

Cambium Dynamics of *Pinus sylvestris* and *Betula* spp. in the Northern Boreal Forest in Finland

Uwe Schmitt, Risto Jalkanen and Dieter Eckstein

Schmitt, U., Jalkanen, R. & Eckstein, D. 2004. Cambium dynamics of *Pinus sylvestris* and *Betula* spp. in the northern boreal forest in Finland. *Silva Fennica* 38(2): 167–178.

Wood formation dynamics of pine and birch along a south-north transect in Finnish Lapland were determined by the pinning technique. For all trees at all sites a more or less sigmoid shape of the wood formation intensity is characteristic with a slow beginning, a faster growth in the middle and a decreasing activity towards the end of the vegetation period. Wood formation of pine started at sites 1–3 (southern sites) in the second week of June and at sites 4 and 5 (northern sites) only in the last week of June, whereas wood formation ended within the first half of August. Wood formation of birch started in the second half of June and ended around the beginning of August. First cells were laid down by pine and birch when the temperature sum had reached the level of 85 to 90 degree days and 110 to 120 degree days, respectively. The intensity of wood formation in pine was highest in July, in birch within two weeks in the middle of July. Wood formation in pine lasted for about seven weeks at the southernmost and about six weeks at the northernmost site. In birch, the duration of wood formation was about five weeks at the southernmost site and around three weeks at the other sites.

Keywords boreal forest, Scots pine, birch, cambium dynamics, wood formation, pinning technique, light microscopy

Author's addresses *Schmitt* and *Eckstein*, Federal Research Centre for Forestry and Forest Products, Institute for Wood Biology and Wood Protection, and University of Hamburg, Chair for Wood Biology, Leuschnerstr. 91, P. O. Box 800209, D-21002 Hamburg, Germany; *Jalkanen*, Finnish Forest Research Institute, Rovaniemi Research Station, Box 16, FI-96301 Rovaniemi, Finland

E-mail u.schmitt@holz.uni-hamburg.de; risto.jalkanen@metla.fi

Received 16 November 2001 **Revised** 26 January 2004 **Accepted** 16 April 2004

1 Introduction

Boreal forests cover worldwide about 36% of the total forest area (Bemmann 1995). Apart from their cultural and economic value, they have attracted increasing scientific attention as an appropriate ecosystem to study plant responses to global warming. Temperature has turned out to determine the onset of the vegetation period (e.g. Lundmark et al. 1988, Kellomäki and Karjalainen 1997, Häkkinen et al. 1998, Kirilyanov et al. 2003), whereas the end of the vegetation period is induced by the shortening of the photoperiod (Partanen et al. 1998). Antonova and Stasova (1993) revealed for pine trees at the northern tree line that in addition to temperature also water availability is responsible for the cambium reactivation in spring but also for the cessation in autumn. Also Brooks et al. (1998) correlated tree-ring widths both with temperature as well as with water availability and found a species-specific response to these boreal growing conditions. According to Holtmeier (1997), the growing season at the northern tree line is around three months long as expressed by the number of days with an average daily temperature of more than 5°C. Low temperature with snow until late spring as well as rapidly decreasing day length and early frost in autumn mark the boundaries of the vegetation period. Trees respond to these extreme environmental conditions at different morphological levels. Their annual radial growth is one of the most prominent structural features; another one is latewood density (Mielikäinen et al. 1998). Both features largely depend on summer temperature and therefore are used to reconstruct summer temperature along the boreal forest border around the globe for several centuries back in time (e.g. Briffa et al. 1990, 2000, D'Arrigo and Jacoby 1993).

Boreal forests represent a highly sensitive and possibly vulnerable ecosystem. Therefore, various joint efforts are undertaken to predict the effects of an anticipated near-future global warming on trees growing at or near tree-line situations (Hicks et al. 2000, McCarroll et al. 2003). The aim of our study in this context was to unravel the wood formation dynamics of pine and birch with a high time resolution within

one vegetation period in the north of Finland in order to get a base line for further studies, such as dendroclimatology (e.g. Lindholm et al. 2000, Helama et al. 2002), boreal forest silviculture (e.g. Mäkitalo 1999) and forest dynamics research (e.g. Jalkanen and Tuovinen 2001) both for the present as well as for future climatic situations.

2 Material and Methods

2.1 Sites

A 400 km long transect from the Arctic Circle (Rovaniemi, site 1) up to the northern tree line (Kevo, site 5) was established in May 1996 (Fig. 1); all sites were dry or dryish and site 2 (Sodankylä) was extremely over-grazed by reindeer (Fig. 2). The sites and the study trees are characterised in Table 1. In each of the plots, three Scots pines (*Pinus sylvestris* L.) and three birches (*Betula pendula* Roth and *B. pubescens*

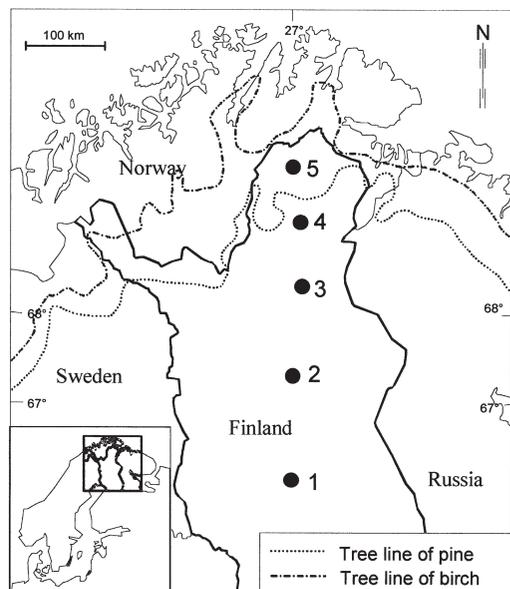


Fig. 1. Location of the five study sites along a south-north transect and the tree lines of *Pinus sylvestris* and of tree-forming *Betula* species in northern Finland, site 1 is located at the Arctic Circle.



Fig. 2. Pine stand at site 2 (Sodankylä).

Table 1. Description of the sampling sites along the latitudinal transect in northern Finland: vegetation types according to Cajander (1949); climate data, based on the models of Ojansuu and Henttonen (1983), represent averaged values from 1961–1990 and are calculated separately for each site.

Site no.	Site name	Vegetation type	Latitude	Longitude	Altitude [m]	Annual precipitation [mm]	Average annual temp. [°C]	Average July temp [°C]
1	Rovaniemi	Empetrum-Vaccinium	66°22′	26°43′	150	540	−0.1	14.6
2	Sodankylä	Uliginosum-Vaccinium-Empetrum	67°22′	26°38′	180	500	−1.1	13.8
3	Laanila	Uliginosum-Empetrum-Myrtillus	68°30′	27°30′	220	460	−1.6	13.1
4	Kaamanen	Uliginosum-Vaccinium-Empetrum	69°07′	27°15′	155	430	−1.5	13.0
5	Kevo	Empetrum-Vaccinium	69°40′	27°05′	110	410	−1.9	12.7

Site no.	Thermal sum degree days	No. of trees/ha	Stand age [years]	Pines		Birches	
				Average height [m]	Average diameter [cm]	Average height [m]	Average diameter [cm]
1	880	1800	45	9.7	13.0	12.5	13.7
2	770	1950	65	10.7	11.7	12.0	11.0
3	670	1200	45	9.5	13.0	7.0	10.0
4	670	1450	50	9.8	12.3	8.4	9.7
5	630	1700	65	9.6	12.0	6.6	6.6

Ehrh.) were selected. Their age and height varied from 45 to 65 years and from 7.5 to 9.4 m, respectively; the diameter at breast height was for all trees around 10 cm. Phenological events such as bud break, shoot flush, foliage expansion, shoot growth and bud set were monitored in regular intervals.

2.2 Pinning Technique

For the determination of the cambium dynamics, the so-called pinning-technique was used, which was introduced as early as in 1968 by Wolter and variously applied thereafter (e.g. Yoshimura et al. 1981, Kuroda 1986, Nobuchi et al. 1995, Dünisch et al. 1999, Schmitt et al. 2000). In principle, a pin is inserted through the bark into the outer xylem in order to wound the cambium (Fig. 3). As a consequence, wood formation immediately stops within a narrow zone around the pinning canal. Further apart, the cambium remains alive but develops modified xylem that can be microscopically differentiated from the xylem laid down prior to the pinning. The distance between this point and the tree-ring border of the previous year can be taken as a measure of the cambium activity in a given time. Repeated pinning throughout the vegetation period provides a series of data with a high time resolution. In the present study, throughout the growing season of 1996 altogether thirty sample trees (three pines and three birches per site) were pinned weekly or fortnightly with a pin of 1.2 mm in diameter, beginning on June 3 and ending on September 3, resulting in a maximum of fourteen pinning dates per tree. Three pinning holes at one time were set at breast height of the stems. The horizontal and vertical distance between adjacent pinning holes was 2.5 cm. In the 2nd week of September 1996, the experimental trees were felled and breast-height discs containing the pinnings were cut off and deep-frozen.

2.3 Microscopy

Small cubes of $1 \times 1 \times 1 \text{ cm}^3$ around the pinning canals as well as from unaffected xylem tissue close to the pinnings were removed with a chisel from the frozen discs and reduced with a razor

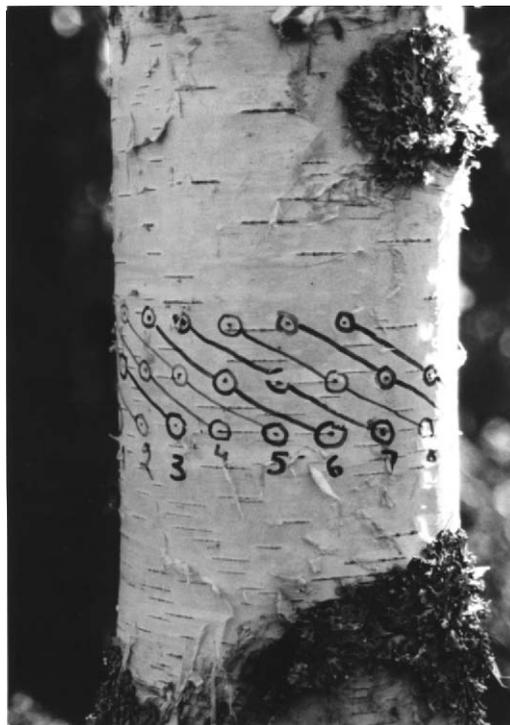


Fig. 3. Pin insertions on a birch stem (encircled), the three pinnings per date are connected by a line; horizontal and vertical distance between adjacent pinning holes is about 2.5 cm.

blade to a final size of about $5 \times 5 \times 5 \text{ mm}^3$. Unaffected xylem was additionally used for total ring-width measurements. The specimens became immersed for fixation in a citrate buffered formaldehyde solution for two to four days. After dehydration in a graded series of propanol, samples were infiltrated with glycolmethacrylate (Technovit 7100) for two months and polymerized after adding an accelerator. With a rotary microtome $8 \mu\text{m}$ thick sections were prepared for light microscopy and stained for two hours with a standard Giemsa solution (see also Schmitt et al. 2000). The weekly or bi-weekly increment was given in percent of the total tree-ring width at the same spot. Hereby, the circumferential variability of growth was accounted for.

3 Results

3.1 Pinning Reactions

In all samples, the pinning caused distinct wound reactions in a very narrow portion around the canal of pin insertion. Disturbances from adjacent pinnings were not observed. The cambium around the canal died immediately and further xylem formation was stopped. This histological feature was clearly visible in most of the samples. In few samples, however, the differentiating xylem collapsed along the pinning canal, which made the microscopic evaluation in this area impossible. Then, alternatively the parenchymatic tissue formed instead of regular xylem was used as reference line for determining the amount of the increment formed prior to the pinning. The observations and measurements gave detailed results on the onset, intensity and end of wood formation within the growing season 1996. Some uncertainty of a few days still remained as to the exact day of the beginning and end because of the weekly or fortnightly pinning intervals. The beginning of wood formation was derived as that pinning date when earlywood cells of the new tree ring were distinctly visible. This means that wood formation started within the week prior to this pinning date. The end of wood formation was determined when no further cells were laid down, again within one week prior to the pinning date.

3.2 Wood Formation Dynamics

3.2.1 *Pinus sylvestris*

In the growing season 1996 the tree-ring widths of the pine trees varied between around 0.5 and 1.6 mm with a high within-site variation; it was on average narrowest at sites 2 and 5 (Fig. 4).

At all sites the trees revealed a more or less sigmoid shape in their wood formation dynamics with a slow beginning, followed by a fast growth in the middle of the vegetation period and a decreasing wood formation activity towards the end of the period (Fig. 5). The trees at the southernmost site 1, for example, started to grow uniformly around June 10. On June 17 several layers of earlywood cells had been laid down (Fig. 6a). This amount represents about 10% of the total tree-ring width. On June 24 the amount of xylem formed was around 20 to 30% of the entire increment (Fig. 6b), on July 15 it was about two third (Fig. 6c). Wood formation intensity was highest between the fourth week of June and the second week of July. On August 5 cell deposition had already been completed (Fig. 6d). Altogether, at the southernmost site wood formation lasted for seven weeks. The thickening of the secondary walls in the latest-formed xylem cells as well as their subsequent lignification proceeded for another two to three weeks until the end of August.

The trees at sites 2 to 5 from south to north showed a slight tendency for an increasingly later initiation of wood formation with a maximum of nearly two weeks at the northernmost site as compared with site 1 (Fig. 5). At all sites first cells were laid down when temperature sum had reached 85 to 90 d.d. (degree days, i.e., sum of degrees by which the daily average temperature exceeds the threshold value of +5°C). At site 5 30–60 % of the tree ring were formed until July 10 (Fig. 6e), 80–90 % until July 24 (Fig. 6f), and xylem formation was completed between August 7 and August 19 (Fig. 6g). At all sites, wood formation was finished within the first half of August.

The pine buds started to swell about one week before wood formation at all sites except at the northernmost site, where this gap was two to three weeks (Fig. 5). At sites 1–3, the cur-

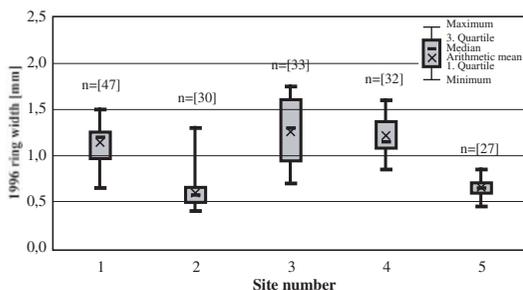


Fig. 4. Pine, total tree-ring widths in the vegetation period 1996, based on measurements at altogether n places within three trees per site.

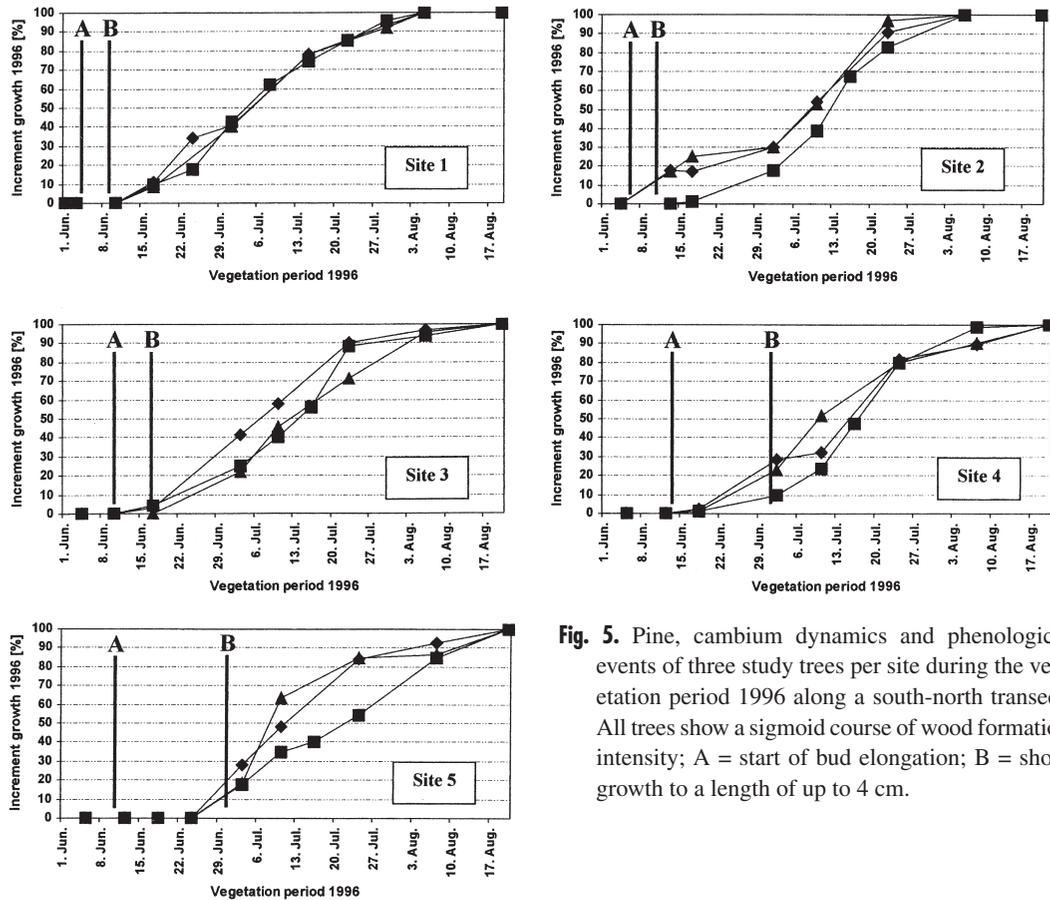


Fig. 5. Pine, cambium dynamics and phenological events of three study trees per site during the vegetation period 1996 along a south-north transect. All trees show a sigmoid course of wood formation intensity; A = start of bud elongation; B = shoot growth to a length of up to 4 cm.

rent-year shoots were 2–4 cm long when wood formation began. However, at site 4 shoot growth reached 2–4 cm two weeks after wood began to form. For the trees at sites 1–3, the interval between bud break and distinct shoot elongation was one week, but three weeks at the two northernmost sites.

The transition from earlywood to latewood formation could also be determined for all the pine trees along the south-north transect for the period of one week around middle of July (Fig. 6c). There were no distinct differences between the five sites.

3.2.2 *Betula* spp.

In 1996, the birch trees showed a large within-site variation of their ring widths which varied between about 1.3 mm at the southernmost site 1 up to less than 0.1 mm at the northernmost site 5; the average ring width at site 4 with a value of about 0.7 mm was higher than at sites 2, 3 and 5 (Fig. 7).

The onset and end of wood formation was determined for sites 1 to 4 only; at site 5 it was impossible to measure the wood formation because two of the three study trees did not show a distinct tree ring. It can only be suggested from the unusual large number of latewood-like cell rows that at least some of them may have been formed in 1996. Therefore, both the beginning and the end of wood formation has not been

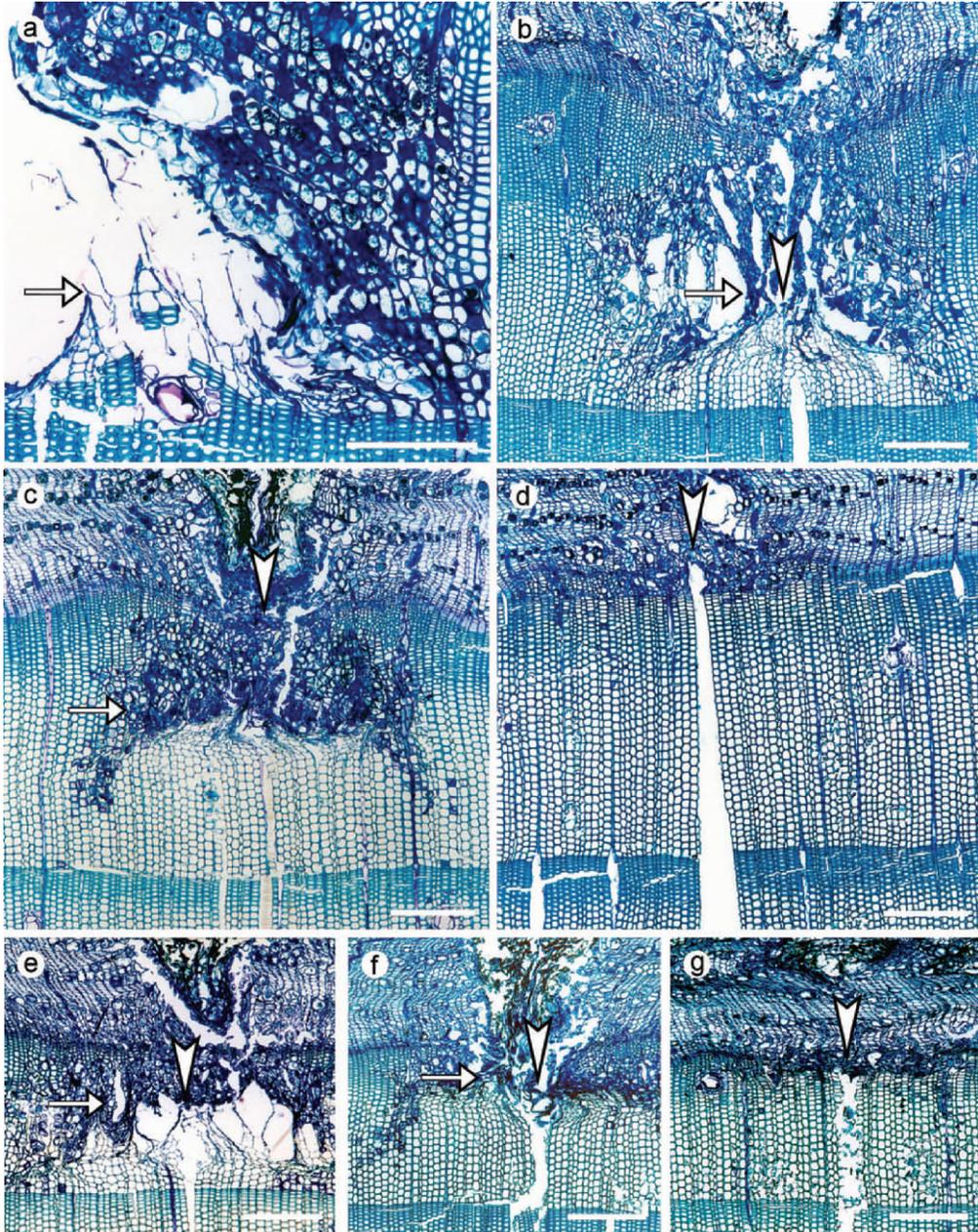


Fig. 6. Pine, light micrographs of xylem cross-sections along the pinning canal. Scale bars = 150 μ m; a–d: site 1/Rovaniemi; e–g: site 5/Kevo. Arrowheads indicate the pin insertion, arrows the assumed position of the cambium at the time of pinning. a. Pinning on June 17, several layers of earlywood cells are laid down indicating an early stage of tree-ring formation in 1996. b. Pinning on June 24, about one third of the 1996 increment is formed. c. Pinning on July 15, two thirds of the increment are formed. d. Pinning on August 12, cell deposition is completed, secondary wall thickening is still going on. e. Pinning on July 10, about 50% of the increment are formed. f. Pinning on July 24, 80–90% of the increment are formed. g. Pinning on August 7, cell deposition is completed, secondary wall thickening is still missing.

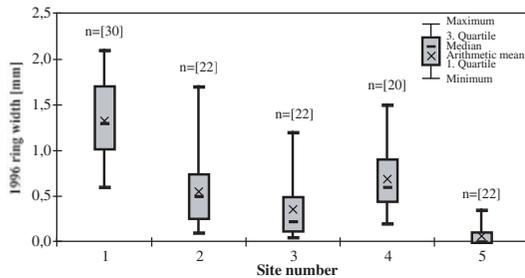


Fig. 7. Birch, total tree-ring widths in the vegetation period 1996, based on measurements at altogether *n* places within three trees per site.

determined for these two trees. The third tree revealed a clearly visible but narrow tree ring with two to three rows of earlywood fibres and a few small diameter vessels followed by a latewood portion of several cell rows (Fig. 8a).

At sites 1 to 4, wood formation followed a more or less pronounced sigmoid pattern in all trees (Fig. 9). Wood formation at the southernmost site 1 started in two trees in the week before June 24, in one tree in the week after June 24. It ended a few days before July 28 in one tree and a few days before August 5 in the other two trees

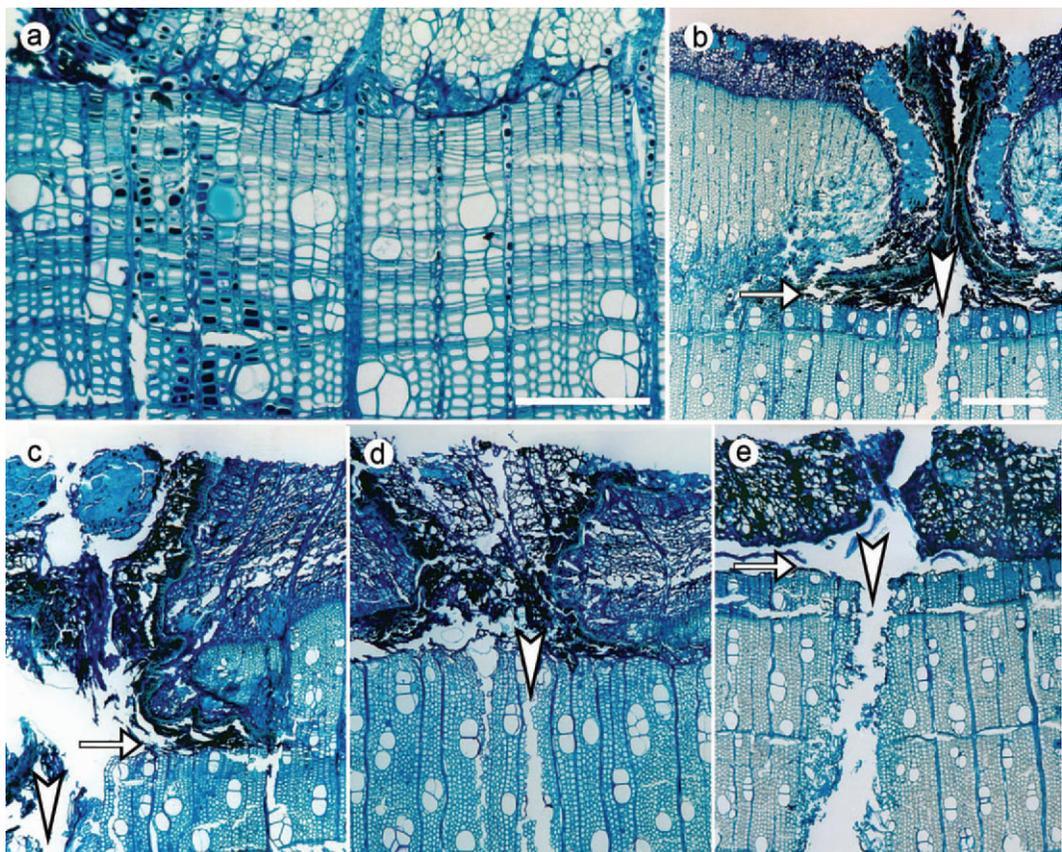


Fig. 8. Birch, light micrographs of xylem cross-sections. Scale bars = 150 μm . a. without pinning; b–e. pinning. Arrowheads indicate the pin insertion, arrows the assumed position of the cambium at the time of pinning. a. Site 5, tree ring with a narrow earlywood zone, a few small diameter vessels and a distinct latewood zone of several rows of flattened, thick-walled cells are visible. b–d. Pinning at site 1, cross sections along the pinning canal. b. Pinning on July 1, distinct earlywood portion is laid down. c. Pinning on July 15, about half of the tree ring is formed. d. Pinning on July 29, completion of the tree ring, secondary wall thickening of latewood cells is still missing. e. Pinning at site 4 on July 17, about two thirds of the final tree-ring width are achieved after two weeks.

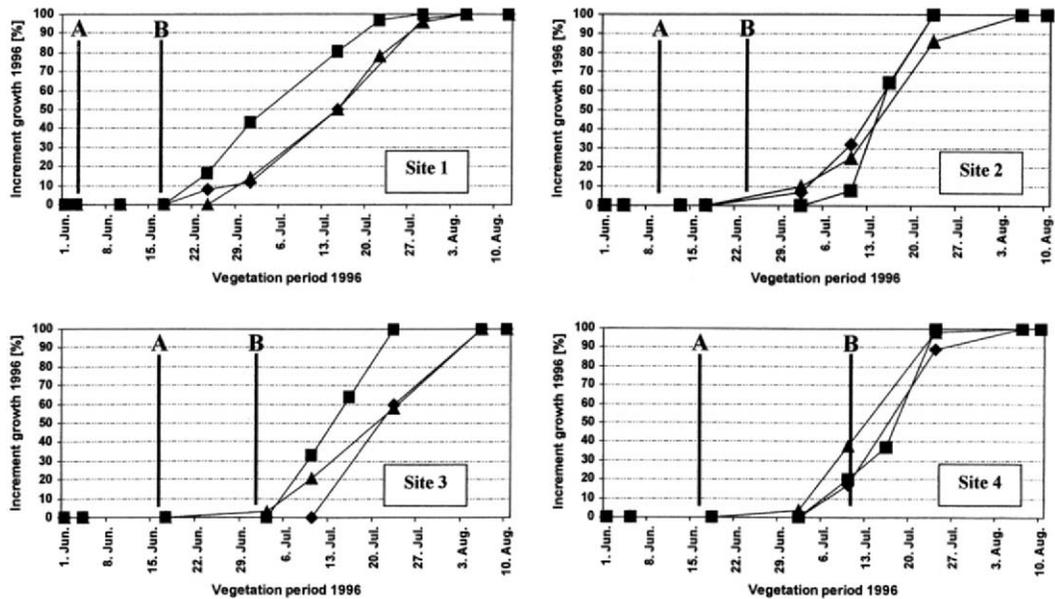


Fig. 9. Birch, cambium dynamics and phenological events of three study trees per site during the vegetation period 1996 along a south-north transect. All trees show a more or less sigmoid course of wood formation intensity; A = bud break/first leaves just visible; B = first leaves fully developed.

(Fig. 9). Altogether, the tree rings were formed within a period of six weeks. On July 1, about one week after the beginning of wood formation, a distinct portion of earlywood was laid down (Fig. 8b). About half of the increment was formed until the middle of July (Fig. 8c), except one tree, which had already formed about 80% of its tree ring. Wood formation was completed on July 29 (Fig. 8d) or in the following week. At site 2, in two trees wood formation already ended in the week before July 24, in the other tree within the week before August 7. Sites 3 and 4 were characterised by a duration of wood formation of three to four weeks (Fig. 9). Figure 8e shows a sample from site 4 with the pinning date July 17; wood formation began two to three weeks earlier and had achieved about one third of the final tree-ring width. Birch laid down its first cells when 110 to 120 d.d. of the temperature sum had been reached.

The interval between bud break and distinct wood formation was two to three weeks. Leaf development took about two weeks at the three southern sites and was completed about one

week before or at the time when wood formation started. At the northern sites 4 and 5 leaf development took three weeks and ended about one week after the beginning of wood formation (Fig. 9). A comparison between the southern sites 1 and 2 and the northern sites 3 and 4 revealed that buds broke two weeks later and leaves were completely developed two to three weeks later in the north. Also the duration of leaf development extended from two to three weeks from sites 1 to 5.

Because of the gradual transition from early- to latewood there were no distinct within-tree-ring characteristics in birch for additional structure/time relationships. Close to the border of the next tree ring there were always one to three rows of thick-walled fibres laid down, which were produced at the very end of the wood formation period of each individual tree.

4 Discussion and Conclusion

The northern tree lines are extremely sensitive boundaries, which vary over time depending on anthropogenic and climatic factors. From our observations it can be concluded that a pine population cannot survive in the long run, if the average prevailing temperature does not enable the cambium of pines to be active over about six weeks. For birch, whose area of natural distribution extends beyond the tree line of pine, this period of cambium activity necessary to survive is about only three weeks. However, it has to be taken into account that June and July 1996 were abnormally cool and moist, whereas only August was more or less normal. It was striking that pines ended their growth at all five sites in northern Finland in the first half of August, whereas the birches ended their cambium activity somewhat earlier around the beginning of August.

Our observations regarding the onset and end of cambium activity are in good agreement with earlier results obtained for pine. For example, Zumer (1969 a, b) determined both the beginning and end as well as the weekly amount of wood formation for several tree species along an altitudinal transect in the south-east of Norway. It was shown that wood formation in pine began with a slight delay with increasing altitude, whereas it stopped simultaneously at the end of the vegetation period independent of altitude. Close to our northernmost site, Hustich (1956) revealed for pine trees that wood formation started around middle of June. Recently, Mielikäinen et al. (1998) determined for pine trees between 1993 and 1996 that the amount of warmth necessary for the onset of wood formation, measured in degree days, is achieved at around end of May/beginning of June at a site 100 km south to the southernmost site of the present study. For spruce in southern Finland, Mäkinen et al. (2003) found that tracheid production started in June and ceased in August. For birch no such detailed studies at tree-line situations have hitherto been made, although there are few dendroclimatological studies (for further references see Eckstein et al. 1991). Based on our present results, the temperature-sum threshold for pine and birch is 85 to 90 d.d. and 110 to 120 d.d., respectively.

Our observations are particularly meaningful for dendroclimatology. They confirm that the window for the climatic signal to directly enter the trees at the northern forest border is only open for a short time of a few weeks.

It was revealed that bud burst in pine occurred one to two weeks and in birch two to three weeks before the onset of wood formation. There was only a slight tendency for an increase of this interval along the south-north transect. At the two northern sites, the shoots of pine obviously elongate more slowly and leaf development in birch is delayed. This indicates a reduced cell division rate as well as a prolonged time for cell differentiation. Wood formation in pine, however, did not show a distinct relationship between the length of the vegetation period and tree-ring width. Obviously, the cambial activity during earlywood formation, once initiated in pine by the prevailing temperature conditions, to a large extent follows a pattern independent of the current-year temperature. Tuovinen et al. (2000) found a correlation between late summer temperature of the previous year and current year earlywood width. Consequently, reserves deposited in the previous year are believed to be responsible for the amount of earlywood. In contrast, latewood width appears to depend on mid to late summer temperatures of the current season, mainly July temperature. Antonova and Stasova (1993) investigated the effects of environmental factors on wood formation of pine in central Siberia and, in contrast, found that throughout the season current-year temperature and precipitation are positively correlated with the rate of cambial divisions and with the radial diameter of the tracheids. Additionally, they found that in May and June the influence of temperature dominates in wood formation, the influence of precipitation increases in July and August.

Regarding the involvement of plant hormones in the context of wood formation, Sundberg et al. (2000) modified the hitherto accepted concept for the role of auxins. They found that auxin transport from the activated buds is not necessarily a prerequisite for cambium reactivation in spring. Their assumption is based on observations on slow growing Scots pine, where the auxin concentration in the cambial tissue is at

the same level during dormancy as during active growth. In these cases, photoperiodic or temperature-dependent reasons appear responsible for the cambium reactivation. Both parameters are well known for the timing of bud burst in spring. Häkkinen et al. (1998) for birch and Partanen et al. (1998) for Norway spruce revealed that bud burst in the boreal zone depends to a large extent on the length of the photoperiod rather than on temperature which plays only a subordinate role. In contrast to the cessation of cambium activity, the transition to dormancy of the buds seems to be related to both day length and temperature.

In conclusion, wood formation in pine and birch at the tree line in the north of Finland is largely initiated by temperature. The duration of the vegetation period, as already shown and expected to be distinctly prolonged by the anticipated global warming (Menzel and Fabian 1999, Kellomäki and Karjalainen 1997), not necessarily results in wider tree rings. Future investigations on the cellular level should focus on climate effects on the radial cell expansion, cell wall thickening, and lignification. All these parameters may provide additional information about the relationship between climate and wood formation as variously laid down (e.g. Antonova and Stasova 1993, Mielikäinen et al. 1998, Gindl et al. 2000, Deslauriers et al. 2003, Schmitt et al. 2003).

Acknowledgements

Financial support by the EU (Contract ENV4-CT95-0063) is gratefully acknowledged.

References

- Antonova, G.F. & Stasova, V.V. 1993. Effects of environmental factors on wood formation in Scots pine stems. *Trees* 7: 214–219.
- Bemmann, A. 1995. Der boreale Wald als CO₂-Senke. *Allg. Forstzeitschrift/Der Wald* 50: 288–290.
- Briffa, K.R., Bartholin, T.S., Eckstein, D., Jones, P.D., Karlen, W., Schweingruber, F.H. & Zetterberg, P. 1990. A 1,400-year tree-ring record of summer temperatures in Fennoscandia. *Nature* 346: 434–439.
- , Baillie, M.G.L., Bartholin, T., Bonde, N., Kalela-Brundin, M., Eckstein, D., Eronen, M., Frenzel, B., Friedrich, M., Groves, C., Grudd, H., Hantemirov, R., Hillam, J., Jansma, E., Jones, P.D., Karlen, W., Kuschner, H.H., Lindholm, M., Makowka, I., Naurzbaev, M.M., Nogler, P., Osborn, T.J., Reimer, T., Salmon, M., Sander, C., Schweingruber, F.H., Shiyatov, S.G., Spur, K.M., Timonen, M., Tyers, I., Vaganov, E.A., Wazny, T. & Zetterberg, P. 2000. Analysis of dendrochronological variability and associated natural climates in Eurasia – the last 10,000 years (ADVANCE – 10K). In: Proc. Europ. Climate Science Conf., Vienna, 19–23 October 1998, Austrian Federal Ministry of Science and Transport, 2000. 13 p.
- Brooks, J.R., Flanagan, L.B. & Ehleringer, J.R. 1998. Responses of boreal conifers to climate fluctuations: indications from tree-ring widths and carbon isotope analyses. *Canadian Journal of Forest Research* 28: 524–533.
- Cajander, A.K. 1949. Metsätyypit ja niiden merkitys. Summary: Forest-types and their significance. *Acta Forestalia Fennica* 56: 69 p.
- D'Arrigo, R.D. & Jacoby, G.C. 1993. Secular trends in high northern-latitude temperature reconstructions based on tree rings. *Climatic Change* 25: 163–177.
- Deslauriers, A., Morin, H. & Begin, Y. 2003. Cellular phenology of annual ring formation of *Abies balsamea* in the Quebec boreal forest (Canada). *Canadian Journal of Forest Research* 33: 190–200.
- Dünisch, O., Bauch, J., Sack, M. & Müller, M. 1999. Growth dynamics in wood formation of plantation-grown *Swietenia macrophylla* King and *Carapa guianensis* Aubl. *Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft Hamburg* 193: 79–96.
- Eckstein, D., Hoogesteger, J. & Holmes, R.L. 1991. Insect-related differences in growth of birch and pine at northern treeline in Swedish Lapland. *Holarctic Ecology* 14: 18–23.
- Gindl, W., Grabner, M. & Wimmer, R. 2000. The influence of temperature on latewood lignin content in treeline Norway spruce compared with maximum density and ring width. *Trees* 14: 409–414.
- Häkkinen, R., Linkosalo, T. & Hari, P. 1998. Effects of dormancy and environmental factors on timing of bud burst in *Betula pendula*. *Tree Physiology* 18: 707–712.
- Helama, S., Lindholm, M., Timonen, M., Meriläinen, J. & Eronen, M. 2002. The supra-long Scots pine record for Finnish Lapland: Part 2, interannual to centennial variability in summer temperatures for 7500 years. *The Holocene* 12: 681–687.
- Hicks, S., Eckstein, D., Schmitt, U., Tuovinen, M., Jalkanen, R., McCarroll, D., Pawellek, P., Edouard,

- J.-L., Gagen, M., Birks, H., Serres, R., Hyvärinen, H. & Nivala, V. 2000. Forest response to environmental stress at timberlines: sensitivity of Northern, Alpine and Mediterranean forest limits to climate. In: Proc. Europ. Climate Science Conf., Vienna, 19–23 October 1998, Austrian Federal Ministry of Science and Transport, 2000. 13 p.
- Holtmeier, F.-K. 1997. Timberlines: Research in Europe and North America. In: L.Loven & S. Salmela (eds.). Pallastunturi Symposium. Finnish Forest Research Institute, Research Papers (Metäntutkimuslaitoksen tiedonantoja) 623: 23–36.
- Hustich, J. 1956. Notes on the growth of Scotch pine in Utsjoki in northernmost Finland. *Acta Botanica Fennica* 56: 1–13.
- Jalkanen, R. & Tuovinen, M. 2001. Annual needle production and height growth: better climate reconstructors than radial growth? *Dendrochronologia* 19: 39–44.
- Kellomäki, S. & Karjalainen, T. 1997. Auswirkungen von möglichen Klimaveränderungen auf die borealen Wälder. *Allgemeine Forstzeitschrift/Der Wald* 52: 758–761.
- Kirchhefer, A.J. 1999. Dendroclimatology on Scots pine (*Pinus sylvestris* L.) in northern Norway. Doctoral thesis, University of Tromsø, Norway.
- Kirdyanov, A., Hughes, M., Vaganov, E., Schweingruber, F. & Silkin, P. 2003. The importance of early summer temperature and date of snow melt for tree growth in the Siberian Subarctic. *Trees* 17: 61–69.
- Kuroda, K. 1986. Wound effects on cytodifferentiation in the secondary xylem of woody plants. *Wood Research* 72: 67–117.
- Lindholm, M., Lehtonen, H., Kolström, T., Meriläinen, J., Eronen, M. & Timonen, M. 2000. Climatic signals extracted from ring-width chronologies of Scots pines from the northern, middle and southern parts of the boreal forest belt in Finland. *Silva Fennica* 34: 317–330.
- Lundmark, T., Hällgren, J.-E. & Hedén, J. 1988. Recovery from winter depression of photosynthesis in pine and spruce. *Trees* 2: 110–114.
- Mäkinen, H., Nöjd, P. & Saranpää, P. 2003. Seasonal changes in stem radius and production of new tracheids in Norway spruce. *Tree Physiology* 23: 959–968.
- Mäkitalo, K. 1999. Effect of site preparation and reforestation method on survival and height growth of Scots pine. *Scandinavian Journal of Forest Research* 14: 512–525.
- McCarroll, D., Jalkanen, R., Hicks, S., Tuovinen, M., Gagen, M., Pawellek, F., Eckstein, D., Schmitt, U., Autio, J. & Heikkinen, O. 2003. Multiproxy dendrochronology: a pilot study in northern Finland. *Holocene* 13: 829–838.
- Menzel, A. & Fabian, P. 1999. Growing season extended in Europe. *Nature* 397: 659.
- Mielikäinen, K., Nöjd, P., Pesonen, E. & Timonen, M. 1998. Puun muisti. Metsäntutkimuslaitoksen tiedonantoja 703. 71 p. (In Finnish)
- Nobuchi, T., Ogata, Y. & Siripatanadilok, S. 1995. Seasonal characteristics of wood formation in *Hopea odorata* and *Shorea henryana*. *IAWA Journal* 16: 361–369.
- Ojansuu, R. & Henttonen, H. 1983. Kuukauden keskilämpötilan, lämpösunnan ja sademäärän paikallisten arvojen johtaminen Ilmatieteen laitoksen mittauksista. *Silva Fennica* 17: 143–160. (In Finnish)
- Partanen, J., Koski, V. & Hänninen, H. 1998. Effects of photoperiod and temperature on the timing of bud burst in Norway spruce (*Picea abies*). *Tree Physiology* 18: 811–816.
- Schmitt, U., Möller, R. & Eckstein, D. 2000. Seasonal wood formation dynamics of beech (*Fagus sylvatica* L.) and black locust (*Robinia pseudoacacia* L.) as determined by the “pinning” technique. *Journal of Applied Botany* 74: 10–16.
- , Grünwald, C., Cufar, K., Koch, G. & Gricar, J. 2003. Maturation of latewood tracheids in healthy and declining silver fir trees in the Dinaric region in Slovenia. *IAWA Journal* 24: 41–51.
- Sundberg, B., Uggla, C. & Tuominen, H. 2000. Cambial growth and auxin gradients. In: Savidge, R.A.; Barnett, J.R.; Napier, R. (eds.). *Cell and Molecular Biology of Wood Formation*. BIOS Scientific Publ., Oxford. p. 169–188.
- Tuovinen, M., Sonninen, M. & Edouard, J.-L. 2000. The relationship between tree-ring latewood width, early- and latewood density and climate. In: Hicks, S. et al. (eds.). *Forest response to environmental stress at timberlines final report of the EU project ENV4-CT95-0063*. p. 46–48.
- Wolter, E. K. 1968. A new method for marking xylem growth. *Forest Science* 14: 102–104.
- Yoshimura, K., Itoh, T. & Shimaji, K. 1981. Studies on the improvement of the pinning method for marking xylem growth. II. Pursuit of the time sequence of abnormal tissue formation in loblolly pine. *Mokuzai Gakkaishi* 27: 755–760.
- Zumer, M. 1969a. Vekstrytme hos noen skogstraer i forskjellige hoedelag – Growth rhythm of some forest trees at different altitudes. *Scientific Reports from the Agricultural College of Norway* 48(5): 31 p.
- 1969b. Aarringdannelse hos gran i fjellskog – Annual ring formation in Norway spruce in mountain forest. *Meddelelser fran det Norske Skogforsoksesvesen, Vollebekk, XXVII* 2: 165–184.

Total of 39 references