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Original article

Structure and development of vegetative buds, from the lower crown of *Picea abies*

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Summary — Seasonal changes in the development of Norway spruce (*Picea abies* (L) Karst) vegetative buds in the lower crown position of 4 18-year-old free standing grafts in the climatic conditions of Poland are described. Bud awakening varies with the season while the end of shoot elongation, after about 6 weeks, seems to be weather independent. Mitotic activity of the embryonic shoot starts about 1 month before bud-burst. The new winter bud develops in 2 periods of bud scale primordia initiation (autumn and spring) and 1 period of needle primordia initiation (during summer). The curves of apical dome size (width and height) have 2 peaks: the 1st one, in late April just before the 1st spring bud scale primordium emerges, and the 2nd one, during the time of rapid needle initiation (mid-August). There is seasonal variation in starch accumulation. Starch is absent in the dormant bud. In the developing bud, starch is associated with areas of high morphogenic activity.

***Picea abies* / spruce / vegetative bud / anatomy / development**

Résumé — Structure et développement des bourgeons végétatifs de la partie basse de la couronne de *Picea abies*. *L'étude porte sur les changements au cours du temps, et dans les conditions climatiques de la Pologne, observés dans le développement de bourgeons végétatifs situés dans la partie basse de la couronne d'épicéas communs (*Picea abies *(L) Karst). Elle concerne 4 arbres greffés, âgés de 18 ans, et poussant hors concurrence. La reprise de croissance des bourgeons varie selon les conditions saisonnières propres à chaque année, alors que la fin d'élongation des pousses, environ 6 sem après le débourrement, semble indépendante du climat. L'activité mitotique de la jeune pousse située dans le bourgeon commence environ un mois avant le débourrement. Le nouveau bourgeon hivernal se développe en 2 temps pour ce qui est de l'initiation des primordia d'écailles de ce bourgeon (à l'automne et au printemps), et en un seul temps pour l'initiation des primordia d'aiguilles (durant l'été). Les courbes de croissance en diamètre et en hauteur du dome apical présentent 2 pics : le premier fin avril, juste avant que n'émergent les primordia des premières écailles de printemps, le second durant la période de rapide initiation des primordia d'aiguilles (mi-août). On observe une variation saisonnière dans l'accumulation de l'amidon. Il est absent dans les bourgeons dormants alors que, dans les bourgeons en développement, il est associé aux zones présentant une forte activité morphogénétique.*

Picea abies */ épicéa / bourgeon végétatif / anatomie / développement*

INTRODUCTION

Development of vegetative buds from the lower crown in *Picea abies* was studied. There are several reports on this topic concerning *Picea* species other than *Picea abies* (*eg,* Owens *et al,* 1977; Pillai and Chacko, 1978; Tompsett, 1978; Harrison and Owens, 1983; Skupchenko, 1984). Our 6 years of study on bud development in Norway spruce concerned:

i) seasonal development of the vegetative bud (manifestation of bud awakening, morphogenic and mitotic activity of the apical meristem);

ii) seasonal changes in apical meristem dimensions;

iii) dates of onset and termination of shoot elongation;

iv) seasonal changes of starch accumulation in the embryonic shoot; and

v) changes in the metabolism of tannin vacuoles.

MATERIALS AND METHODS

In 1986, 4 free-standing 18-year-old grafts of 1 clone in a clonal archive at Zwierzyniec near Kórnik (longitude 17°04', latitude 52°15', altitude 70 m) were selected for morphological and anatomical studies. The selected clone K-15-33 originates from Stronie Śląskie. Chosen grafts were approximately of the same height (7–8 m) and vigor.

Studies were carried out on shoots from the lower crown zone (excluding 3 or 4 lowest living branch whorls). This zone was selected for experimental studies on male buds initiation.

The time table (month.day) for collecting and fixing of specimens for histological studies was as follows:

years: 1986 – 04.25, 05.08, 05.27, 06.27, 07.23, 08.11, 09.09, 10.20, 12.03

1987 – 01.26, 02.25, 03.26, 04.15, and from 04.27 to 12.28 weekly

1992 – from 03.05 to 11.10 weekly.

Also information was used from another study on the same clone and on ramets of the same age. Material was collected:

1988 – from 01.06 to 05.16 weekly, and 07.11, 08.23

1989 – 01.27, 05.02, 05.03, 05.11, 05.12, 06.20, 07.25, 09.19

1990 – 03.23, 10.10.

Buds with or without scales (depending on the stage of bud development) were fixed in Craf solution (in proportion: 0.8 g chromic acid, 3 ml glacial acetic acid and 20 ml 40% formaldehyde). Specimens were dehydrated in ethyl alcohol and through benzene embedded in paraffin. Transverse and longitudinal sections 9 μm thick were stained with Ehrlich hematoxylin by the progressive method (modified Gerlach, 1969). For cytochemical analysis, specimens were treated with Schiff's reagent for Feulgen (counterstained with Fast green) or PAS (periodic acid Schiff) reaction (modified Berlyn and Miksche, 1976). Details of these methods were described in Hejnowicz (1982).

Dimensions of the apices were established on longitudinal median sections using the ocular micrometer. Mitotic indices on permanent specimens were calculated on series of transverse sections after the Feulgen reaction.

Occasionally during the warm winter of 1990, mitotic activity of embryonic shoot was checked on squash specimens with the aceto-carmin method (Gerlach, 1969).

In 1988, 1990, 1991 and 1992, the dates of starting and termination of shoot growth, as well as the rate of shoot elongation, were established on branches from the same part of the crown of 2 trees. Terminal and distal lateral buds/shoots were measured weekly from early spring to mid-June.

RESULTS

Structure and development of the winter buds

The winter resting bud of Norway spruce, encased in bud scales, possesses an

embryonic shoot bearing all of the next year's needle primordia, which delimit stem units (= internode + node; Doak, 1935), but not the lateral bud primordia.

The dormant embryonic shoot averages 2 mm in length and is one-fourth of the whole bud length. At the base of the embryonic shoot in the pith region there is a nodal diaphragm (crown figs 1, 2, 28) built of thick-walled living cells with irregularly thickened but not lignified walls. The walls have many simple pits. Some pith cells are filled with tannins.

Beneath the ventral (adaxial) epidermis of the upper bud scales there are basipetally extending strands of cells resembling those in the pith nodal diaphragm. These strands, in that part of the receptacle where the bases of bud scale join together, form a ring which we have named "peripheral diaphragm" (d_2, fig 2).

Bud length in winter is positively correlated with the mother shoot length (r = 0.70***). This is a consequence of a positive correlation between the length of an embryonic shoot and the number of stem units (fig 4). There is also a positive correlation between needle and shoot length (r = 0.52***). For the studied years, needles were shorter on the 2-year portion than on the 1st year shoot of a branch (fig 5). The correlation between bud and shoot length and between needle and shoot length, could account for the difference of the needle length on terminal and lateral distal shoots (fig 5).

In the winter, the length of a lateral distal bud on a shoot is approximately the same as that of its terminal or is about 1 mm shorter (fig 6).

Two kinds of bud scales, outside ones (dry, rigid, relatively thick) and deflexed and internal ones, cover the embryonic shoot. The youngest internal scales (delicate and living) immediately cover the apical meristem.

The apical meristem of Norway spruce vegetative bud has 4 cytohistological zones. (Terminology used here as first described by Foster (1938) for Gingko.) At the summit of the apex, there are a certain number of apical initials below which lie the central mother cells zone. Further below, there is a pith rib meristem zone which produces vacuolated pith cells. Some of them are filled with tannins colored yellow or red after the PAS reaction. On the flank of the apical meristem lies the peripheral meristem that produces the scale and needle primordia.

The best identifiable zonation especially viewed on slides after the Feulgen reaction is in late April to early June (figs 7–9).

Shoot development

Shoot elongation on branches of the same vigor and approximately of the same length and diameter starts in late April or early May and ends in late May or early June (fig 10).

The years 1988 and 1990 differed substantially in the daily mean air temperatures in the months preceding bud development. In 1988, the temperatures were much lower than in 1990 (fig 11). In May, however, the mean air temperature and the total precipitation (15 mm) were very similar for the 2 years. Reactivation of bud development in 1988 occurred about 1 week later than in 1990, but the elongation of shoots in both years lasted about 6 weeks. The final mean shoot length in 1988 was more than 40% greater than that attained in 1990 (fig 10A). (This difference cannot be explained by differences in the age of trees, since in both years the branches chosen for measurement were of more or less the same size and stem girth.) It appears that elongation rate in 1990 was negatively affected by low air humidity at the time the shoots were in the most advanced stage of development.

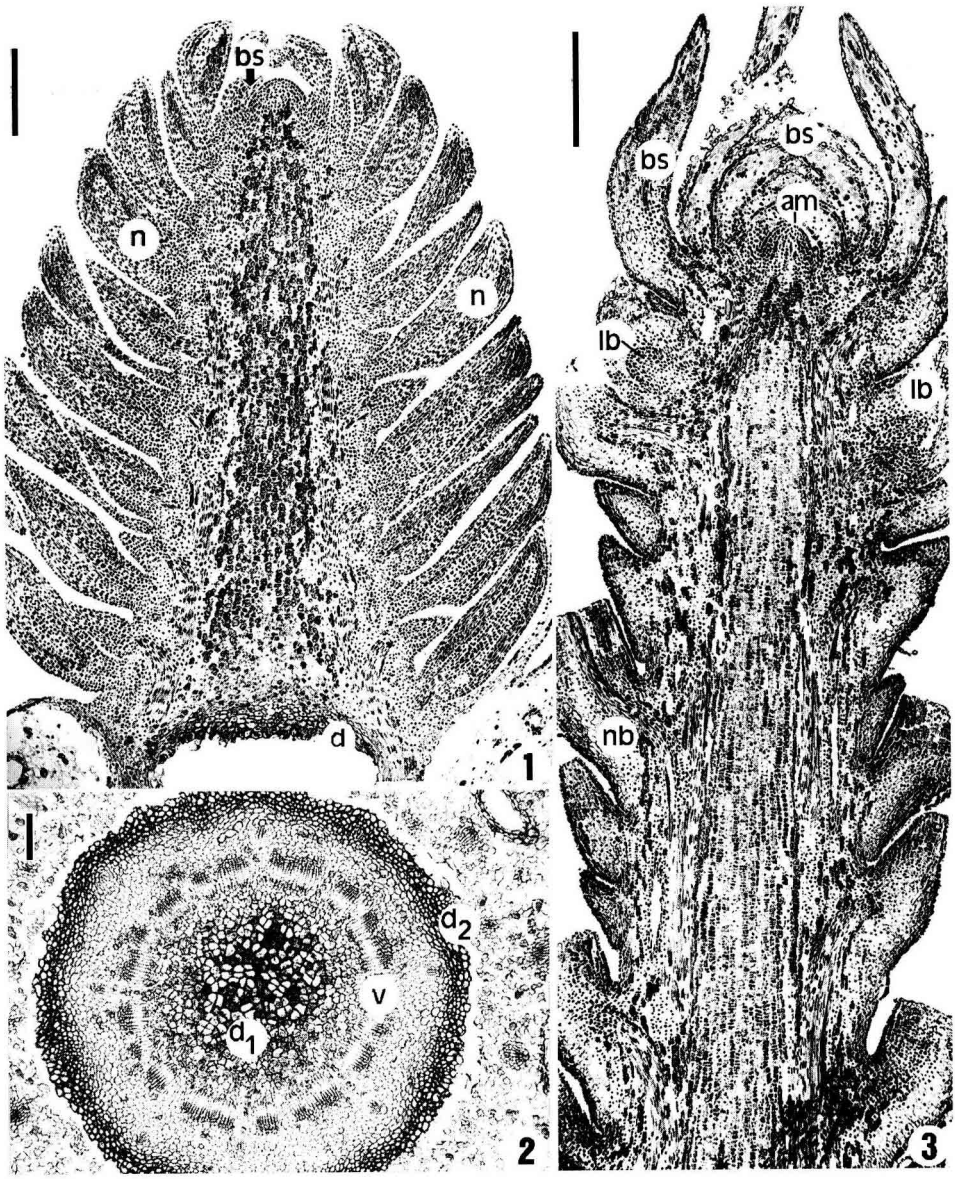


Fig 1. Median longitudinal section of embryonic shoot, mid-April, Feulgen reaction + Fast green. Bar = 0.4 mm. bs = bud scale; n = young needle; d = nodal diaphragm.

Fig 2. Cross section of the basal (proximal) part (black line in fig 28) of the embryonic shoot, early May, PAS reaction. Bar = 0.2 mm. d_1 = pith diaphragm; d_2 = ring of cells of the peripheral diaphragm with collenchymatically thickened walls; v = vascular bundle.

Fig 3. The upper part of an embryonic shoot on median longitudinal section, early May. Feulgen reaction + Fast green. Bar = 0.3 mm; am = apical meristem of the future winter bud surrounded by bud scales; lb = lateral bud primordium; bs = bud scale; nb = basal part of young needle.

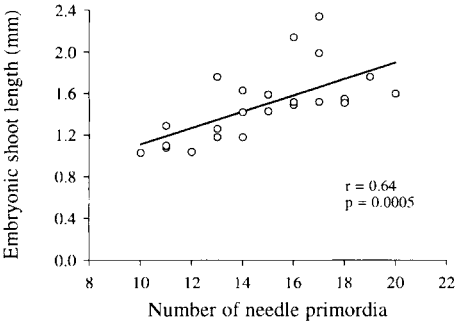


Fig 4. Correlation between length of embryonic shoot and number of needle primordia (*ie*, stem units) on a central longitudinal section, mid-September.

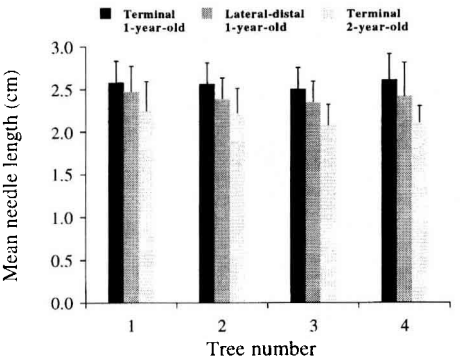


Fig 5. Mean needle length on current-year (1990) and 2-year (1989) portions of a parent branch and lateral-distal shoot on the same branch. Means for each of 4 trees of 10 centrally located needles and 2–9 branches.

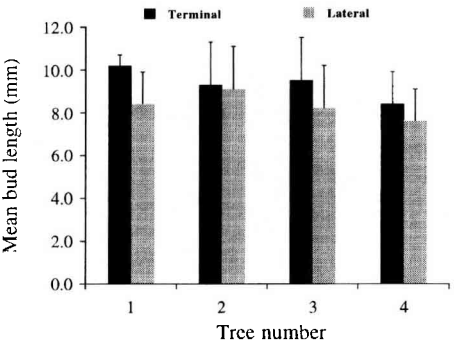


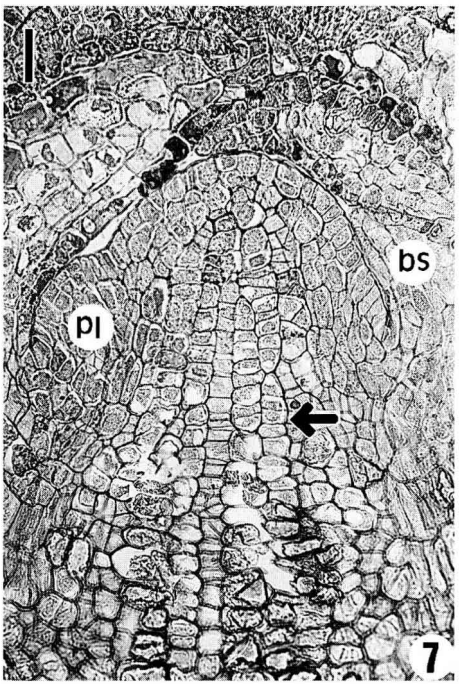
Fig 6. Mean terminal and lateral-distal winter bud length on branches from the lower crown region of 4 trees. Means of 10 buds.

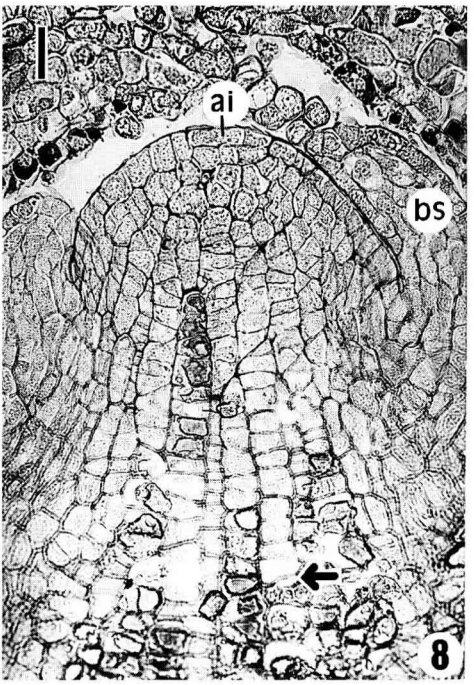
In the years 1991 and 1992, initiation of bud development occurred similarly as in 1988 in the 1st days of May and terminated about 6 weeks later (fig 10); thus there was three times as much precipitation in May (54 mm) as in the years 1988 and 1990.

Resumption of cell divisions was studied precisely only in 1988. The first mitoses arose in cataphyll primordia and in the procambium in the 2nd half of March (about 1 month before bud burst) and then in the apical meristem 2 weeks later. In 1987, after a cold winter (mean temperature of January −9.8°C, February −0.9°C and March −1.8°C), no mitoses were observed in March. In 1990, winter was mild and mitoses were observed in late March just in the apical meristem (fig 11). In 1990 and 1992, dividing cells in young needle were observed in early March and in apical meristem 2–3 weeks later.

The 1st apical meristem cells to divide were those of the peripheral meristem producing bud scale primordia. Cells at the summit of the apex, the apical initials, began to divide about 2–3 weeks later. In late June, the apical meristem began to produce needle primordia. The last one arose in late August or early September. In the next 2–3 weeks, a few bud scale primordia differentiated, but most of them are initiated in the spring of the next year (fig 12C).

Two characteristics distinguish bud scale and needle primordia in the early phase of development. First, procambial cells lie near the adaxial surface in scale primordia (figs 14 and 16), but more centrally in needle primordia (figs 13 and 15). In the needle primordium, mitoses are distributed more reg-





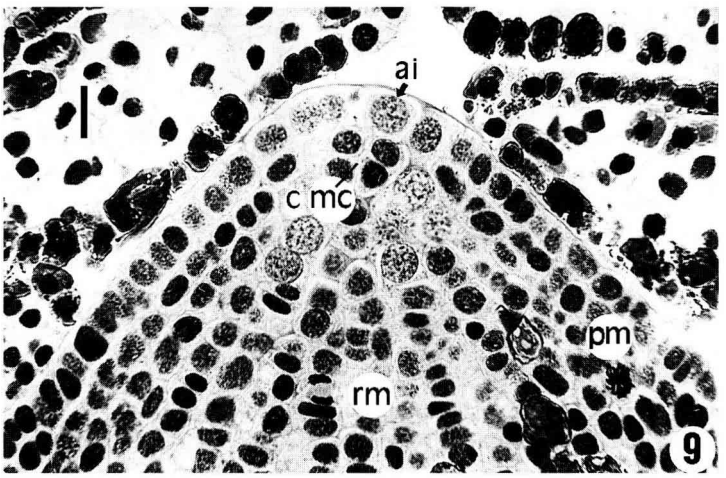


Fig 7. Terminal apex on median longitudinal section, mid-April. Arrow = the border between old and new parts of the embryonic shoot, PAS reaction. Bar = 0.4 mm. pl = bud scale primordium; bs = bud scale.
Fig 8. As in figure 7, 3 weeks later. Three periclinally divided apical initials (ai). Bar = 0.04 mm. bs = bud scale.
Fig 9. Median longitudinal section of apical meristem of terminal bud, early June, Feulgen reaction + Fast green. Bar = 0.02 mm. ai = apical initials; pm = peripheral meristem; cmc = central-mother cells; rm = pith-rib meristem.

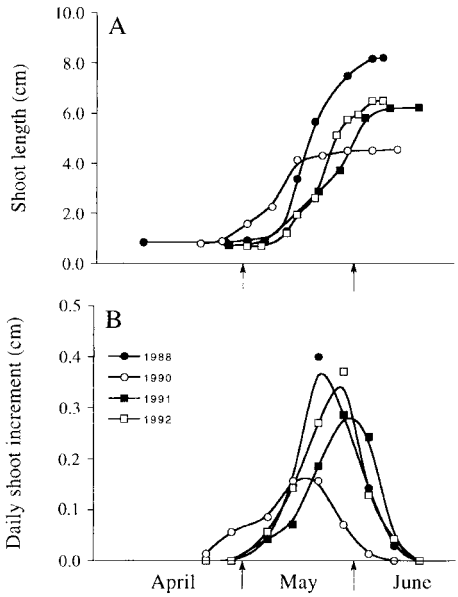


Fig 10. Bud/shoot length (A) and daily shoot length increment (B) in the years: 1988 (means of 20), 1990 (means of 22), 1991 (means of 40), and 1992 (means of 50). Measurements were made weekly from mid-March.

ularly and in the scale primordium they are mainly on the abaxial and marginal parts (viewed on cross sections). Thus, the cross-sectional shape of a young needle is round and of a bud scale is flattened on the adaxial surface.

Before bud burst, the length of the embryonic shoot increases twofold due to internode elongation. The embryonic shoot/bud length ratio thus becomes double that in the winter (0.5 *vs* 0.25). In early July, during needle primordia initiation, the embryonic shoot of a new winter bud is about 0.15 mm long. In mid-October, it reaches a final length of about 2 mm (fig 12B).

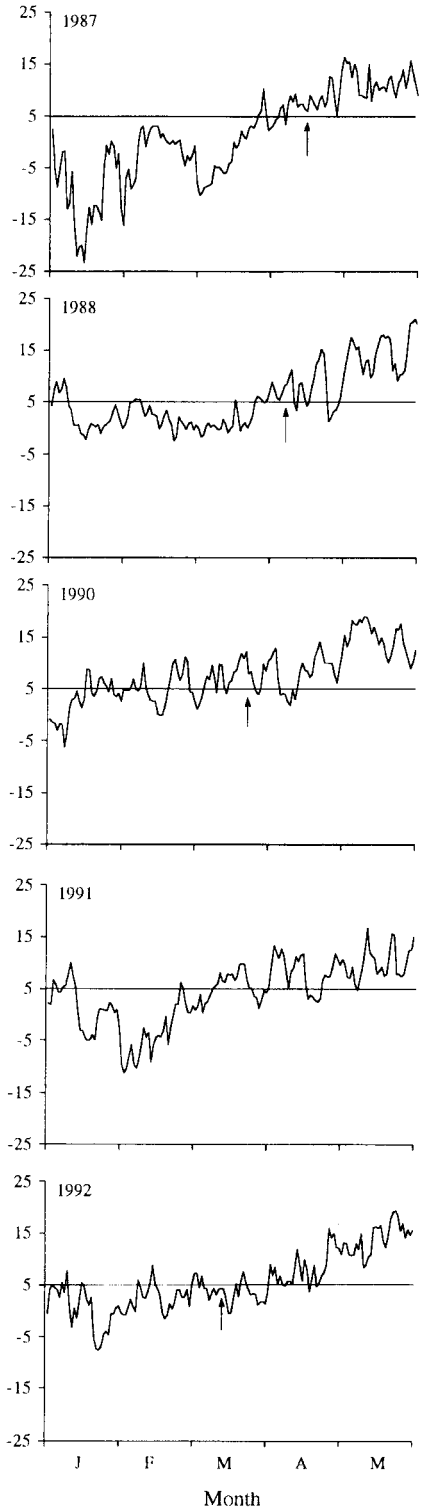


Fig 11. Mean temperature of January–May in 1987, 1988, 1990, 1991 and 1992. Data of meteorological station located 3 km from the site of the clonal archieve. Arrows indicate the 1st mitoses in apical meristem in 1987, 1988 and 1990 and in young needles in 1992.

In the spring, before the apical meristem starts to produce new bud scale primordia, the old ones and young needles begin to elongate and differentiate (fig 1).

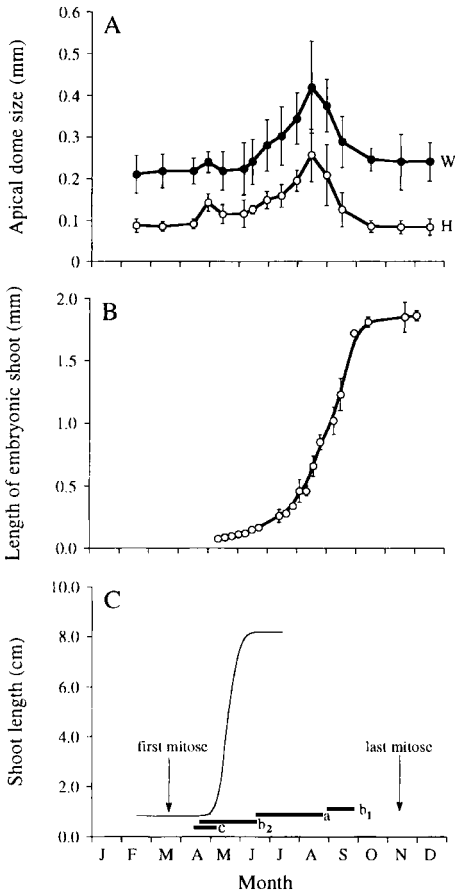


Fig 12. Bud/shoot development on branches of the lower crown in 1987. (A) Seasonal changes of apical dome dimensions (W = width, H = height). Means of 6–17 terminal and lateral-distal buds. (B) Development of a new winter bud. Means of 6–12 terminal and lateral-distal buds. (C) Seasonal winter bud development against a background of shoot growth curve in 1987. a = needle initiation phase for 1988 shoot; b_1 = autumnal phase of bud scale initiation for 1989 shoot; b_2 = spring phase of bud scale initiation for 1988 shoot; c = lateral bud initiation phase for 1988 shoot.

At the end of April, due to high mitotic activity, the dimensions of the apical meristem increase. After the 1st bud scales have been initiated, height and width of the apical dome decreases (fig 12A). During the phase of rapid needle initiation (mid-August), apical dimensions and the ratio of height to width are the greatest. In winter, the ratio is 0.4 and it increases to 0.5–0.6 in mid-August.

About 4–5 weeks after the start of mitotic activity in the embryonic shoot, the 1st lateral bud primordia arose in the axils of young needles from the distal zone of the parent embryonic shoot (figs 3 and 17). This began in the 2nd half of April (fig 12C). The axillary bud primordium enlarged and the apical meristem became organized. Periclinal divisions in the 2 or 3 outer layers of the peripheral meristem gave rise to 2 prophylls. These were situated opposite each other and perpendicularly to the plane of the needle axis and the axis of the mother shoot. During the next 2 months, as on the terminal apex, cataphyll and then needle primordia arose (figs 18 to 20). Before the winter, needle primordia were about 0.5 mm long.

In early September, when needle primordia production terminated, mitotic activity of the apical meristem decreased. Soon thereafter, several bud scale primordia were laid down in the new terminal bud and lateral distal buds.

Almost all cells of the bud axis are meristematic. Dividing cells in the pith region are visible until the end of shoot elongation (end of May). In early May, more or less regularly arranged sclerenchyma cells differentiate, forming transverse plates across portions of the pith (figs 21–23). Sclerenchyma cells are shorter and distinctly less vacuolated than other pith cells. There are tannins in the vacuoles, and the cell walls are thick, unlignified and have simple pits (fig 23).

From the beginning of new terminal and lateral bud initiation, the border between old

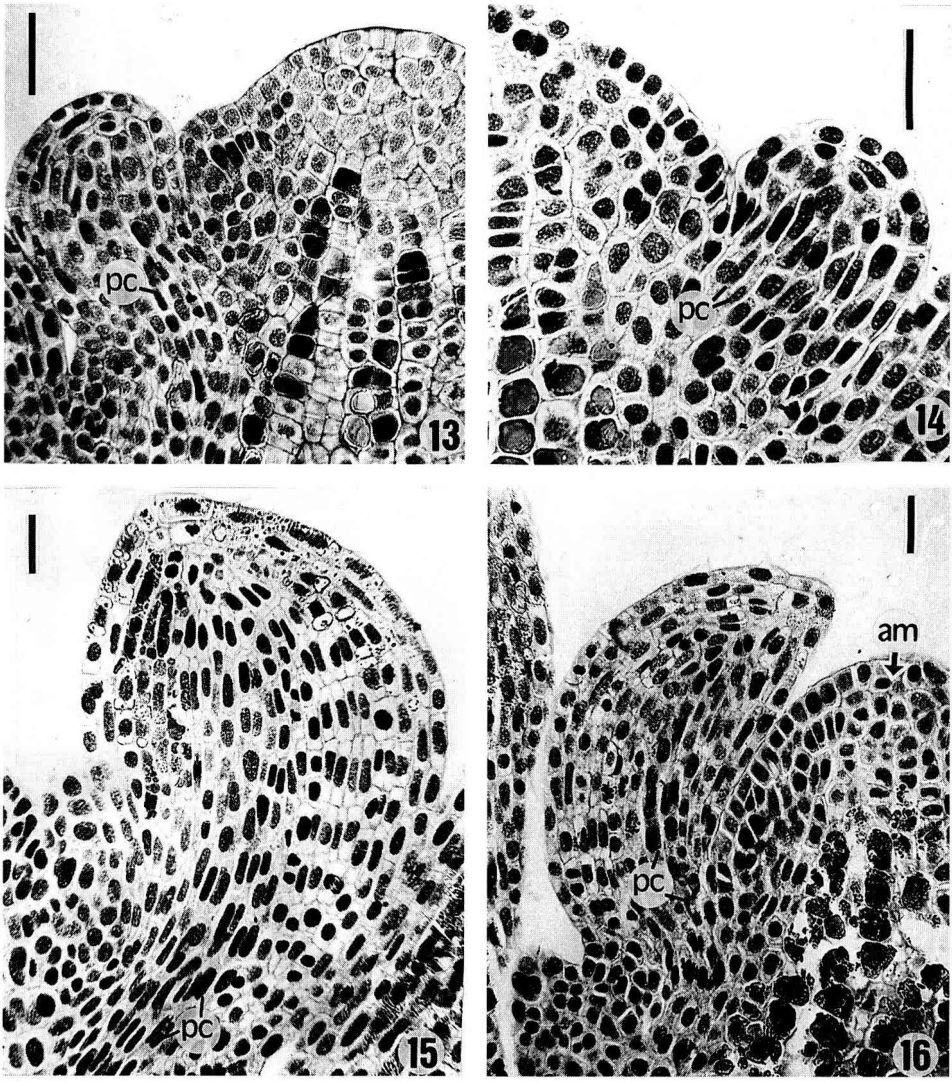


Fig 13. Distal part of an embryonic shoot with last needle primordium on central longitudinal section, late September, Feulgen reaction + Fast green. Bar = 0.05 mm. pc = procambium cell.
Fig 14. Bud scale primordium on longitudinal section in terminal winter bud, February, Feulgen reaction + Fast green. Bar = 0.05 mm. pc = procambium cells.
Fig 15. Median longitudinal section of young needle, late March, Feulgen reaction + Fast green. Bar = 0.04 mm. pc = procambium cells.
Fig 16. Distal part of an embryonic shoot in longitudinal section in Mid-April. Elongating bud scale initiated during the autumnal period of morphogenic activity of the apex, Feulgen reaction + Fast green. Bar = 0.04 mm. am = apical meristem; pc = procambium cells.

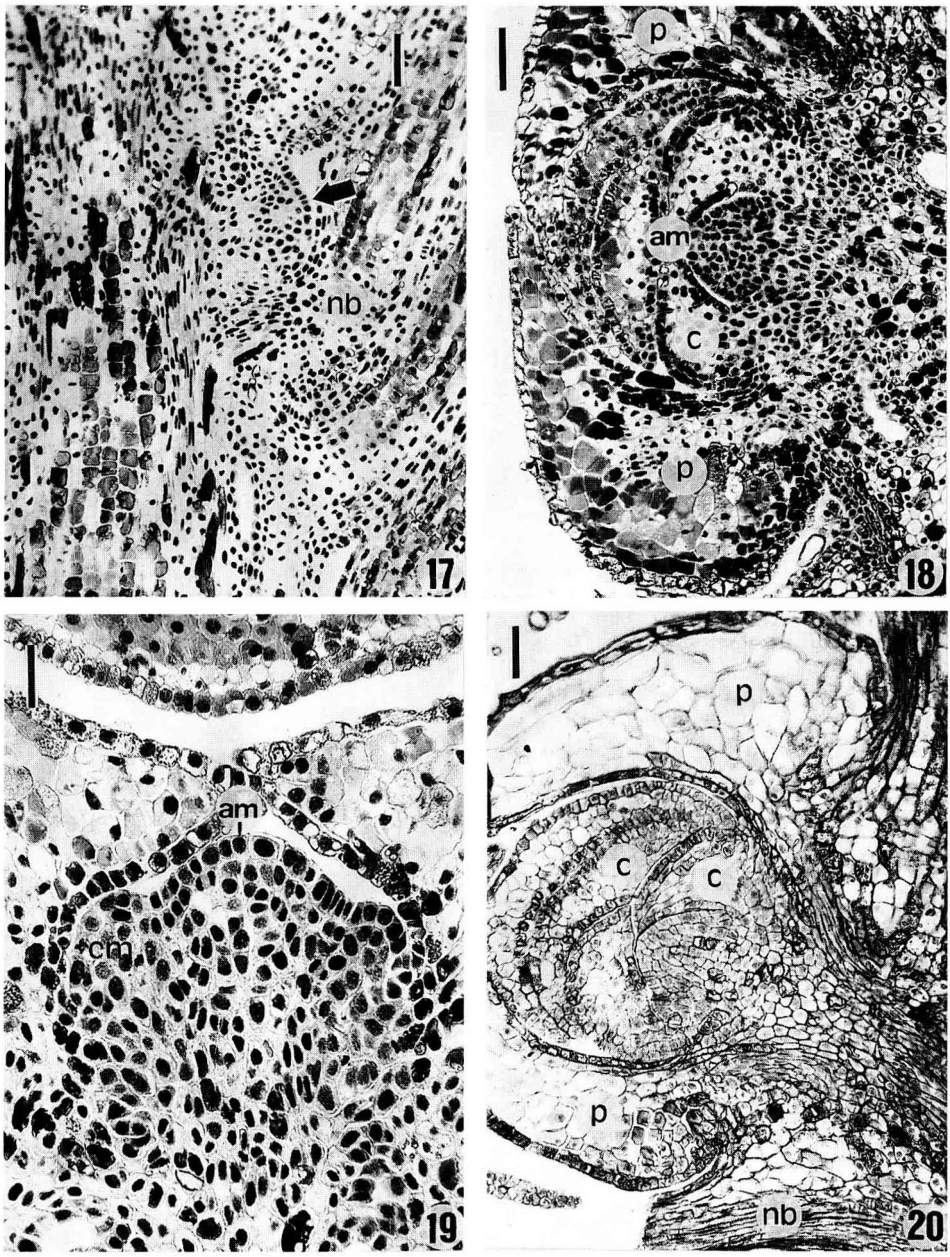


Fig 17. Part of the embryonic shoot on median longitudinal section. Lateral bud primordium in the axil of young needle. Apical meristem (arrow) before prophylls are initiated in late April, Feulgen reaction + Fast green. Bar = 0.08 mm. nb = basal part of young needle subtending the lateral bud primordium.
Fig 18. Longitudinal section of lateral bud primordium at the end of cataphyll initiation, Ehrlich hematoxylin progressive method. Bar = 0.05 mm. am = apical meristem; p = prophyllum; c = cataphyllum.
Fig 19. As in figure 18, 2 weeks earlier, the first 2 cataphyll were initiated (mother shoot on cross section). Bar = 0.05 mm. am = apical meristem; cp = cataphyll primordium.
Fig 20. Median longitudinal section of lateral bud in the stage of bud scale initiation. Apical mersitem is well organized, late May, PAS reaction. Bar = 0.08 mm. p = prophyllum; c = cataphylllum; nb = basal part of needle subtending the lateral bud.

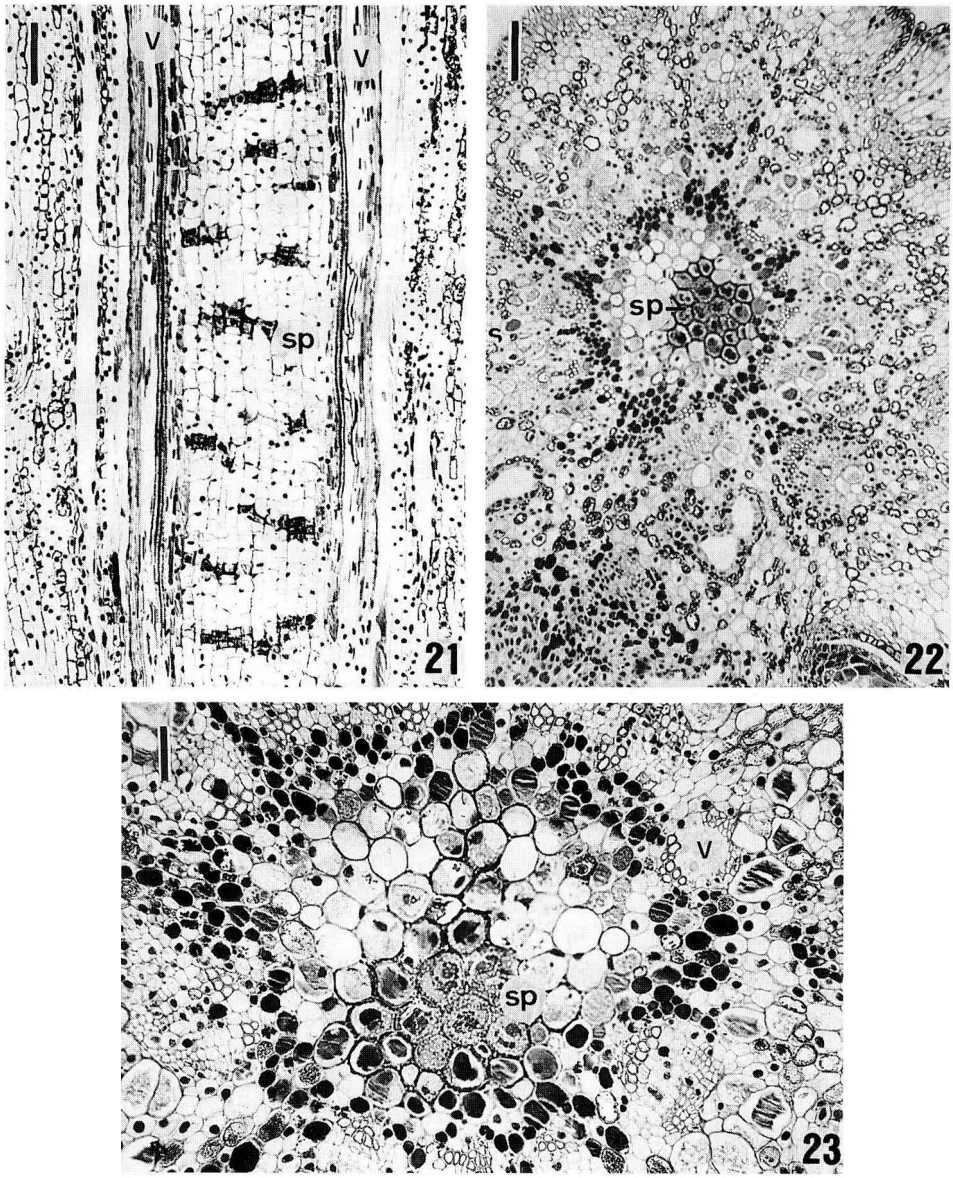


Fig 21. Sclerenchyma plates (sp) in elongating shoot in longitudinal section, mid-May, PAS reaction. Bar = 0.05 mm. v = vascular bundle.
Fig 22. Sclerenchyma plate (sp) on cross section, mid-May, Feulgen reaction + Fast green. Bar = 0.1 mm.
Fig 23. As in figure 22, simple pits in the walls are visible. Bar = 0.05 mm. sp = sclerenchyma plate; v = vascular bundle.

and new parts of the embryonic shoot is visible (figs 7 and 8). In the former tannin, cells are colored red after PAS reaction, and in the latter, light yellow. In August, collenchyma-like cells differentiated in this region (fig 25), forming the future nodal diaphragm or crown (figs 1, 2, 26–28). From mid-July to late September, starch accumulates in this region (figs 24 and 27), while there is little starch in other parts of the embryonic shoot of the new bud. On the other hand, starch is absent in cells of the mature nodal diaphragm while it is relatively abundant in other parts of the bud.

Starch was absent from the winter bud (negative PAS reaction). Only in the oldest bud scales located below the nodal diaphragm were some starch grains visible during the winter. In the initial phase of bud growth (April), starch accumulates in young needles (fig 28) and on sites where the future lateral bud primordia will arise.

In mid-October, the morphogenic activity of the apex ended. Mitotic activity stopped first in the apical meristem and last in the youngest needle and bud scale primordia. Several dividing cells could still be seen in the youngest leaf primordia at the end of November.

Tannin-containing cells of the young pith undergo seasonal changes. In winter, vacuoles of these cells are colored orange or red after the PAS reaction. In the summer, they become light yellow. There is a relation between starch and red coloration of pith cells after PAS reaction. The region of red cells in the winter bud is in the upper half of the embryonic shoot where in the summer and early autumn the most intensive starch accumulation occurs.

DISCUSSION

Our study on the structure and development of the vegetative bud of Norway spruce indicates that it behaves similarly to other spruces (Lewis and Dowding, 1924; Korody, 1938; Camefort, 1956; Anikeeva and Minina, 1959; Fraser, 1966; Schüepp, 1966; Owens and Molder, 1976; Owens *et al*, 1977; Pillai and Chacko, 1978; Tompsett, 1978; Harrison and Owens, 1983; Skupchenko, 1984; and others).

Bud growth resumes when the required heat sum ("degree days" after Sarvas, 1967) is achieved. Cannell (1985) suggested that the date of vegetative bud burst of *Picea sitchensis* depends not only on heat sum required to induce bud burst but also on the number of chilly days experienced during winter and spring. This could explain why

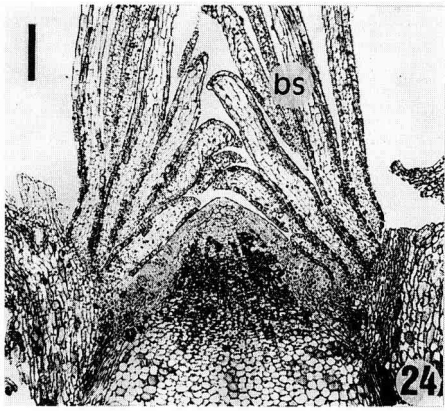
Fig 24. Embryonic shoot at the start of needle intiiation, late June, PAS reaction. Bar = 0.2 mm. bs = bud scale.

Fig 25. Embryonic shoot at the period of the last needle initiation, late August, Feulgen reaction + Fast green. Bar = 0.2 mm.

Fig 26. Embryonic shoot during the first bud scale primordia initiation (arrow) in mid-September, Feulgen reaction + Fast green. Bar = 0.2 mm.

Fig 27. Embryonic shoot in the autumnal phase of bud scale initiation on longitudinal section. Great amount of starch (black) in the subapical part of young pith, and no starch (light cells) below the nodal diaphragm. Late September, PAS reaction. Bar = 0.2 mm.

Fig 28. Embryonic shoot in mid-April on longitudinal section. Great amount of starch in the pith distributed as in autumn (see fig 27) and also in the distal part of the developing needles and around procambial strands. Below the nodal diaphragm (X) a gap is visible which arose in late autumn due to autolysis of pith cells (compare with fig 27). PAS reaction. Bar = 0.2 mm. Black line = the level of section in figure 2.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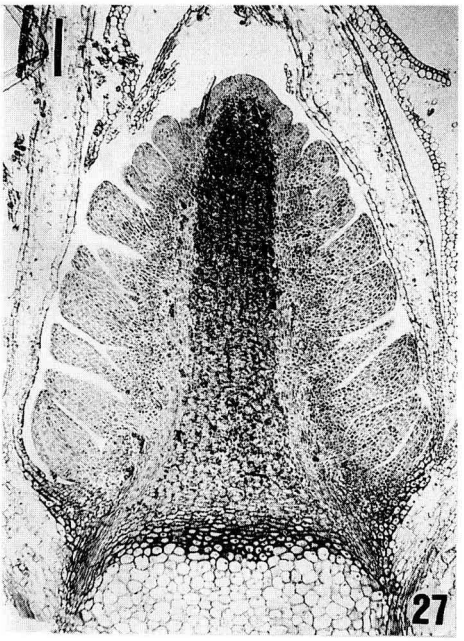
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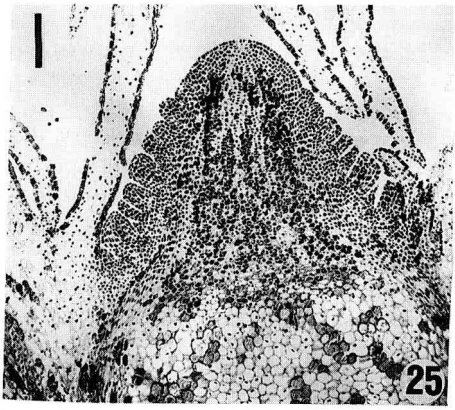
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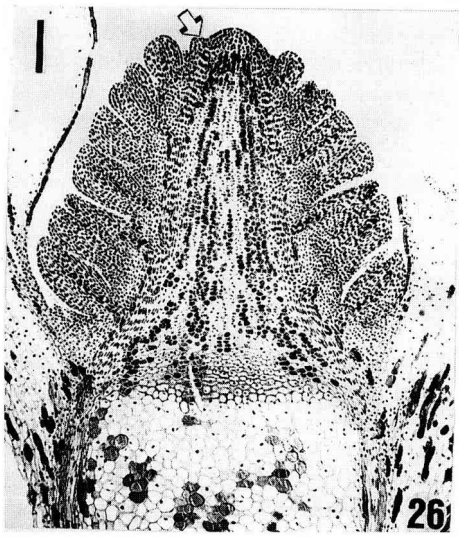
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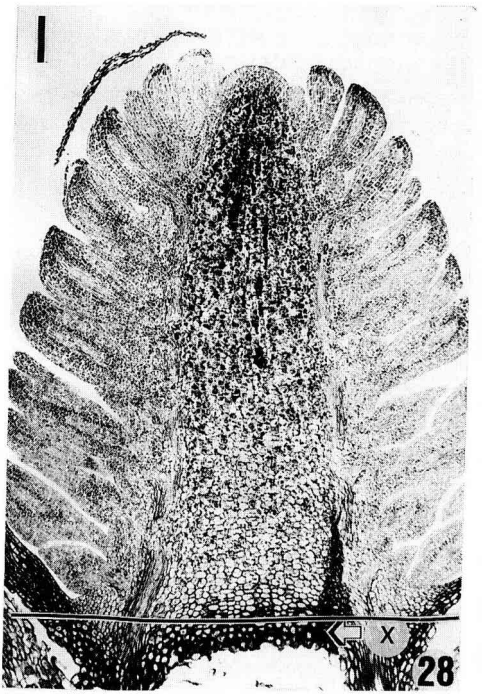
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28

in 1987, in spite of a very cold winter, only a few (counting from January) warm days (mean daily temperature between 5–10°C) preceded resumption of mitotic activity in the apical meristem. In 1990 (a mild winter), the first dividing cells of the apical meristem were observed in late March though in previous months there were nearly 40 days with mean temperature above 5°C (8 days with temperature above 10°C) (fig 11).

Shoot elongation in the lower crown of *Picea abies* lasted about 6 weeks (fig 10) as in *Picea glauca* in the same level of the crown (Fraser, 1962), independently of the date of bud awakening. The cessation of shoot extension varies with the year (fig 10) and with location in the crown (Fraser, 1962; Ford *et al,* 1987). It appears therefore that temperature which determines the initiation of bud elongation in the spring does not affect the duration of bud elongation.

Shoot elongation is achieved both by cell elongation and cell division. In *Picea abies,* cell divisions in the shoot axis were observed until the end of shoot elongation (*eg,* early June 1988). The final shoot length depends therefore on conditions during bud initiation influencing bud length (spring–summer of year n–1) as well as on conditions during bud/shoot elongation (May of year n).

Cytohistological zonation of the apex was most visible when the rate of mitotic activity of the peripheral and pith-rib meristems was high and in distal zone (apical initials + central-mother cells), there were no cells in division (fig 9).

At the end of the morphogenic activity of the apical meristem, the first bud scale primordia arise. No autumnal phase of bud scale initiation was previously noted in the genus *Picea* (*eg,* Owens and Molder, 1976; Harrison and Owens, 1983). Assuming that those observations were exact, this would make *Picea abies* an exception. In this species, Camefort (1956) also found scale primordia in the winter bud. Schüepp (1966) wrote that in *Picea abies* the 1st bud scales are initiated at the beginning of the season; nevertheless, in his fig 153, he has the starting point of the first 10 scale primordia placed in September of the previous year. These two authors did not give any explanation of this.

Two periods of bud scale primordia initiation, which are characteristic for all pines (*eg,* Hejnowicz, 1982), may also be characteristic of spruces, at least in some crown locations. Because of the difficulty in distinguishing scale and needle primordia at an early stage of their development, this could have gone unnoticed before. The distribution of procambial cells, identified by their shape and density of protoplasm, allows one to distinguish bud scale and needle primordia. (Procambium cells were clearly visible on slides stained with Fast green at low pH because of the more intensive color of cytoplasmic compounds than in neighboring cells. That was not easy to show on black and white microphotos.) In scale primordia, procambium cells lie near the adaxial surface and in needle primordia, more centrally (figs 14–16).

There are 2 kinds of bud scales in the winter bud of *Picea abies* (Kaniewski *et al,* 1971): outside and inside ones. The former are thick and narrow. The inside bud scales are broad, flattened in the tangential plane and undifferentiated. The basal part of the inside scales is meristematic, becoming thin and membranous during the spring. When elongating the dead, upper part of scales are raised above the embryonic shoot. These scales become detached and are shed. Outside bud scales do not come off in the spring. They form a rigid, dead collar at the base of an elongating shoot (as in Scots pine; Hejnowicz, 1982). We suggest that the outside bud scales were initiated a year earlier, in the autumnal phase of apical meristem activity. In the opinion of Harrison and Owens (1983), in the *Picea engelmannii,* both kinds of bud scales arise in the

spring of the same year. The difference in their structure would be due to the various rates of activity of the apical meristem. The 1st arise in the slow, and the 2nd during the rapid phases of bud growth.

In Norway spruce, as in Scots pine (Hejnowicz, 1979, 1982), there may exist a causal relationship between seasonal changes in tannin and starch metabolism. Tannins occur in vacuoles and are hydrolyzable. Released glucose may be utilized for starch synthesis. In the initial period of embryonic shoot elongation (mid April), starch accumulates in the axils of some young needles. Thus, starch accumulation there can be considered as an indication of the onset of lateral bud primordium development.

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