of the fields is made). The growth of a part results from its position in the growth field.

All these properties determine the growth of the apex parts.

Mention must also be made of the individual cell properties. A cell is not an entirely passive component of an organism, but is to some extent a separate unit for itself. The individual cell properties are shown by such features as, for instance, the additional differentiation in the cell wall growth and details in cell division which also have an influence on the cell pattern. This influence varies in the various kinds of tissues and seems to be very slight in the apical meristematic cells. When considering definite cases it must neither be underrated nor overrated while in theoretical deliberations it may be neglected.

It is the object of the present paper:

(i) to establich a relation between the growth rates in the different directions and to define the possibilities for growth differentiation in an apex of a constant shape and size,

(ii) to give a graphical method for illustrating the distribution of growth,

(iii) to distinguish and characterize the growth distribution types,

(iv) to establich the principal features of cell arrangement patterns which correspond to the various growth types,

(v) to state the principles for the classification of cell patterns in connection with the modes of apex growth.

The present considerations are concerned with those theoretically possible modes of growth of the convex apex which condition the shape and size stability of the apex. In these cases the growing apex changes neither its shape nor size. The whole increase in bulk is, so to speak, passed on to the building of the organ terminated by the apex.

In root apices it is evident that the shape does not change, but in shoots doubts may arise. It is a well known fact that the shape of the shoot apex changes with time and together with the successive plastochrone stages. This change of shape consists in successive initations of leaf primordia, but refers only to small side areas on the apex and, in a sense, the growth process which conditions the „stability" of the apex may be separated from the external and additional processes of leaf formation.

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[1] The expression "growth gradient" is to be understood as a progressive change in growth rate of the "smallest elements" along an axis. The expression "gradient" is explained by Prat, **1945.**

The growth process which conditions the "stability" of the apex in the case of shoot apices is concealed by the additional process of leaf formation. Nevertheless it is the same basic growth process both in shoot and in root apices.

There is also an ontogenetic change in shape and size of the apex, but in most cases this change may be assumed to be so slow that, for the period during which the cell arrangement in question is being formed, it may be neglected.

It has been said previously that all theoretically possible modes of growth which condition the shape stability in the growth of a convex apex are to be discussed here. It will be for future investigations based on experimental methods to decide which of these possible growth manners are to be found in natural conditions.

All the present considerations refer to the relations and condition on the axial plane and this is in accordance with the traditional investigations on the apex.

## GROWTH OF THE APEX

Although the growth of the apex is a growth in volume it may be regarded in terms of linear growth.

The growth in length which takes place in the axial plane of the apex, whatever its direction, can be resolved into two components of which one is the longitudinal growth, i. e. parallel to the axis, and the other transversal growth, i. e. at right angle to the axis. These directions are strictly oriented in space and are better suited for describing the growth than the anticlinal and periclinal directions. Longitudinal growth is here defined as elongation.

The axis of the apex is denoted by the $x$-axis, the origin of which corresponds to the tip. The distance from the apex surface to the $x$-axis is denoted by h and may be expressed as the function of $x$, then $h = f(x)$. As a result of elongation the points lying on the axis are displaced away from the tip. The increment of the distance between point x and the tip during some time interval is the rate of displacement of point $x$ and is denoted as $r_x$ (Goodwin and Stepka 1945), consequently $r_x = dx/dt$. To the displacement of a given point $x$ corresponds an increment in the distance from the point $x$, which lies on the axis, to the apex surface, this is denoted by $r_h$ and $r_h = dh/dt$. For various points the value of $r_x$ is different. It can then be said that $r_x$ is a function of $x$ and $r_x = G(x)$. The function G(x) and better still its derivative, characterize the gradient of longitudinal growth. This is illustrated by Fig. 2 which represents the elongation gradient of the *Phleum pratense* root, reproduced after G o o d w i n and S t e p k a (1945).

The definition "the distance increment of a point" must be distinguished from the growth at the point itself, because the distance increment of point x from the tip during some time interval, that is $r_x$, is the sum of growth which takes place during this time interval at the various points between x and the tip. The growth at the point is only one of the elements which compose the sum of growth.

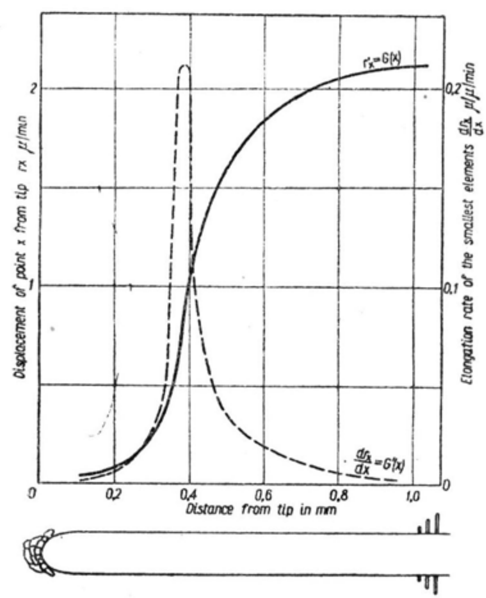


Fig. 2. Elongation of Phleum pratense root (after Goodwin and Stepka 1945).

First of all, the relationship must be established between the longitudinal and transversal growth in conditions in which the shape of the apex remains unchanged.

From the assumption of uniform shape it follows thas the basic growth must develop so as not to change the shape of the apex.

Let us assume that the growth affects the region ABCD of the apex shown in Fig. 3 (for the sake of simplicity only a longitudinal half of the apex is represented), and let us assume further that in this region an elongation has taken place, the level CD is then displaced in respect to the tip. If no transversal growth takes place C'D' = CD. Consequently, the shape of the apex changes. To counteract this change in shape of the apex the longitudinal growth must be accompanied by transversal growth. The line CD in Fig. 3 must attain the length C'D''. The displacement of CD corresponds to $r_x$. The growth along the line CD (C'D'' minus CD) corresponds to $r_h$. To establish the mutual relation of $r_x$ and $r_h$ for a given apex shape the following relations must be examined (Fig. 4):

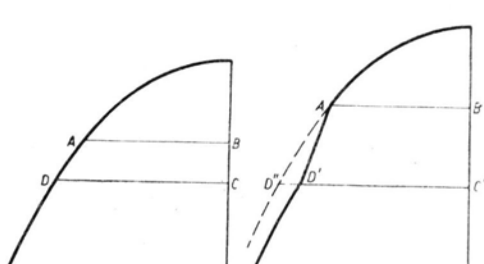


Fig. 3. For details see text.

$$h = f(x); \quad r_x = \frac{dx}{dt}; \quad r_h = \frac{dh}{dt}; \quad \text{hence} \quad \frac{r_h}{r_x} = \frac{\frac{dh}{dt}}{\frac{dx}{dt}} = \frac{dh}{dx} = f'(x);$$

hence $\frac{r_h}{r_x} = f'(x)$; equation I.

From this equation it follows that to the sum of the longitudinal growth of the smallest elements lying on the apical axis between the tip and the point x corresponds at the level x the sum of transversal growth of the smallest elements lying between the point x and the surface. This latter sum is defined by the tangent of the angle formed by a line tangent to the apex surface at the level of point x.

By transforming the equation I the following equations are obtained: $r_h = r_x f'(x) = G(x) f'(x)$. The curve corresponding to this function characterizes the change in the transversal growth rate at the various levels of the apex and will be here defined as the transversal growth gradient parallel to the axis.

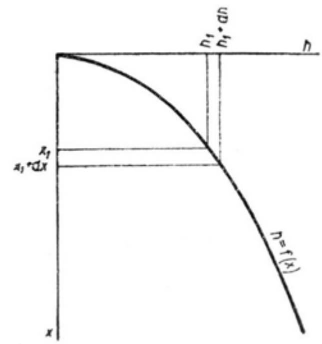

Fig. 4. For details see text.

Next must be discussed the differences which may appear in the growth of apices with similar shapes.

The longitudinal growth gradients of the smallest elements lying on the axis may differ. To these various gradients correspond of course various transversal growth gradients parallel to the axis, which is in agreement with the equation $r_h = G(x) f'(x)$, where, as it has already been mentioned, the function $G(x)$ represents the longitudinal growth gradient.

Similarly, the distribution of transversal growth on one level may vary within the limits of the value $r_h = r_x f'(x)$ — the various, perpendicular to the axis growth gradients of the smallest elements. The growth taking place between the axis and the surface may consist in growth uniformly distributed along the axis or in growth not uniform, concentrated at some one spot.

Further differences become apparent when the elongation between the various points of a transverse section and the tip level are compared.

There are two possibilities in the mutual displacement, in respect to the zero level, of points from a transverse section, i. e. of points lying on a plane perpendicular to the axis (the distance from these points and the zero level is measured along the perpendiculars to the zero level):

(*i*) the points of the transverse section may move away from the zero level at a uniform rate, or
(*ii*) the points of the transverse section may move away from the zero level at various rates.

In the former case after the displacement takes place the mutual position of the points from the transverse section will not change and the points will still lie on one transverse section, in the latter after the displacement the points will no longer lie on the same transverse section.

The displacement of a point depends on the elongation between the point and the tip level. It follows that in the first case the elongation is the same for all the points from one transverse section. On the other hand, in the second case the elongation may be either greater or smaller on the periphery than at the centre (at the apex axis) of the section.

To establish the changes in the mutual positions of points which take place in the course of growth the expression "growth line" (the „Zuwachslinien" of Reinke 1880, Schüpp 1917, 1926) may here be introduced. The growth lines are here defined as the lines which connect the same freely chosen points displaced by growth.

Thus starting with points lying on one transverse section the final arrangement will consist: in the first case of growth lines parallel in respect to each other and transversal in respect to the axis, and in the second case of curved growth lines. The differentiation of elongations at various points on the transverse section is not optional. It can easily be noticed that the total elongation which takes place between the various points on the base of the apex and the zero level (reckoned along lines parallel to the axis) is the same for all the points, and only when the apex bends this is not the case. The case when all the points of a transverse section move with same rate away from the zero level, i. e. the type with parallel transversal growth lines, is a particular instance of growth. All other instances, when the points of a transverse section are displaced in a different manner, may be regarded as deviations from this particular type and estimated by the value of this deviation. In the present work the growth type with parallel growth lines will be taken as a standard. At the same time the growth type of this kind is the simplest to describe, because the displacement of all the points from the transverse section can be represented with one function only.

The preceding considerations refer to the behaviour of points resulting from their presence in the growth field. The differentiation or uniformity in the displacement of the points in respect to the zero level is considered to be a characteristic of the growth field.

There is, however, another source for differentiation in the displacement of the points, and this lies in the individual properties of the cell.

In this case the differentiation in the displacement of a point is connected with one particular cell and not with the position of the cell in the apex. It is for instance evident that, in the cylindrical part of the root apex, growth lines parallel to each other and transverse to the root axis should be found. However divergences from this rule are found in living cells and the points selected in the cell-wall net may part after some time, as is to be seen in Fig. 5 (S i n n o t t and B l o c h 1939). Nevertheless this does not mean that it is erroneous to predict transversal growth lines when characterizing the growth of the apex as a whole. In such a case the displacement of the points from a transverse section is differentiated

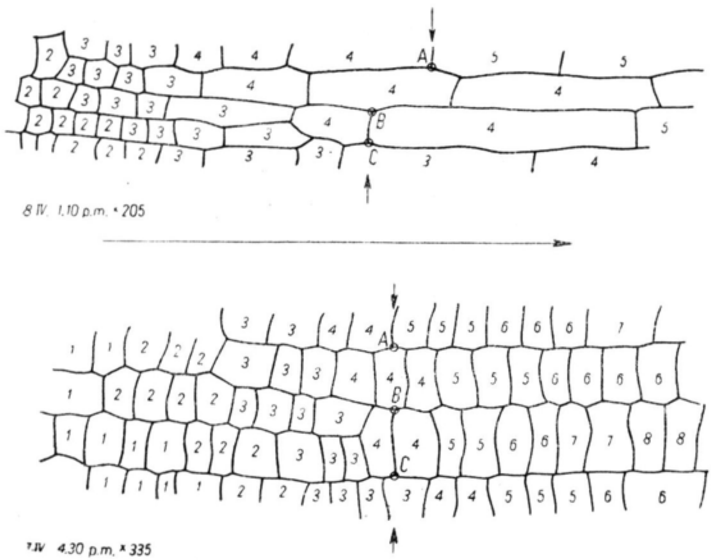


Fig. 5. Two successive stages in the development of the *Phleum pratense* root epidermis showing the mutual discplacement of points A, B and C which lay previously on the straight line perpendicular to the root axis, according to S i n n o t E. and B l o c h R. 1939. Points A, B, C, marked by the author.

because an additional differentiation in the cell growth occurred. The differentiation caused by the individual cell properties and defined as additional growth differentiation is not within the scope of this paper.

Thus, even within the range set by the unchangeability of the apex shape various growth distributions are possible. To understand the growth distribution in the apex the aspects which must be considered are:

(*i*) the elongation gradient for points lying on the axis,

(*ii*) the possibility of differentiation in elongation for the various points lying on the perpendicular to the axis,

(*iii*) transversal growth gradient parallel to the axis,
(*iv*) transversal growth gradient perpendicular to the axis.

If there is a causal relation between the growth distribution and cell arrangement patterns, then to the differentiation occurring on one side of the relation (various cell patterns in an apex of uniform shape) must correspond a differentiation on the other side (various kinds of growth distributions). It has been shown that this condition may be fulfilled.

## DELINEATION OF GROWTH DISTRIBUTION

In the preceding paragraph it has been shown that various growth distributions are possible in the apex. The question now arises how growth distribution is to be characterized? Hitherto, in studies on apical growth, and especially in works undertaken in the least ten o twenty years, the approach has been limited to specifying the directions of the highest growth rate in the different apical regions. Such an approach is manifestly unsufficient in the present considerations.

Reinke (1880) and Schüpp (1926) introduced into the considerations on growth the growth lines. In Schüpp's method the growth distribution (or more exactly distribution of periclinal growth) is deduced from the distances between the neighbouring growth lines, each of the lines being by one time unit younger than the other. If in some apex region these distances increase rapidly, rapid growth in that region is to be inferred, and on the contrary, in regions where the distances do not change no growth takes place.

The method may greatly be improved by introducing an exact definition of the distance changes between the growth lines or otherwise — by defining the elongation distribution in terms of the $r_x$ function. In this way the estimation of elongation in the apex would consist in plotting the growth lines and determining the function $r_x$ and its derivative. The function $r_x$ and its derivative define the elongation distribution on the apical axis, while the elongation in the other parts of the apex in respect to the elongation along the axis is defined by the growth lines.

If starting from points lying on a line perpendicular to the axis parallel growth lines are obtained, then it is to be deduced that elongation at all points of the transverse section is the same. If convex growth lines are obtained, then elongation between the tip level and the peripheral points of the transverse section is greater than the corresponding value for the points lying near or on the axis. This relation will be inversed if concave growth lines are obtained.

The plotting of the growth lines may be very difficult. The direct method for plotting these lines consists in repeated observations at successive time intervals of the relative positions in the points picked out at the start. Such a procedure is of course extremely troublesome. Where the cycle of structural changes is again and again fully repeated during growth, e. g. in apices with solitary apical cells, an indirect method based on examination of cell patterns may be used. However in other kinds of apices structural changes are not usually repeated exactly at successive stages and it is not easy to reproduce the life history of the individual cells for plotting growth lines.

It is not surprising therefore that so little data on growth lines are available. The informations are restricted to apices of a few pteridophytes in which growth lines are indicated by the segment walls. Indeed, Schüpp generalizes this kind of growth lines to root and shoot apices in angiosperm plants, though, as more definite evidence is lacking, such a generalization seems doubtful. The kind of growth lines as given by Schüpp is only one from all possible in apices of angiosperms.

The transversal growth gradient perpendicular to the axis is represented by the displacement lines (the "Verschiebungskurven" of Schüpp 1926). Transversal growth will be considered to be uniform when the points which are being displaced (their displacement traces the displacement lines) divide the distance between the surface and the axis at a constant ratio. When the transversal growth is uniform the displacement lines together with the line tracing the apical shape form the family kf(x), where $0<k<1$.

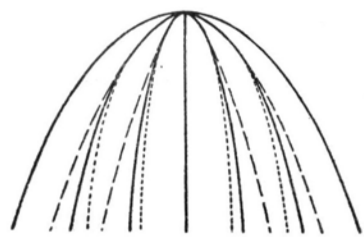

Fig. 6. Displacement lines, for details see text.

The displacement lines are shown in Fig. 6 with continuous lines indicating uniform transversal growth, dash lines indicating growth most rapid near the axis, and dotted lines growth most rapid on the periphery.

## CHARACTERISTICS OF GROWTH TYPES

In the first place it must be stressed that the present paper deals only with the embryonic region in the apex and consequently all that will be said refers only to this region.

For cell patterns, as it will be demonstrated later, the consequences of elongation are of the greatest importance. Hence the growth types are classified here in respect to the elongation gradient as follows:

(*i*) the apical type of elongation when the elongation rate of the smallest elements decreases simultaneously as they move away *from the tip,*

(*ii*) the basal type of elongation when elongation rate increases together with the movement away from the tip.

In Fig. 9 the curves on the right side of the axis illustrate simple instances of elongation gradients: $A$ and $B$ respectively — gradients distinctly and weakly apical, $C$ — basal gradient. On Fig. 9, in addition to the curves $r_x$ and $dr_x/dx$ which have been discussed previously, the curves corresponding to the elongation gradients are traced, in these the distance from the points of the apex to the tip is plotted against time. These curves and their function may be established when the function $r_x$ is known.

$$r_x = \frac{dx}{dt} = G(x); \quad \text{whence} \quad t = \int \frac{dx}{G(x)} + C.$$

The curve will be very convenient for tracing the displacement of points on growth models.

Uniform elongation is to be classified as the intermediate type, then the increment per unit distance is constant everywhere:

$$r_x = ax; \quad \frac{dr_x}{dx} = a; \quad t = \frac{1}{a} \ln x + C.$$

It has been stated previously that in the apical and the basal elongation types respectively the maximum and the minimum of elongation are at the apex tip. Let us now compare the transversal growth at various levels in a convex apex relatively to elongation distribution.

First, it must be established in what manner the longitudinal growth should be distributed so that the relative transversal growth rate — i. e. the growth during some time interval per unit distance — might be the same at various levels. This condition can be stated thus: $r_{h_x}/h_x = \text{const}$ where $h_x$ is the distance between the axis and the apex surface at the level $x$.

For a parabolically shaped apex where $h = \sqrt{2px}$ it is a uniform elongation. $r_h/h_x = \text{const}$; after substitution $r_h = r_x f'(x)$, $h_x = f(x)$ and $f(x) = \sqrt{2px}$ the equation obtained is $r_h/h_x = r_x/2x = \text{const.}$ and this can only be when $r_x = kx$, $dr_x/dx = k$ that is when elongation is uniform.

Let us consider again the equation $r_x f'(x)/h_x = \text{const}$. In this equation the denominator increases simultaneously as the distance from the tip increases, and therefore for the quotient to remain constant the numerator must also increase. Because, as has been said, $f'$ ($x$ also decreases, the increase of $r_x$ must be correspondingly rapid. When the apex is paraboloid the increment of $r_x$ must be directly proportional to $x$ ($r_x = kx$), which corresponds to uniform elongation. When the increment of $r_x$ is too slow, and this takes place when elongation is of the apical type, the quotient $r_x f'(x)/h_x$ decreases as the distance from the tip increases, which means that the transversal growth rate per unit distance diminishes. In this case the relative transversal growth is at a maximum at the tip. When $r_x$ rises too rapidly, and such is the case with the basal elongation type, the quotient $r_x f'(x)/h_x$ assumes an ever greater value and the transversal growth per unit distance is ever increasing. In that case the minimal relative transversal growth is at the tip.

These conclusions refer to paraboloid apices. A generalization may, however, be made and the conclusions may be referred to all convex apices as well as to these parts of flat and concave apices which are displaced along convex displacement lines, but only in those cases when the elongation type is markedly apical or markedly basal.

It follows that the maxima of elongation and of transversal growth are essentially coincident in the case of both elongation types. The apical elongation type is thus simultaneously the apical type of growth and similarly such is the case with the basal type. Therefore, instead of speaking of elongation types, growth types of apices may be reffered to.

So far growth types have been discussed in terms of linear growth. It must be noted, however, that volumetric growth types of various apices growing according to the same linear growth type might be different and this depends upon the shape of growing mass. To the uniform elongation of a convex apex which does not thicken at the base corresponds the apical type of volumetric growth (as the distance from tip increases the growth per volume unit decreases).

## GROWTH DISTRUBUTIONS AND CELL PATTERNS

The arrangements of daughter cells depend on the manner in which the mother cells grow (when the manner of cell division is known). When growth in one direction is predominant the ensuing arrangement of the daughter cell is more or less filamentous. Let us consider the relation between growth in the apex in directions perpendicular to each other, longitudinal and transversal.

Transversal growth at a certain level in the apex depends upon elongation between that level and the tip, and on the angle formed at the level by the tangent to the surface and the apical axis which follows from equation I (page 8).

A similar relation was formulated in 1863 by Nageli and Leitgeb: "Es hängt dies (das Breitenwachstum) mit der Gestalt des Kegels und mit der Verteilung des Längenwachstums zusammen". Nevertheless, these authors did not understand correctly the relation between transversal and longitudinal growth, as is shown by the following quotation: "Wenn das letztere (das Langenwachstum) überall gleich gross wäre, so würde das Breitenwachstum lediglich eine Funktion des Neigungswinkels sein, den die Oberfläche mit der Achse bildet". The statement just quoted is not correct, because when elongation is uniform — i. e. when according to definitions here used $dr_x/dx = a$; $r_x = ax$; then $r_h = r_x f'(x) = ax f'(x)$ — then transversal growth is not only a function of the angle formed by the tangent but also of the distance from the tip. It must be stressed that the transversal growth at a certain region depends not on the elongation which takes place within the region, but on elongation which takes place in between the region and the tip. A region may grow transversally even when it does not elongate but is moved away from the tip by growth occurring in the parts on the apical side of the region.

In the apical type of elongation the apex grows out in that part in which the elongation is accompanied by a strong transversal growth. On the other hand, in the basal type the apex grows out in the part where the elongation is connected with a weak transversal growth (except in the case when the apex thickens at the base).

In the preceding paragraph it has been assessed that in the apical type the relative transversal growth rate diminishes simultaneously with the displacement away from the tip (a convex apex not thickening at the base is being considered), while in the basal type the relative transversal growth rate is highest at some distance from the tip. Let the breadth of the cell — i. e. as measured in the direction perpendicular to the apical axis — be a unit of length. Further, if the size of the cell which is to divide is constant, then, because the frequency of longitudinal cell division is directly proportional to the relative transversal growth rate, longitudinal partition walls will be most frequent at and near the tip when the growth type is apical in a convex apex, and at some distance from the tip when the growth type is basal. When the growth type is apical such splits in the eventual filamentous series of cells will run from the tip and when it is basal from the base.

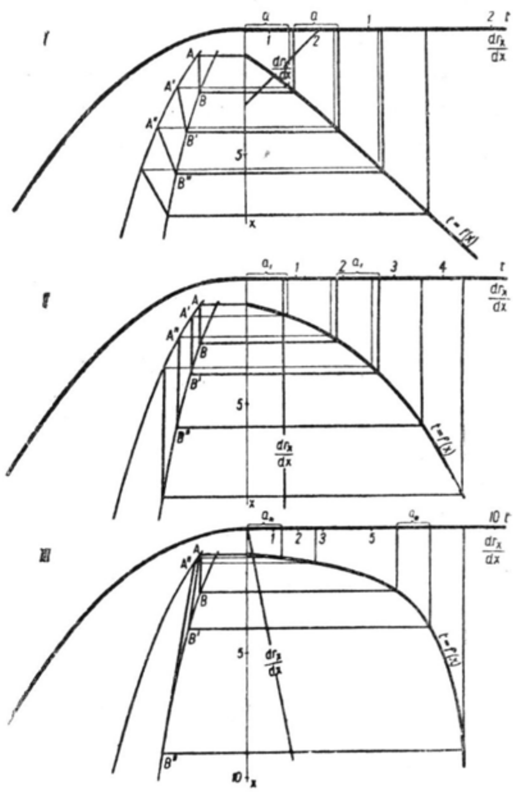


Fig. 7. Aspect and position of segment AB in the models of growing apices at successive time intervals corresponding to various elongation gradients.

The possibilites of growth of the longitudinal cell walls in the different growth types are shown by the diagrams in Fig. 7 which illustrate the behaviour of longitudinal segments in a growing paraboloid apices.

The three diagrams in the Fig. 7 represent respectively apical, uniform, and basal elongation types. In all the cases transversal growth is uniform and the points of a segment are displaced along displacement lines from the family kf(x).

The longitudinal growth gradients are represented in all the diagrams by the line $dr_x/dx$ traced with the light line on the right of the axis. The displacement magnitude of the points is estimated from the curve $t=p(x)$ and the manner to do it is to shift at one stage all the points of a segment along the displacement lines through the same distance corresponding to the time interval a. This is illustrated by the construction of the distance increment lines and of time interval lines — the light straight lines in the diagrams. During the first time interval the point A is displaced to A', during the second interval to A" and so on. Point B is displaced similarly.

In the diagram I representing the apical growth type the segment AB elongates little, while on the other hand it is markedly moved away from the tip. Simultaneously the segment slants away from the axis. For the sake of simplicity the two moving points A and B are joined with a straight line, but if the true positions of the points lying between A and B were plotted, it would appear that the segment AB, straight at first, bends gradually. In diagram I it would curve towards the axis.

When elongation is uniform the segment AB elongates in the same degree as it is displaced away from the tip, at the same time the segment remains parallel to the axis.

In diagram III representing the basal growth type the segment AB grows considerably, but is moved away from the tip only slightly.

Let it be assumed that in Fig. 7 the segment AB represents a cell wall. In the different growth types the cell wall will elongate in different manner:

(*i*) in the apical type the longitudinal walls grow only a little and are strongly displaced away from the tip,

(*ii*) in the basal type their elongation is considerable, but the displacement away from the tip is slight.

Let us now examine what is the behaviour of the cell at the tip and of the daughter cells in the different growth types. The question then arises in what manner does the grown cell divide? Let us assume a division which conforms best to the requirements thus defined:

the new wall must be at right angles to an already existing wall and perpendicular to the direction of the strongest growth (the direction of the strongest growth runs along the resultant of longitudinal and transversal growths).

In Figs. 8 and 9 may be seen diagrams representing the successive stages in the growth of the cell at the tip for various elongation gradients (in the type of transversally arranged growth lines).

The diagrams in row A represent a markedly apical type. Almost all the elongation of the apex takes place in the tip itself. The transversal

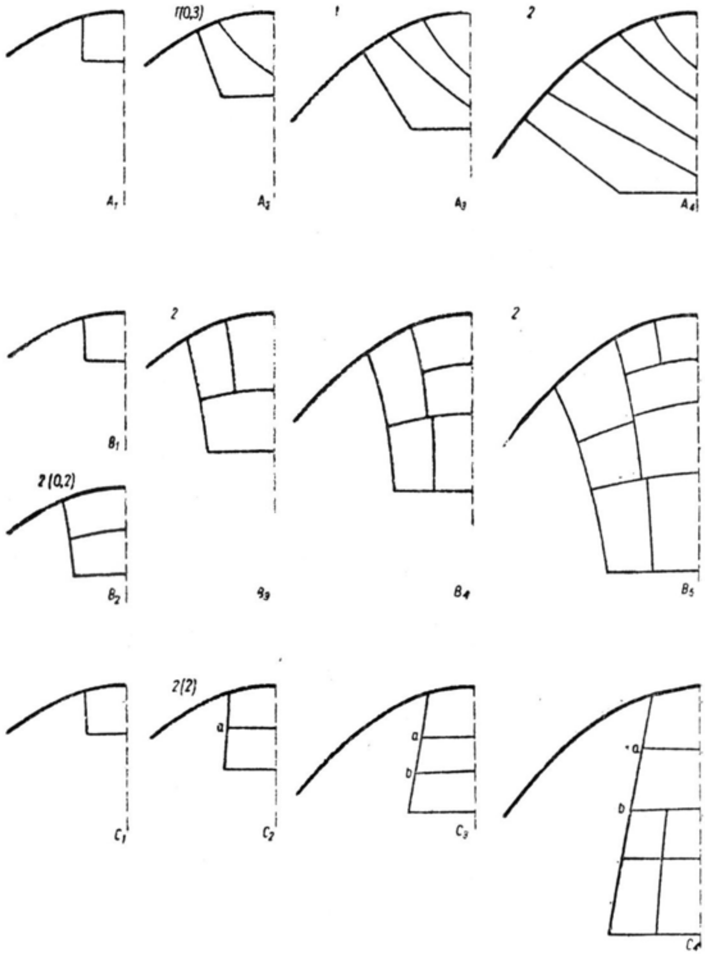


Fig. 8. Diagramatic representation of cell behaviour corresponding to various elongation gradients in the apex. Top row A corresponds to strongly apical growth ($dr_x/dx = 3 - x$ when $X \leqslant 3$ and $dr_x/dx = 0$ when $x > 3$); the middle row corresponds to not too pronounced apical growth ($dr_x/dx = 3 - 1x/4$); bottom row C corresponds to basal growth ($dr_x/dx = 1/5x$). The numbers in between the diagrams in one row indicate the relative number of time units which passed between stages represented.

growth in the tip is fairly strong. Consequently the resultant strongest growth line slants rapidly away from the axis. The segments which are pushed away from the tip enter the region where elongation is small and the resultant cell pattern may be described as segmental (Fig. 9 diagram $A_5$).

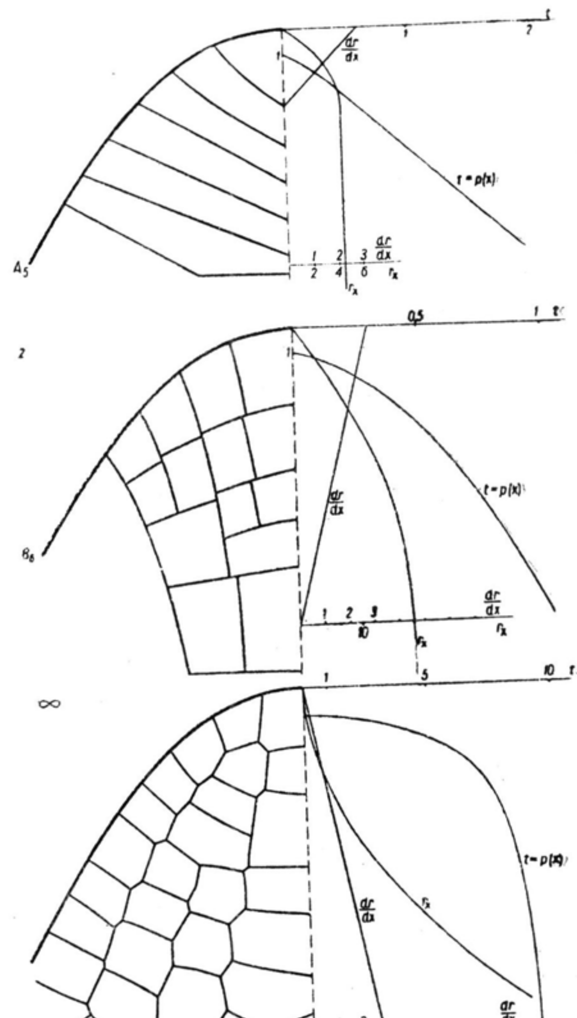


Fig. 9. Continued from Fig. 8. The numbers in brackets on Fig. 8 between the first two diagrams in each row represent the time in units accepted for the t-axis. The t-axis and the curves representing the elongation gradient are on the right in the diagrams $A_5$, $B_5$, and $C_5$. In diagram $C_5$ the local changes in the cell wall pattern have been accounted for.

If the cell at the tip divided in a different manner, the pattern of the daughetr cells would be affected. Less regular divisions would cause less regular cell patterns. Anyway, when the growth is markedly apical there are no conditions for the formation of filamentous cell series. None of the growth directions is predominant in no part of the apex. It is as if the cells at the tip were building up the apex.

When the apical growth type is not very pronounced (diagrams in row B) elongation becomes somewhat predominant and as a result elongated cell groups of common origin are formed in which the split runs from the tip.

Finally in the basal growth type (diagrams in row C) elongation dominates the transversal growth, and consequently cell filaments running along the displacement lines are clearly formed and the splitting starts at the base. In this case it is as if the apex were being developed by cells situated at some distance from the tip.

From the considerations on cell growth in the apex it appears that:

(*i*) the more strongly pronounced is the apical growth type, the smaller is the possibility for the formation of filamentous cell series,

(ii) the more strongly pronounced is the basal growth type, the more distinct are the cell filaments converging in the initial group at the tip and diverging at the base.

Hitherto the various kinds of elongation distribution have been discussed on the assumption that the transversal growth is uniform, though the final conclusions are valid regardless of the transversal growth distribution. However, usually in the apices of higher plants the transversal growth is differentiated. Such a state has its biological reflection in the more frequent periclinal divisions in some parts of the transverse section which is plainly visible on slides. It is not difficult to realize the effect on cell patterns resulting from the transversal growth not being uniform. When constructing growth patterns the points must be displaced along lines modified accordingly.

For some given growth distribution, manner of cell division, and unchaging apex shape a specific cell pattern becomes stabilized after some time. The factors mentioned and the cell pattern are then in equilibrium. Any other cell pattern must change until it attains the form characteristic for the balanced pattern.

When a balanced pattern is observed, growth distribution in the apex may be deduced from the characteristic features of the cell arrangement.

On the basis of present deliberations a continuity may be expected in cell arrangement differentiation corresponding to the theoretically possible continuity in the different modes of growth. To two slightly different modes of growth two slightly different cell arrangement patterns should correspond. To numerous and varied modes of growth greatly diversified cell patterns should correspond.

The continuous differentiation which is theoretically possible in the modes of growth forms a sequence of growth modes ranging from the strongly apical to eminently basal. In other words, the modes of growth form an *ordered set.* To each element in this set a corresponding element from a set of cell patterns is attached. A knowledge of the natural order in the set of the modes of growth makes it possible to foresee the place that some cell pattern will occupy in a corresponding set of cell patterns. For example, the diagrams representing cell patterns from Fig. 9 should be listed in the following order: segmental pattern, filamentous cell series running from the tip, and filamentous cell series with splits running from the base. It follows that the segmental pattern is more closely related to the filamentous cell series in which the cell filaments split from the tip than to the pattern in which the cell filaments split from the base. Another conclusion is that in the phylogenetic chain joining the apices of pteridophytes with angiospermous apices one of the links ought to be formed by apices similar to those represented by diagram $B_6$ in Fig. 9.

## SUMMARY

The paper deals with the growth of the apex as a whole and with the influence the growth has on patterns of cell arrangements.

The objects aimed at in the paper are:

(i) to establish a relation between the growth rates in the different directions, and to define the possibilities for growth differentiation in an apex of a constant shape and size,

(ii) to give a graphical method for illustrating the distribution of growth,

(iii) to distinguish and characterize the growth distribution types,

(iv) to establich the principal features of cell arrangement patterns corresponding to the various growth types,

(y) to state the principles for the classification of cell patterns in relation to the modes of apex growth.

The conclusions reached are summarized as follows:

1. The relation between the elongation rate and the transversal growth rate is given by the equation $r_h/r_x = f'(x)$, where $r_x = dx/dt$ represents the elongation rate between the point x lying on the axis and the tip, $r_h = dh/dt$ represents the transversal growth rate between the point $x$ and the surface of the apex, and $h = f(x)$ is a function describing the apical shape (Fig. 4).

2. The growth variations appearing in apices of the same shape may be listed as follows:

a — differences in the elongation rate gradient of the smallest elements lying on the apical axis,

b — differences in elongation between the various points of a transversal section and the tip level; as a result the points of the transversal section move away from the tip level at various rates, or at a uniform rate in one particular case,

c — differences in the transversal growth rate gradient parallel to the apical axis. The gradient of transversal growth rate parallel to the axis depends on the elongation rate gradient according to the equation $r_h = r_x f'(x)$,

d — differences in the transversal growth rate gradient of the smallest elements lying on the perpendicular to the apical axis.

3. The elongation distribution on the apical axis is defined by the function $r_x = G(x)$ and its derivative $dr_x/dx = G'(x)$ (see Fig. 2). Elongation rate in other parts of the apex in respect to the elongation rate along the apical axis is defined by the growth lines (Zuwachslinien).

The transversal growth rate gradient parallel to the axis may be plotted from the apical shape and the curve of the function $r_x = G(x)$.

The transversal growth rate gradient perpendicular to the axis is characterized by the displacement lines (Verschiebungskurven, Schüpp 1926). As uniform is considered that kind of transversal growth in which the points in their displacement divide at a constant ratio the distance between the axis and the surface. In Fig. 6 are shown the displacement lines when transversal growth is uniform — heavy black lines, when growth near the axis is strongest — dashed lines, and when growth is strongest in the peripherical parts — dotted lines.

4. Two elongation types are distinguished: the apical type, when the elongation rate of the smallest elements decreases as the distance from the tip increases, and the basal type when the elongation rate of the smallest elements increases as the distance from the tip increases. In the intermediate type the elongation is uniform. In Fig. 9 on the right of the apical axis these growth types are characterized with simplest examples of curves representing the functions: $r_x = G(x)$, $dr_x/dt = G'(x)$ and $t = p(x)$; the last of these functions is obtained from a transformation of the function $r_x = dx/dt = G(x)$ and hence $dt = dx/G(x)$.

In strongly apical elongation types the greatest relative transversal growth $r_h/h$ is at the tip. In distinctly basal growth types it lies at some distance away from the tip. (In both cases the maxima of transversal growth rate are given for apices not thickening at the base). As the maxima of elongation and of transversal growth coincide the apical elongation type is also the apical growth type in general. Such is also the case with the basal type.

The distinguished growth types pertain only to the embryonic region in the apex regardless of what takes place in the region of active elongation.

5. The possibilities of longitudinal cell wall growth in the different growth types are shown by the diagrams in Fig. 7. The diagrams show what changes take place in a longitudinal segment during the growth of the apex; the diagrams I—III show respectively the changes that take place in the case of apical, uniform and basal types of growth. The displacement of the points of the segment along displacement lines is governed by the curve $t = p(x)$. All the points of a segment are shifted simultaneously at each stage by the same time interval „a" on the t-axis. When the diagrams are compared it appears that in the various growth types there are different possibilities for cell wall elongation. In the apical type the cell wall elongation is small, but the walls are strongly displaced from the tip. On the other hand, in the basal type, cell walls elongate strongly and are pushed away from the tip only slightly.

6. From considerations on the relation between growth types and cell patterns it appears that the more pronounced is the apical mode of growth the less likely is the formation of filamentous cell series, while the more basal the mode of growth the more distinctly are the filaments converging towards the initial tip group and diverging at the base.

7. The classification of cell arrangement patterns is to be based on an *a priori* ordered set of modes of growth.

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## STRESZCZENIE

Praca niniejsza obejmuje teoretyczne rozważania nad wzrostem wierzchołka i jego wpływem na układ komórek.

Schemat zależności między wzrostem wierzchołka a układem komórek przedstawia się następująco:

Układ komórek merystematycznych na wierzchołku zależy od sposobu dzielenia się i sposobu wzrostu tych komórek. Ponieważ jednak sposób podziału komórki jest funkcją jej wzrostu, a wzrost komórki podporządkowany jest wzrostowi wierzchołka jako całości, w rezultacie układ komórek na wierzchołku zależy od sposobu wzrostu wierzchołka.

Znajomość tej złożonej zależności jest znikoma, większość bowiem prac zajmujących się przyczynami danego układu komórek zatrzymała się na pierwszym jej stopniu. Prace te określono jako prace o ujęciu atomistycznym w przeciwstawieniu do prac o ujęciu całościowym, w których punktem wyjścia jest wierzchołek jako całość i które uwzględniają obydwa stopnie wymienionej zależności.

Praca niniejsza stosuje ujęcie całościowe.

Rozważając wzrost wierzchołka jako całości i wzrost komórek jako części składowych wzięto pod uwagę:

a) stałość kształtu i rozmiarów rosnącego wierzchołka,

b) kompensacyjny charakter różnicy we wzroście części składowych wierzchołka,

c) rozmieszczenie wzrostu na wierzchołku, które daje się scharakteryzować w przestrzeni jako pole wzrostu, a wzdłuż pewnej osi jako gradient wzrostu.

Wymienione właściwości determinują wzrost części składowych wierzchołka.

Praca stawia sobie następujące zadania:

1. ustalić powiązania między szybkością wzrostu w różnych kierunkach i możliwości zróżnicowania wzrostu na wierzchołku, który nie zmienia swego kształtu ani rozmiarów;

2. podać sposób opisywania rozmieszczenia wzrostu;

3. przeprowadzić podział sposobów wzrostu na typy wzrostu i podać ich charakterystykę;

4. ustalić zasadnicze cechy układów komórkowych, odpowiadających różnym typom wzrostu;

5. podać zasadę porządkowania układów komórkowych w oparciu o sposób wzrostu wierzchołka.

Uzyskano następujące wyniki:

1. Opisano zależność między szybkością wzrostu podłużnego i szybkością wzrostu poprzecznego za pomocą równania: $r_h/r_x = f'(x)$; przy czym $r_x = dx/dt$ — szybkość wzrostu podłużnego między punktem $x$ leżącym na osi wierzchołka a szczytem; $r_h = dh/dt$ — szybkość wzrostu poprzecznego między punktem $x$ a powierzchnią wierzchołka; $h = f(x)$ — funkcja opisująca kształt wierzchołka (rys. 4).

2. Ustalono, że możliwe są następujące zróżnicowania wzrostu wierzchołka:

a) różne gradienty szybkości wzrostu podłużnego najmniejszych odcinków leżących na osi wierzchołka;

b) zróżnicowanie wzrostu podłużnego między różnymi punktami przekroju poprzecznego a poziomem szczytowym (w rezultacie punkty przekroju poprzecznego oddalają się od poziomu szczytowego z różną szybkością albo w szczególnym przypadku z szybkością jednakową);

c) różne gradienty szybkości wzrostu poprzecznego — $r_h$, równoległe do osi. Gradient szybkości wzrostu poprzecznego równoległy do osi uzależniony jest od gradientu szybkości wzrostu podłużnego zgodnie z równaniem $r_h = r_x f'(x)$;

d) różne gradienty szybkości wzrostu poprzecznego najmniejszych odcinków, leżących na prostopadłej do osi wierzchołka.

3. Podano sposób opisu rozmieszczenia wzrostu na wierzchołku. Gradient wzrostu podłużnego dla punktów osi charakteryzuje funkcja $r_x = G(x)$, a jeszcze lepiej jej pochodna $dr_x/dx = G'(x)$. Dla przykładu podano charakterystykę gradientu wydłużania korzenia *Phleum* wg Goodwina i Stepki (1945) na rys. 2.

Wzrost podłużny dla różnych punktów przekroju poprzecznego w porównaniu ze wzrostem dla punktu leżącego na osi charakteryzują linie przyrostów (Zuwachslinien — Shüpp 1926).

W szczególnym przypadku, gdy punkty przekroju poprzecznego odsuwają się od poziomu szczytowego z jednakową szybkością, linie przyrostów są równoległe do siebie i prostopadłe do osi.

Gradient szybkości wzrostu poprzecznego równoległy do osi można wyznaczyć na podstawie kształtu wierzchołka i krzywej odpowiadającej funkcji $r_x = G(x)$.

Gradient wzrostu poprzecznego prostopadły do osi charakteryzują linie przesunięć (Verschiebungskurven — Schüpp 1926). Za równomierny wzrost poprzeczny przyjęto uważać taki wzrost, w którym przesuwające się punkty dzielą odległości między osią a powierzchnią stale w tym samym stosunku. Na rys. 6 przedstawiono linie przesunięć: przy równomiernym wzroście poprzecznym — linie ciągłe, przy silniejszym wzroście części przyosiowej — linie kreskowane, przy silniejszym wzroście części peryferycznej — linie kropkowane.

4. Wyróżniono dwa typy wydłużania: apikalny typ wydłużania, gdy tempo wydłużania najmniejszych odcinków zmniejsza się w miarę oddalania od szczytu i bazalny typ wydłużania, gdy tempo wydłużania najmniejszych odcinków wzrasta w miarę oddalania się od szczytu. Pośredni typ wydłużania to wydłużanie równomierne. Charakterystykę tych typów (najprostsze przykłady) za pomocą krzywych odpowiadających funkcjom: $r_x = G(x)\, dr_x/dx = G'(x)$, i $t = p(x)$ (ta ostatnia funkcja wyznaczona z przekształcenia funkcji $r_x = dx/dt = G(x)$, stąd $dt = dx/G(x)$) podaje rys. 9 po prawej stronie osi wierzchołka. Schemat $A_5$ przedstawia silnie apikalny typ, $B_6$ słabo apikalny typ, $C_5$ bazalny typ wydłużania.

W silnie apikalnym typie wydłużania najsilniejszy względny wzrost poprzeczny $r_h/h$ występuje na szczycie. W silnie bazalnym typie wydłużania — w pewnej odległości od szczytu. (W obydwu wypadkach maksimum szybkości względnego wzrostu poprzecznego podano dla wierzchołków nie rozszerzających się u podstawy). Ponieważ maksima wzrostu podłużnego i wzrostu poprzecznego pokrywają się, zatem apikalny typ wydłużania to apikalny typ wzrostu w ogóle. Podobnie w wypadku typu bazalnego. Wyróżnione typy dotyczą wzrostu strefy embrionalnej wierzchołka bez wglądu w to, co się dzieje w strefie wydłużania.

5. Możliwości wzrostu podłużnego ścian komórkowych na wierzchołku w różnych typach wzrostu przedstawiono na schematach rys. 7. Schematy te pokazują zmiany, jakim ulega podłużny odcinek w czasie wzrostu wierzchołka: w apikalnym typie wzrostu — schemat I, przy równomiernym wzroście — schemat II i w bazalnym typie wzrostu — schemat III. Punkty odcinka przesuwano wzdłuż linii przesunięć na podstawie krzywej $t = p(x)$. Wszystkie punkty odcinka przesuwano w tym samym etapie o taki sam przyrost czasu „a" na osi t. Z porównania schematów wynika, że w różnych typach wzrostu istnieją różne możliwości wzrostu podłużnego ściany komórkowej. W apikalnym typie ściany wydłużają się słabo, ale są silnie odpychane od szczytu. W bazalnym typie wydłużają się silnie, a odpychane są słabo.

6. Omówiono zależności, jakie istnieją między danym typem rozmieszczenia wzrostu na wierzchołku a układem komórek stwierdzając, że im bardziej apikalny typ wzrostu, tym słabiej jest zaznaczony słupowy układ komórek, a im bardziej bazalny typ wzrostu, tym wyraźniejsze są słupy zbieżne ku szczytowej grupie inicjalnej i ulegające rozszczepianiu od podstawy.

7. Przedstawiono wykształcanie się układu komórek w danym typie wzrostu na schematach wzrostowych na rys. 8 i rys. 9. Przy konstruowaniu schematów przyjęto, że nowa ściana, powstająca w czasie podziału komórki, spełnia postulat prostopadłego ustawienia względem kierunku najsilniejszego wzrostu i mniej więcej prostopadłego ustawienia względem ściany już istniejącej. Szereg A odpowiada silnie apikalnemu, szereg B słabo apikalnemu i szereg C bazalnemu typowi wzrostu. We wszystkich wypadkach założono równomierny wzrost poprzeczny i jednakową szybkość odsuwania się punktów przekroju poprzecznego od poziomu szczytowego.

8. Omówiono sprawę porządkowania zbioru układów komórkowych w oparciu o *a priori* uporządkowany, metryczny zbiór sposobów wzrostu wierzchołka, dochodząc do wniosku, że układ segmentowy, występujący na wierzchołkach wielu paprotników, bliższy jest układowi, w którym słupy komórek ulegają rozszczepianiu od szczytu, niż układowi, w którym słupy ulegają rozszczepianiu od podstawy.

Pracę niniejszą wykonałem w Zakładzie Anatomii i Cytologii Roślin Uniwersytetu Wrocławskiego pod kierunkiem prof. dra Henryka Teleżyńskiego, któremu pragnę gorąco podziękować za cenne rady i pomoc w czasie jej pisania. Pragnę również wyrazić wdzięczność prof. drowi J. Perkalowi za cenne uwagi dotyczące ujęcia matematycznego.

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