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Variations of growth in shoot apical domes of spruce seedlings: A study using the growth tensor

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Abstract

Variations of the relative elemental rate of growth within apical domes, for the case when dome geometry changes during development, were modeled. It was ascertained that: 1) the domes of spruce seedlings have a paraboloidal shape; 2) the shape is maintained during growth, but the domes become higher and wider; 3) the relative elemental rate of growth in area on dome surface is isotropic, as indicated by analysis of cell packets in the surface layer. These data were used in modeling by means of the growth tensor and natural coordinate system. Growth of the dome was considered a superposition: 1) of relatively fast steady shape growth, where the isotropy of growth in area on the surface of the dome, was determined, and 2) of relatively slow isogonic growth, which does not disturb the isotropy. The convergent parabolic system was selected as the natural coordinate system. Distributions of the growth rates in the form of computer-made maps for three domes differing in age, were obtained. It appears that the growth rates within the dome are relatively high in the distal part and smaller in the central and peripheral regions. This variation decreases progressively with seedling age when the dome becomes wider. The relative elemental rate of growth in volume, averaged for the whole dome, also decreases.

Key words: apical dome, spruce seedlings, growth variations

INTRODUCTION

The apex growth of spruce seedlings has been studied by Gregory and Romberger (1972a, b) and Romberger and Gregory (1977). The authors concluded that the volumetric growth rate, when averaged for the

whole dome, decreases with age and at the same time, the size of the dome increases. There is an accumulation of leaf primordia beneath the dome, which indicates that the caulis grows less than the apical dome itself. It is possible that the rate of volumetric growth decreases with the distance from the vertex, and that the reason why the mean rate for the whole dome decreases with age is the acquisition of a slower growing part at the base.

The problem of growth rate distribution inside the dome can be solved by using the growth tensor (Hejnowicz and Romberger 1984, Hejnowicz et al. 1984a, b). The spruce represents a very interesting case for such an analysis because the geometry of the dome changes in this species during development: although the dome maintains its shape, it becomes higher and wider. This phenomenon offers an unusual opportunity for modeling the case where dome geometry changes. Until now, modeling was done for such cases only in which the domes maintained their geometry during growth. They were either abstract domes (Hejnowicz et al. 1984a, b, Nakielski 1987) or a real dome of barley (Hejnowicz et al. 1988).

The significant steps of the modeling procedure for any real dome are as follows: 1) determination of the dome geometry, 2) the choice of the appropriate natural coordinate system and formulation of the growth tensor in this system, 3) determination of the vector field of displacement velocity $\bar{V}$, 4) calculation of the growth rates at different points within the dome.

Preliminary studies indicated that in the case of spruce shoot apex, the vector field $\bar{V}$ can be determined by means of analysing the cell packets in the surface layer.

MATERIAL AND METHODS

Picea abies seedlings were grown in laboratory in nearly natural conditions. From the moment of germination, successive collections of about 30 seedlings were made at random in 4-7 day intervals. All leaves, including cotyledons and leaf primordia, were removed under a bionocular and counted to determine the plastochron age of each plant. The apical part of the caulis, including the dome and the youngest primordia, was then cut off and investigated. The entire material was divided into 3 parts: one was used for the determination of the dome shape, the second — for analysis of the cell packets in the surface layer, and the third — for semithin sectioning.

The first part was fixed in acetic acid-ethanol 1:3, then stained in toto with the PAS method, and finally each dome was photographed en profile under a microscope. The second part of the material was fixed and stained

as previously, afterwards, however, it was dehydrated in an ethanol series and transferred to euparal. The dome was dissected under a binocular by a transverse cut, placed on a slide with the top upwards, mounted in euparal, and photographed under an epi-microscope. The third part of the material was fixed in glutaraldehyde, mounted in epon, cut into sections 3 μm thick, stained by the PAS method and photographed.

The determination of the dome shape consisted in finding the parameter p of the parabola representing the profile (Fig. 1). This parameter was
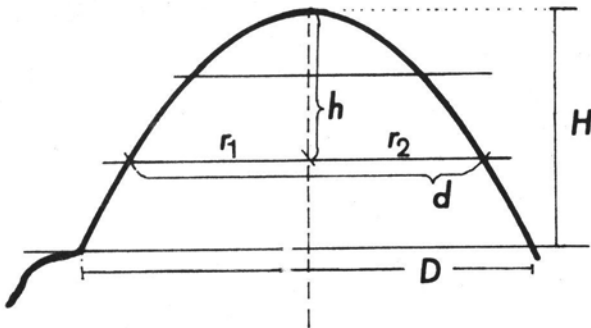

Fig. 1. Outline of a paraboloidal dome: H — dome height, D — basal diameter, d — diameter at the distance h below the vertex. For one level h, two parameters p were evaluated, namely $p' = \dfrac{r_1^2}{2h}$ and $p'' = \dfrac{r_2^2}{2h}$, where $r_1 + r_2 = d$

calculated from the formula $\left(\dfrac{d}{2}\right)^2 = 2ph$, where d is the diameter of the dome in the distance h from the tip. For each dome the d was measured at 3-4 distances, and the mean p was determined. For calculation of the parameter p, the d and h in the scale 265* to a milimetres, were measured.

Packets of cells on the dome surface could be seen in the surface layer. A packet is a group of cells enclosed within a wall which once was the wall of a single cell. All of the cells in the packet originated from this cell by successive divisions (Fig. 2). On the photographs of the dome surfaces, the sharply outlined packets were contoured. For each packet the dimensions: meridional, l_{mer}, and latitudinal, l_{lat}, as well as the distance q_{mer} between the center of packet and the vertex (along the meridional line), were measured. The ratio $l_{mer} : l_{lat}$ at the different q_{mer}, was evaluated for the apices of different age. These data were to answer the question, whether the growth on the dome surface is isotropic or anisotropic.
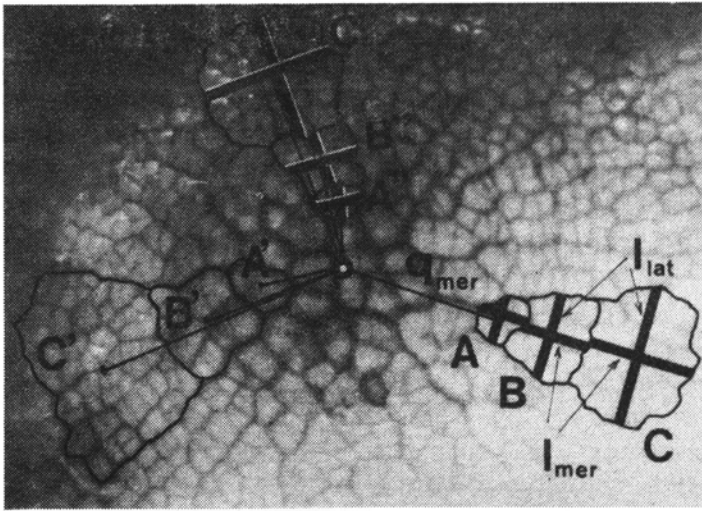
Fig. 2. Explanation to the calculation from cell packets in the surface layer of the relative rate of growth in length in meridional (i.e. periclinal on the surface of the dome) and latitudinal directions. Selected cells and cell packets derived from them are outlined. Each packet is characterized by the ratio $\frac{l_{mer}}{l_{lat}}$ and q_{mer}, where l_{mer} and l_{lat} are two dimensions of the packet in the meridional and latitudinal directions, respectively and, q_{mer} is the distance of the packet center the vertex (along the meridional line)

RESULTS

GEOMETRY OF THE DOME AND NATURAL COORDINATE SYSTEM

The apical dome in spruce has a rotational symmetry, thus the shape of a dome is fully defined by a single profile. Figure 3 shows the shapes of typical domes at different ages. It can be ascertained from these pictures that the profiles are parabolas, i.e., they fulfill the relation $\left(\frac{d}{2}\right)^2 = 2ph.$ The parameter p increases with the seedling age (Fig. 4). There was an increase of h at nearly constant p during each plastochron, and at the end of the plastochron, a distal portion was exported from the dome as a frustum. This caused shortening of the dome height, but the shortening was slightly less than the increase during one plastochron. Thus, the dome entered the next plastochron with a slightly greater height. There was also a slight increase of the parameter p.

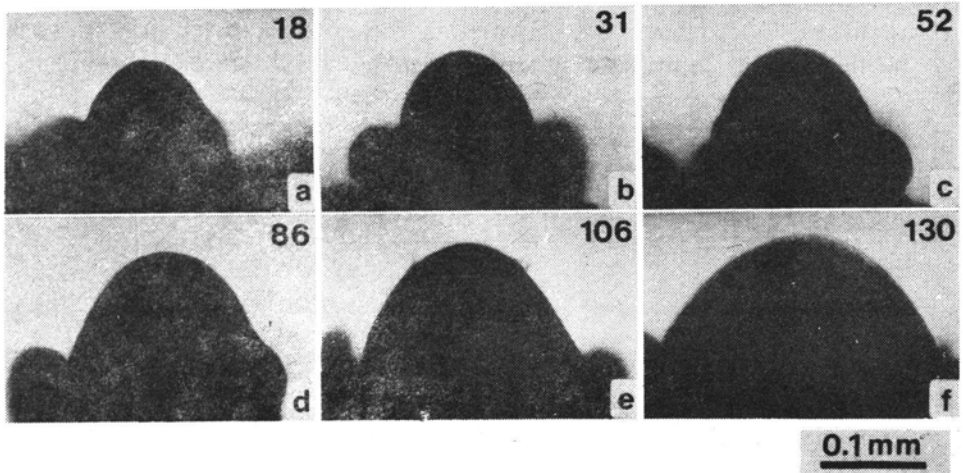The pericline on the dome surface in longisection was a parabola.

Fig. 3. Dome profiles for the shoot apices of seedings at different age from 18 plastochrons (a) to 130 plastochrons (f). The age in plastochrons is shown in the upper right-hand corner
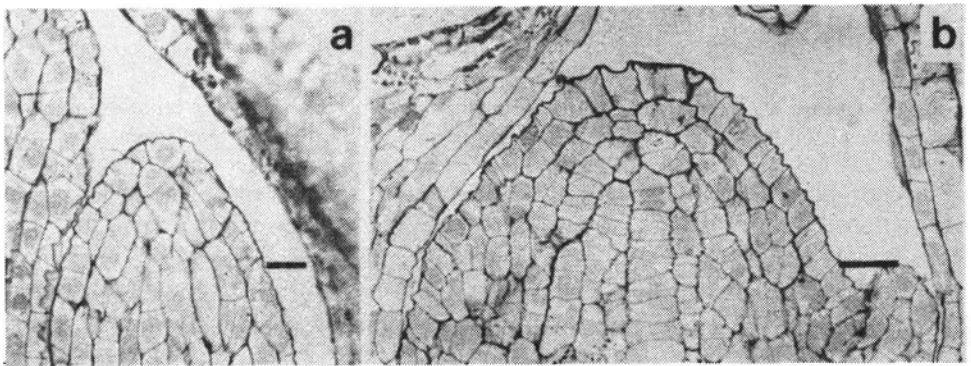

Fig. 5. Medial longitudinal sections from seedling shoot apices at about 10 plastochrons of age, (a), and at about 100 plastochrons of age (b). The base level is denoted for both domes

Inspection of the cell arrangement indicated that inside the apex, the periclines were parabolas too (Fig. 5). In the apical domes of the spruce lacking tunica typically (there are some periclinal divisions in the surface layer of cells in axial plane), and one can consider that periclines in longisection are convergent at the vertex. The convergent parabolic system (Nakielski 1987) (shown in Fig. 6) was therefore assumed in this work, to be the natural coordinate system (Hejnowicz 1984) for the spruce.
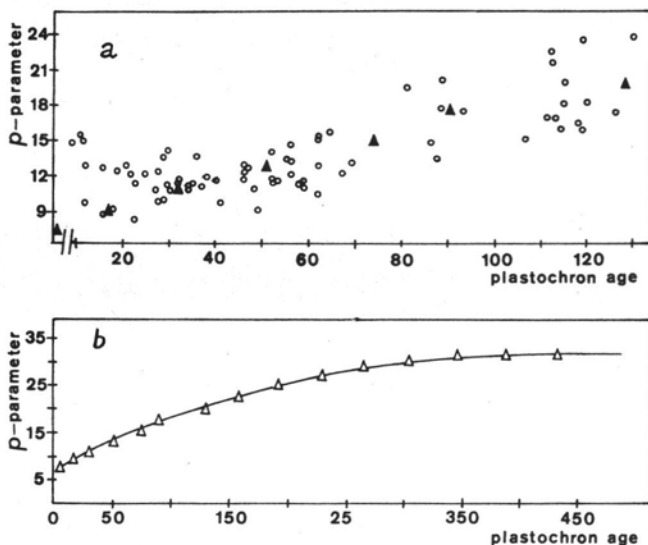

Fig. 4. Change in p parameter with plastochron age for the parabolas representing dome surfaces: a) for the range of plastochron age up to 130 plastochrons, data from own study, b) for the age up to about 400 plastochrons, based on Romberger and Gregory (1977), the data which are in the range to 130 plastochrons are marked on the upper plot as triangles

In Fig. 6 the profiles of three domes at different age, are shown. If we denote the curve representing the profile of a given dome as $v = v_s$, then for the parabola describing the profile we have $v_s = \sqrt{p}$.

DESCRIPTION OF DOME GROWTH BY MEANS OF THE GROWTH TENSOR

It is a feature of parabolas that, if we have two parabolas differing in their parameter p: $r_1^2 = 2p_1 h_1$ and $r_2^2 = 2p_2 h_2$, where $p_2 > p_1$, the latter can be transformed into the first by decreasing its scale. If $p_2 = ap_1$, $a > 1$, then the scale should be changed by a, namely by putting $r_2 = ar_1$ and $h_2 = ah_1$, the second parabola becomes then identical with the first. In this sense the increase of p equals the increase of the scale.
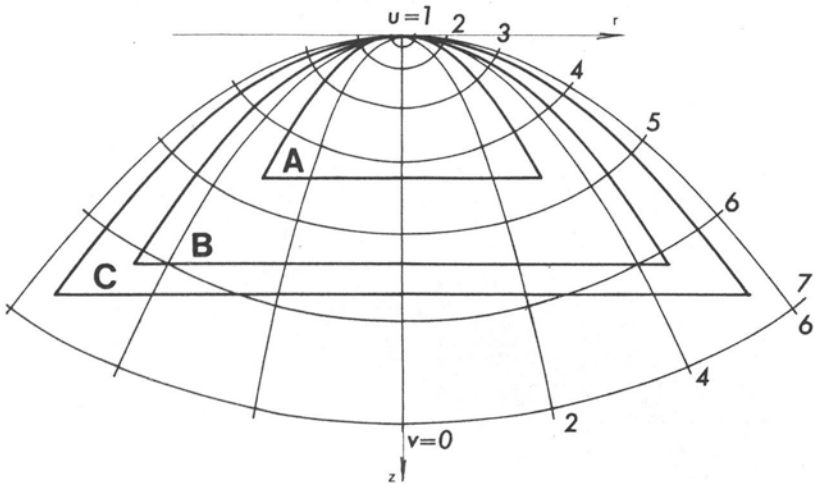
Fig. 6. The convergent parabolic system assumed as the natural coordinate system for spruce domes. The domes (*A, B, C*) for which the distributions of the growth rates were evaluated in this work, are outlined against the system

The growth of the dome of spruce can be considered as consisting of two superposed parts: I) relatively fast growth connected with the production of frusta at a constant *p* parameter, II) relatively slow growth connected with increasing of parameter *p*. The first is called a steady shape growth, the second is called an isogonic growth. Both of these growths can be described separately by means of their growth tensors $T(I)$ and $T(II)$. The total growth tensor for a given dome is equal to $T(I)+T(II)$.

Steady shape growth, cell packets in the surface layer of the dome

In general, vector $\bar{V}$ of the displacement velocity has three components in mutually orthogonal directions: periclinal, anticlinal and latitudinal. In natural coordinate system (u, v, φ), the components of $\bar{V}$ are: V_u, V_v, V_φ. The domes of spruce grow without rotation around the symmetry axis, thus $V_\varphi = 0$. Since in the steady shape growth, the parameter *p* is maintained in time, this means that the $V_v = 0$, and only V_u remains, V_u has to be known along one pericline to determine the field $V_u(u, v)$ for a whole dome (Hejnowicz 1984). It was obtained for the pericline on the dome surface, from analysis of the cell packets.

Figure 7 shows the surface of the domes at different stages of development. The cell packets are well recognizable. They originate from cells which earlier were located close to the vertex. The meridional and latitudinal dimensions of the complexes are similar (Fig. 8). This indicates that at least in a distal part of the apices of the seedlings 18-33 and 75-90 plastochrons old. the growth in area on the surface is isotropic. Older
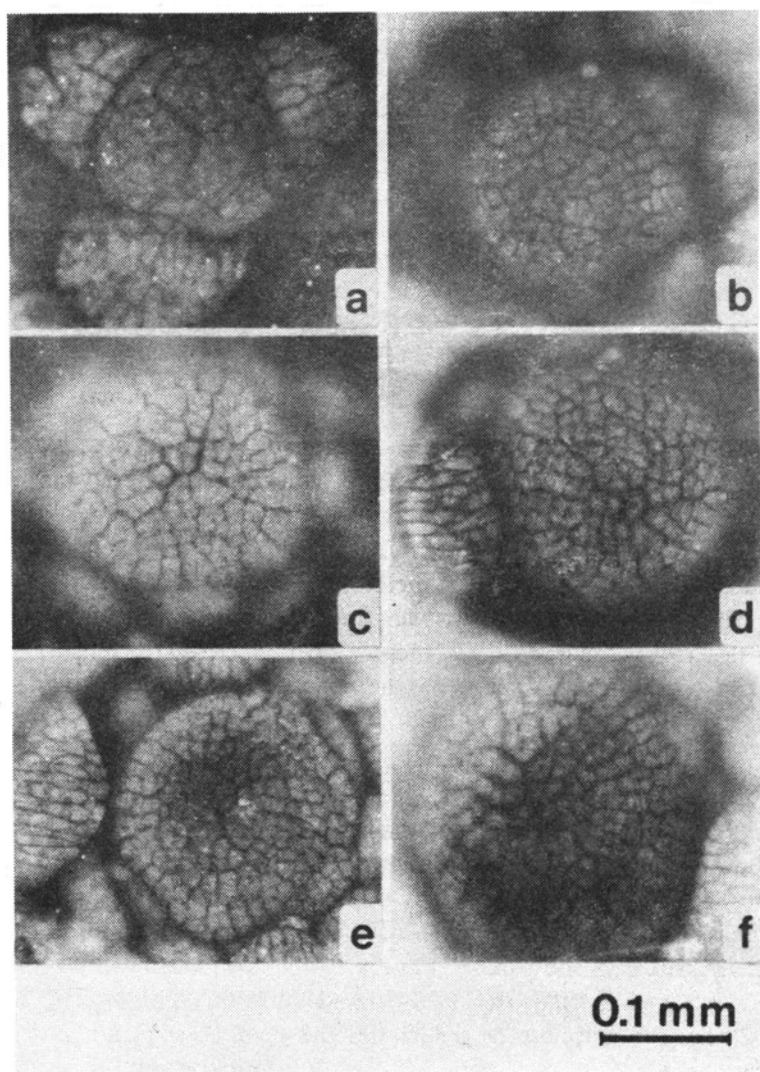
Fig. 7. The surface cellular configuration of shoot apices in the spruce seedlings. The apices: *a*, *b*, *c* — have from 20 to 35 plastochrons, *d*, *e*, *f* — have from 75 to 90 plastochrons

seedlings had not been investigated but the analysis of cell packets in the apices of old trees indicates that the growth on the dome surface is also rather isotropic there.

The fact that surface growth is isotropic means that the relative elemental rate of growth in length, $RERG_l$ (Richards and Kavanagh 1943, Hejnowicz and Romberger 1984), is the same in any directions in the plane tangent to the surface at given point (Nakielski 1987). Thus, from the condition $RERG_{l(per)} = RERG_{l(lat)}$ for $v = v_s$, where $RERG_{l(per)}$ and $RERG_{l(lat)}$
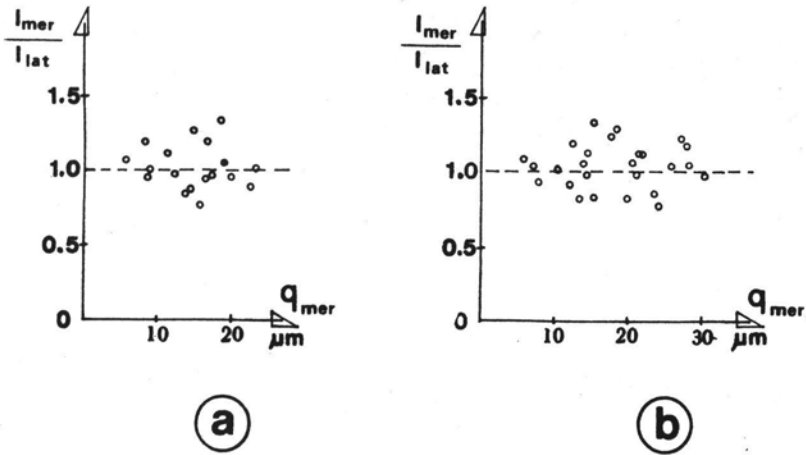

Fig. 8. The ratio $\dfrac{l_{mer}}{l_{lat}}$ as a function of q_{mer} (see Fig. 2) for the domes in two ranges of plastochron age: from 20 to 35 plastochrons (a) and from 75 to 90 plastochrons (b)

there are two the $RERG_l$ in the periclinal and latitudinal direction, respectively, the field $V_u (u, v)$ can be calculated. For the convergent parabolic system the following formula was obtained (Nakielski 1987):

$$V_u (u, v) = c \, \frac{v_s^2 \, \sqrt{\tilde{m} (\tilde{m} - 1)}}{v^2 \, \sqrt{m (m - 1)}} \sqrt{\tilde{m} - 1} , \qquad (1)$$

where $m = \dfrac{1}{v^2} \sqrt{4u^4 + v^4}$ and $\tilde{m} = \dfrac{1}{v_s^2} \sqrt{4u^4 + v_s^4}$. In the same paper the growth tensor for V_u described by (1), was given. This tensor is taken as T (I) for the modeled domes of spruce seedlings. Specification of T (I) depends on determining two constants v_s and c. This will be done in the next section.

Isogonic growth

The isogonic growth is a case of growth in which the relative elemental rate of growth in length, $RERG_l$, is the same at every point throughout

the organ, as well as being the same in any direction $\bar{e}_s$ from any given point (Richards and Kavanagh 1943). It is obvious that such a growth does not disturb the isotropy on the surface of the dome. Because no direction is favoured, the growth tensor $T(\mathrm{II})$ may be written in every coordinate system as:

$$T(\mathrm{II}) = \left\{ \begin{matrix} d & 0 & 0 \\ 0 & d & 0 \\ 0 & 0 & d \end{matrix} \right\}, \tag{2}$$

where $d = \mathrm{const}$ and $d = RERG_{l(s)}$ for any direction $\bar{e}_s$.

One can take the cylindrical coordinate system (r, h, φ) coaxial with
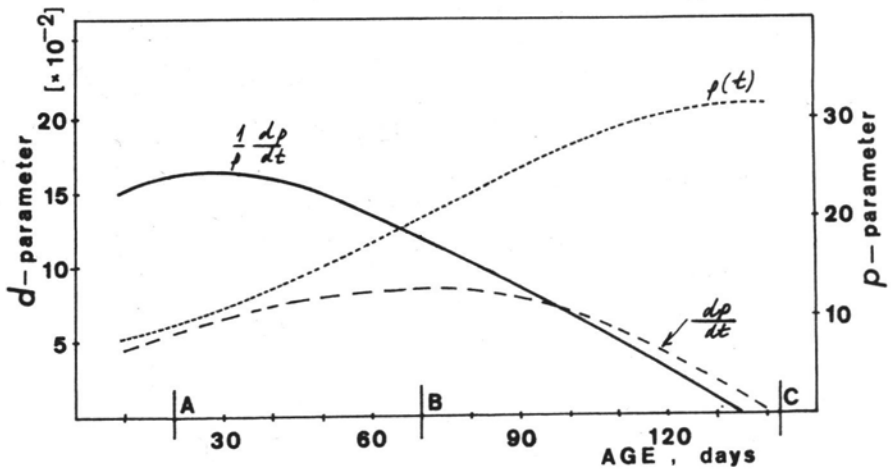

Fig. 9. The parameter d as a function of seedling age, in days. Two broken curves show the functions $p(t)$ and $\dfrac{dp}{dt}(t)$ from which the $d(t)$ was evaluated. The ages of domes selected for modeling are denoted on horizontal axis

the dome (where h is a symmetry axis). For isogonic growth, from the growth tensor $T(\mathrm{II})$, the $RERG_l$ in longitudinal and radial directions are the following:

$$RERG_{l(h)} = \frac{d}{dh}\left(\frac{dh}{dt}\right) = d, \quad RERG_{l(r)} = \frac{d}{dr}\left(\frac{dr}{dt}\right) = d.$$

Thus, by integration we have:

$$\frac{dh}{dt} = hd, \quad \frac{dr}{dt} = rd,$$

and finally:

$$\frac{1}{h}\frac{dh}{dt} = \frac{1}{r}\frac{dr}{dt} = d. \tag{3}$$

Differentiating the equation of the parabola $r^2 = 2ph$, the following relation it can be obtained:

$$\frac{dp}{p} = 2\frac{dr}{r} - \frac{dh}{h}.$$

Thus, dividing by dt and substituting (3), we have:

$$\frac{1}{p}\frac{dp}{dt} = \frac{2}{r}\frac{dr}{dt} - \frac{1}{h}\frac{dh}{dt} = 2d - d = d.$$

Accordingly, the value of d in $T(II)$ may be evaluated from the relative rate of change of p. The plot of $d(t)$ as a function of seedling age for the domes of spruce is shown in Fig. 9. With increasing age, the $d(t)$ decreases, and this means that the participation of isogonic growth in the growth of the domes as a whole, is smaller and smaller.

SELECTION OF THE DOMES FOR MODELING, SPECIFICATION OF THE GROWTH TENSOR

Three domes, differing by parameter p, were chosen for modeling: A — at the age of about 18 plastochrons, $v_s = 3$, B — at the age of about 130 plastochrons, $v_s = 4.6$, and C — at the age of about 400 plastochrons, $v_s = 5.6$. The fields V_u and the growth tensors $T(I)$ and $T(II)$ for this domes are different because the constants v_s, c and d in (1) and (2), are different there. The v_s and d, from own study, were specified for each of the domes. The c can be obtained from Romberger and Gregory's (1977) data referring to the height of the first internode in the shoot apices of spruce.

For the point at the dome base (the base is defined as transverse section of the dome at the level of youngest leaf axil) on the axis, the value of V_u, when its dimension is μm per plastochron, depends upon the increment of the dome height during one plastochron. If the dimension of V_u is μm per day, it then also depends on the plastochron duration. From Romberger and Gregory's studies, the distance of the first primordium below the base (IS), and the plastochron duration (PD), are known. Denoting velocity at the base level, by which the dome increases during one plastochron as $V_{u(b)}$, there is:

$$V_{u(b)} = \frac{IS \cdot 24\ hrs}{PD}. \tag{4}$$

Table 1

The constants: v_s, c, d determining growth tensors for domes A, B, C and the data from which these constants were calculated; v_s — coordinate describing dome profile, u_b — coordinate at which the base cuts the dome axis, IS — distance of the first primordium below the base, PD — plastochron duration, $V_{u(b)}$ — velocity at the base level on the axis of the dome, c — constant in the growth tensor T (I), d — constant in the growth tensor T (II)

Dome	A	B	C
v_s	3.0	4.6	5.6
u_b	4.25	5.40	5.74
IS^* (μm)	8.50	4.79	2.71
PD^* (hr)	20.10	7.96	5.07
$V_{u(b)}\left(\dfrac{\mu m}{day}\right)$	10.15	14.44	12.85
c	6.39	12.03	13.31
d	0.019	0.012	0.001

* From Romberger and Gregory (1977).

In the relation above, $V_{u(b)}$ pertains to the u (denoted as u_b), at which the base cuts the dome axil $v = 0$ (see Fig. 6). Thus, from (1) and (4), the parameter c is:

$$c = \frac{2V_{u(b)}\, u_b^2\, v_s}{\sqrt{4u_b^4 + v_s^4}\left(\sqrt{4u_b^4 + v_s^4} - v_s^2\right)}. \tag{5}$$

The values of IS, PD and $V_{u(b)}$ from which the c for the domes A, B, C were computed, are shown in Table 1. In the same table the parameters d are given, as they are read from the plot $d(t)$ on Fig. 9. Knowing the constants: v_s, c and d for a given dome, the specific growth tensors T (I) and T (II) can be written. For example, the total growth tensor for dome A has following final form:

$$T(\mathrm{I}) + T(\mathrm{II}) = \frac{57.5\sqrt{\tilde m}\,(\tilde m - 1)}{t^4\, m\,(m-1)} \begin{vmatrix} H & \dfrac{-\sqrt{m-1}}{m} & 0 \\ \dfrac{\sqrt{m-1}}{m} & \dfrac{m+1}{m} & 0 \\ 0 & 0 & 1 \end{vmatrix} + \begin{vmatrix} 0.019 & 0 & 0 \\ 0 & 0.019 & 0 \\ 0 & 0 & 0.019 \end{vmatrix},$$

where $m = \dfrac{1}{v^2}\sqrt{4u^4 + v^4}$, $\tilde m = \dfrac{1}{9}\sqrt{4u^4 + 81}$,

and $H = \dfrac{m^2(\tilde{m}-1) - \tilde{m}^2(m-1)}{\tilde{m}^2 m(m+1)} + \dfrac{m(\tilde{m}+1)}{\tilde{m}(m+1)}.$

DISTRIBUTION OF GROWTH RATES

The results of modeling are shown together for domes A, B, C in the forms of computer-made maps (Figs. 10, 11 and 12). The maps on Fig. 10
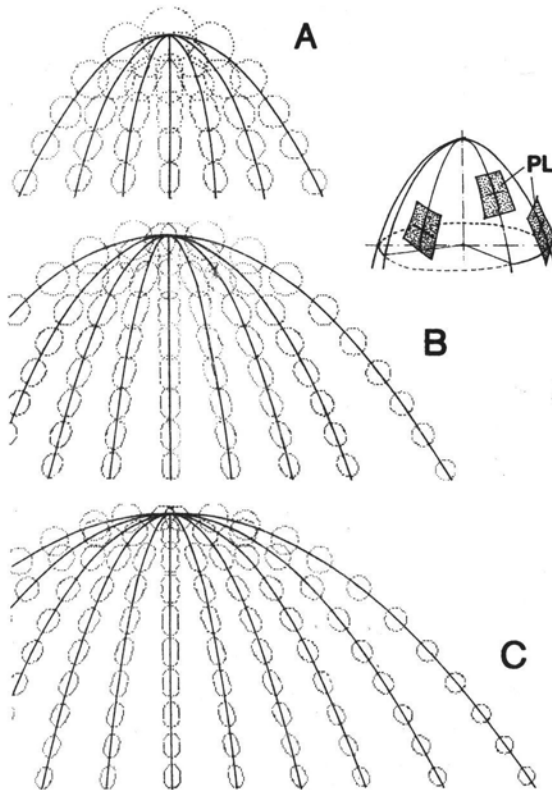

Fig. 10. Spatial and directional variations of the linear growth rates for domes A, B, C in PL planes. The three-dimensional drawing shows the orientation of some of the PL planes. Values of the $RERG_l$ are displayed in the form of two-dimensional computer-made plots of $RERG_l$ around a number of points lying on the parabolas in the axial plane (for each plot its latitudinal direction is oriented anticlinally as the result of the rotation of the PL plane by $90°$ around the pericline). For a given position, $RERG_l$ in different directions every $10\text{-}15°$, were evaluated. Anticlinal coordinates of the convergent parabolic system are not marked, however, the points for which $RERG_l$ values were calculated lie along the following surfaces: a) for dome A, $v=0$, $v=1$, $v=2$, $v=3$, b) for dome B, $v=0$, $v=1$, $v=2$, $v=3$, $v=4.6$, c) for dome C, $v=0$, $v=1$, $v=2$, $v=3$, $v=4.1$, $v=5.6$. The size of domes is proportional to their length at each stage of their growth. Plots of $RERG_l$ are drawn in the same scale
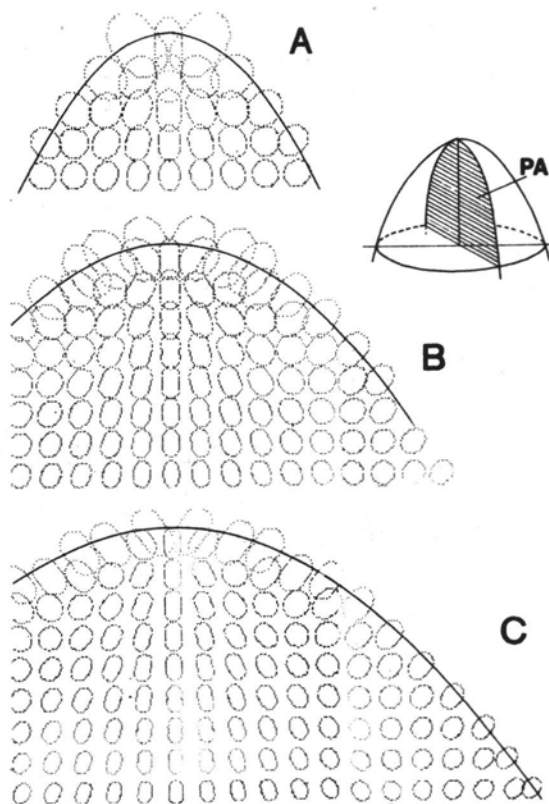
Fig. 11. Spatial and directional variations of the linear growth rates for domes *A*, *B*, *C* in axial plane *PA*. Explanation as in Fig. 10 except that the points for which $RERG_l$ values were evaluated, lie in the nodes of the rectangular net

show the plots of $RERG_l$ in the planes *PL*, fixed by periclinal and latitudinal principal growth directions. The other maps show the $RERG_l$ and $RERG_{vol}$ (the relative elemental rate of growth in volume equal to the sum the $RERG_l$ in three mutually orthogonal directions (Richards and Kavanagh 1943, Hejnowicz 1982) distributions in axial plane *PA*.

It is obvious that in the *PL* planes (Fig. 10), the plots formed by $RERG_l$ around the points on the dome surface are circles because the growth is isotropic there, as was assumed. The circles decrease in radius with the increase of meridional distance from the vertex. The absolute values of $RERG_{l(per)}$ and $RERG_{l(lat)}$ are equal at the points on surface v_s, but then they decrease with increasing u. On the same maps, the growth is not isotropic below the surface of the dome, the $RERG_{l(per)}$ is higher than $RERG_{l(lat)}$. At the dome axis $RERG_{l(lat)}$ amounts to 50-60% of $RERG_{l(per)}$.

From Fig. 11, it can seen that the distribution of $RERG_l$ in the axial plane *PA* is as follows: in peripheral parts of domes at the base level, the $RERG_l$ is nearly isotropic, and it is not so in the other regions;
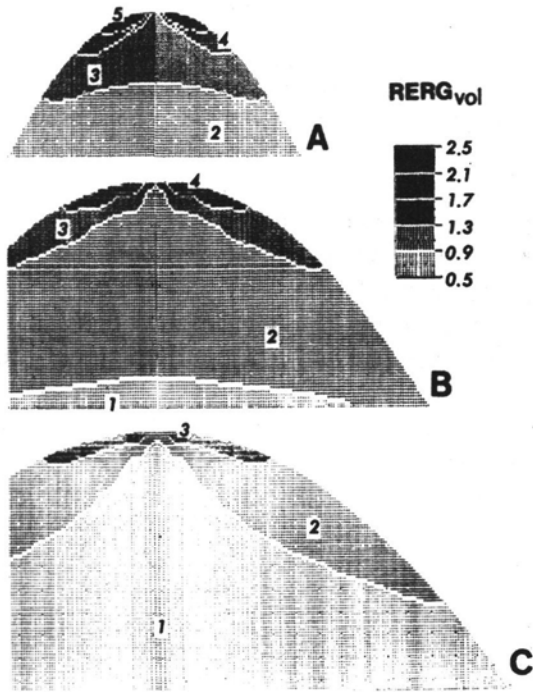
Fig. 12. The distributions of volumetric growth rate $RERG_{vol}$ for domes A, B, C. Within the domes the following numbers of points lying in the nodes of the rectangular net were taken into interpolation: dome A — 120, dome B — 160, dome C — 220. The full range of growth rate variation for all domes was divided by the computer into 5 equal parts, numbered from 1 to 5. The position of each part within the dome is marked by one of five graphical symbols, according to the legend. The unit of $RERG_{vol}$, the same for all maps, represents the increment of small volume element per day. The program SYMAP for the Riad 32 computer was used to obtain the regions on the maps

the maximum of the $RERG_{l(per)}$ is on the dome axis at the vertex, the maximum of the $RERG_{l(ant)}$ is on the dome surface in the distal part, and $RERG_{l(ant)}$ is there the greatest of all. In corresponding regions of different domes, the linear growth rates decrease with increasing parameter p. For instance, the mean value of $RERG_{l(per)}$ at the base of dome C amounts to about 80% of the one calculated for dome B, and about 60% of the one for dome A.

Figure 12 shows the distributions of volumetric growth rates. On the base level of each dome, the $RERG_{vol}$ is about 50% less than in the distal part. The mean $RERG_{vol}$ for dome A is the greatest, all ranges of $RERG_{vol}$ values from the legend, are represented in this dome. With increasing p when domes become wider, the upper ranges disappear one by one, for instance, in dome B — the range 5 disappears, in dome C — the range 4. In this sense, dome A grows more quickly than B, and dome B more quickly than C.

DISCUSSION

The geometry of the apical dome in spruce seedlings changes specifically during development because the profile of the dome remains parabolic. This feature was used to distinguish into steady shape growth and isogonic growth. In the latter, the anticlinal component of the field $\bar{V}$ was assumed in the most simple way, namely by $RERG_l = $ const. (at all points and for any direction). Giving up that particular division would necessitate solving the equation for isotropy surface growth (Nakielski 1987) for both V_u and V_v components together. Because of having two unknown quantities: V_u and V_v in one equation, some second equation should be considered, and then both equations could be solved as a system. There have been attempts to use the feature for nondiagonal elements of the growth tensor that $T_{uv} = -T_{vu}$ (Hejnowicz and Romberger 1984) as the second equation, but it appears that the mathematical description of growth becomes more difficult while the results are similar to these obtained in the present paper. From this point of view, the division into steady shape growth and isogonic growth is convenient.

The choice of the natural coordinate system for spruce shoot apices is a controversial question. There are two possibilities: a paraboloidal system or a convergent parabolic one. The second system was chosen for modeling, in the belief that the first better suits dome with a tunica. In the apical domes of spruce there occur some periclinal divisions in the surface layer of cells at the vertex (in axial plane), which indicates that the tunica, if present, is in the form of a potential tunica rather, according to the terminology of Foster (1939). If the confocal system is appropriate for the tunical dome, why was it not chosen here? It we match the coordinate surface $v = $ const. of the paraboloidal system to the profile of the real dome, it appears that the focus is at a point about $1/3$ of the dome height below the vertex, i.e., the distance between the focus and the vertex is greater than the dimension of two cells. Thus, in confocal system the cells deriving from pariclinal divisions of the initial cell (located at the vertex of the dome) cannot cross the focus during growth, while in the spruce apical initials give the derivative cells inside the dome (Korody 1937, Hejnowicz 1957).

The author of the present paper is aware that the convergent parabolic system has some faults too (Nakielski 1987). Among other things, in consequence of these faults the $RERG_{l(ant)}$ on the surface of the distal part of the dome is too large (Fig. 11). Similarly, at the base level, the $RERG_{l(ant)}$ is too high in peripheral part, and simultaneously is too low in the central part.

The possibilities of comparing the results of the present study with

empirical data are small because the literature pertaining to the dynamics of shoot apex growth in spruce is scarce. We have only Romberger and Gregory's data (1972a, b, 1977) for the seedlings and the paper of Camefort (1956) referring to old trees.

Romberger and Gregory found, as mentioned before, that the mean volumetric growth rate calculated for the dome as a whole decreases with seedling age. It will be seen from our results showed in Fig. 12 that the mean $RERG_{vol}$ for the whole dome A, B, C is decreasing too.

It is known that if the mean cell dimensions in a meristem are nearly constant (such situation occurs at spruce in the first approximation) then from the mitosis pattern, the growth rate distribution may be concluded (Hejnowicz 1980). Camefort (1956) reported that in the distal parts of tree domes there were 2 mitoses only, whereas in peripheral and central parts, there were 198 mitoses all together. Because the volume of the distal part is not less than 10% of the whole dome, this means that the distal part grows much more slowly than other parts. But results presented in this paper are exactly the oppisite! There is no irrefutable argument that the distribution of mitoses in the dome of old trees is the same as for seedlings, however, if this is really the case in spruce, then how can the difference be explained? The two possibilities exist: 1) one can not be sure whether the isotropic surface growth applies to the whole surface of the dome, as it was used in our studies; thick lack of confidence is caused by the fact that when the curvature of the surface is large, cell packets in the basal region of domes are poorly visible, 2) trajectories of the principal directions of growth in a real dome are different from the ones used in our studies; it should be stressed here, however, that these trajectories in the case of periclinal direction, cannot be distinctively different from the parabolas (similar modeling conducted with the paraboloidal system and with the same assumptions referring to the surface growth, gives results which do not change the proportion of growth between different regions of the dome).

It is interesting that in spruce, for the seedling as well as for the tree, cell packets in the surface layer of the dome can be clearly seen. On the basis of the pattern of cell packets, the variant of the surface growth and, in consequence the $\bar{V}$ field for the whole dome, were determined. The cell packets provide essential information for the modeling study. Therefore, it is great satisfaction to learn that at present many authors for various reasons, have become more interested in cell packets studies (Bierhorst 1977, Barlow 1983, Puławska 1986).

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Zróżnicowanie szybkości wzrostu w wierzchołkach pędu siewek świerka: Badania za pomocą tensora wzrostu

Streszczenie

Modelowano rozmieszczenie szybkości wzrostu w wierzchołku pędu w przypadku, gdy kształt apikalnej części wierzchołka się zmienia. Apikalna część wierzchołka u świerka ma kształt paraboloidy obrotowej. W trakcie wzrostu staje się większa i bardziej płaska ale jej profil pozostaje paraboliczny. Z badań kompleksów komórek w warstwie powierzchniowej wynika, że wzrost w płaszczyznach stycznych do powierzchni wierzchołka jest izotropowy. Dane te wykorzystano w modelowaniu. Założono, że wzrost wierzchołka jest superpozycją: 1) stosunkowo szybkiego wzrostu wydłużeniowego, w trakcie którego profil wierzchołka się nie zmienia oraz zapewniona jest izotropia wzrostu powierzchniowego na powierzchni; 2) stosunkowo słabego wzrostu izogonicznego, w trakcie którego wierzchołek rośnie „na grubość" bez zmiany wzrostu powierzchniowego w płaszczyznach stycznych do powierzchni. Oba typy wzrostu opisano oddzielnie w terminach tensora wzrostu, biorąc jako naturalny dla świerka ortogonalny układ współrzędnych oparty na konwergentnych parabolach. Z macierzy tensora wyliczono względne szybkości wzrostu liniowego i objętościowego w różnych punktach organu. Wyniki pokazano w ormie komputerowych map szybkości wzrostu dla wierzchołków siewek w różnym wieku. Okazało się, że szybkości wzrostu wewnątrz wierzchołków są zróżnicowane, największe są w wierzchołku najmłodszym, najmniejsze w najstarszym. Występuje zróżnicowanie wzrostu między różnymi rejonami wierzchołka. Największe szybkości są w strefie dystalnej, najmniejsze przy podstawie, na poziomie najmłodszych zawiązków liściowych. Zróżnicowanie to zmniejsza się z wiekiem siewek, w miarę jak wierzchołki stają się bardziej płaskie.