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Frost-induced reversible shrinkage of bark of mature subalpine conifers

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Abstract

Temporal and spatial patterns of stem and root radius changes were continuously measured on mature, subalpine Norway spruce (*Picea abies* (L.) Karst.) over 2 years. In addition, freezing experiments with stem segments of saplings were carried out in a climate chamber. The dynamics of the radius fluctuations were analyzed in relation to temperature profiles of air, bark, and soil. We found that bark thickness sharply decreases by 1 mm and more within 2–3 days when the air temperature falls below -5°C . In contrast to the elastic tissues of the bark, the rigid xylem remains largely unaffected. This frost-induced shrinkage of the bark is up to 10 times larger than the measured amplitude of diurnal stem radius fluctuations in summer. During periods of rising air temperatures ($>-12^{\circ}\text{C}$), the radius suddenly returns to its original size. We conclude, that the large stem and root radius changes in winter are related to changing bark water content, as is also the case during size fluctuations in summer. For a mature tree with a height of 25 m, the shrinkage of the entire stem bark is equivalent to approximately 20 l of water. A hypothesis is discussed which suggests a frost-induced transport of this water between bark and wood. It is based on the initial freezing of water in the xylem resulting in a water potential gradient between bark (solution) and wood (ice). The hypothesis suggests that the water transport between bark and wood is mainly determined by physical changes and that no biochemical transport energy or physiological control mechanisms are involved. As long as ice is initially formed in the xylem and not in the bark, this mechanism of bark dehydration comes into play and protects the living cells from frost damage. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Tree water relations; Stem contraction; Frost stress; Freezing protection; *Picea abies*

1. Introduction

The elastic living tissues of roots, stems, and foliage sharply diminish their size during periods of temperatures below the freezing point. This was reported as early as the 19th century (Hoffmann, 1857; Sachs, 1860) and has remained a topic of interest to the present day (Lemoine et al., 1999). Wiegand (1906) described the expansion of *Salix* twigs during thawing and reported a much bigger extension of the bark

(13.5%) than of the wood (2.5%). Bryan and Doolittle (1950) noted that shortly after a cold spell the outer layer of living tissues of *Pinus radiata* stems contracted about 10 times the mean daily shrinkage that occurred during the growing season. A similar conclusion was drawn by Winget and Kozłowski (1964) from dendrometer measurements on different tree species (*Betula*, *Tsuga*, *Acer*, and *Tilia*). They noted that the winter shrinkage exceeded the growth rate of a whole season and that spring re-hydration may be readily confused with growth initiation. Winget and Kozłowski (1964) also showed that the winter shrinkage is primarily a function of tree species and stem size. The bark of softwood species commonly

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shrinks less than the bark of hardwood (Larcher et al., 1985).

McCracken and Kozlowski (1965) described the phenomenon of sudden stem shrinkage during freezing periods as ‘thermal contraction’, from its obvious initiation at temperatures $<0^{\circ}\text{C}$. But, temperature alone does not explain the great contraction of the bark because the thermal expansion of wood is too small. However, tissue shrinkage to this extent is possible when living cells are dehydrated and lose turgor (Zweifel, 1999). A plausible explanation for such dehydration is the extracellular freezing of water (Fischer, 1911; Sakai, 1982; Jeffree et al., 1987). The water removed from the protoplasts may either remain in the tissue of its origin or may be moved to a neighboring tissue of different characteristics.

In contrast to investigations about the formation of ice within the tissue of the dehydrated protoplasts (Pook and Hall, 1976; Levitt, 1980; Larcher et al., 1985), only little information is available on frost-induced water transport between different tissues. Sakai (1979, 1982) reported water migration in the crown of conifers due to freezing, and Lemoine et al. (1999) recently showed that excised beech branches exuded water when the temperature dropped below the freezing point. However, we found no work, which explicitly states that water is transported from the bark into the xylem due to freezing. Our present investigations on mature subalpine *Picea abies* provide evidence for such a water transport. To answer the question how the relatively large amount of water is transported between the different tissues at low temperatures, we discuss a hypothesis for a frost-induced bark depletion process.

2. Materials and methods

2.1. Study site

From July 1997 to May 1999, the stem radius fluctuations of mature Norway spruce trees (*P. abies* (L.) Karst.) were continuously investigated in the subalpine Seehorn forest near Davos, Switzerland ($46^{\circ}48'59''\text{N}$, $9^{\circ}51'25''\text{E}$, 1640 m asl). The trees were 150–250 years old and between 15 and 25 m tall. Their stems were between 0.2 and 0.5 m in diameter (measured at 1.5 m above ground) and the thickness of the elastic tissues

of the bark (cambium, phloem, and parenchyma) was between 1.5 and 6.0 mm (Zweifel, 1999). The trees were rooted in a soil classified as a ferric humic podsol (Häsler et al., 1991). The organic layer was between 0.1 and 0.4 m deep.

2.2. Point dendrometer

Twenty point dendrometers (POD, Agricultural Electronics Corporation, USA) were used to continuously measure the stem and root radius fluctuations (ΔR). Each stem of the eight trees investigated was equipped on its west side with a point dendrometer at breast height. Additional dendrometers were mounted at various tree heights (6, 10, 14, and 18 m above ground) and on roots of the trees A, C and F. The dendrometers operate on the basis of a linear variable differential transformer enclosed in an enamel housing on three sides (Gensler and Diaz-Munoz, 1983). Three stainless steel threaded rods are implanted approximately 70 mm into the xylem and connect the mounting struts to the tree. The sensing rod is slightly pressed against the stem of the tree by a force unit. The bias due to the hygroscopic swelling and shrinkage of the bark at its surface was minimized by placing the contact point 2–6 mm below the surface, but still onto the dead outermost layer of the bark. To minimize a detected temperature sensitivity of the dendrometers, we corrected the stem radius measurements with control measurements, derived from dendrometers of the same type mounted on a stone plate and a steel plate, which for the purposes of this study we considered non-contracting and non-expanding. The bias was found to be linearly correlated to the air temperature; an increase of 1°C caused an average contraction (artefact) of $1.4\ \mu\text{m}$. The resolution of the dendrometers was $3.7\ \mu\text{m}$. The dendrometer data were automatically collected at 15 min intervals.

To obtain additional and independent measurements of the stem radius changes we used three point dendrometers, consisting of a precision displacement transducer (TRANS-TEK, Ellington, USA) and a body of stainless steel. The instruments were mounted in the same way as all the other dendrometers but the sensing head was glued with tar to the smoothed bark surface (Trees A, F, and G). The resolution of these dendrometers was $1.5\ \mu\text{m}$ and the recording frequency was 10 min.

2.3. Bark temperature

Eight temperature sensors (10TCRT, Campbell, USA) were set through thin boreholes (diameter: 2 mm) onto the xylem of tree C, mounted circularly around the stem in four directions at two heights (6 and 14 m above ground). The injured part of the bark was sealed with tar. The data of the sensors were collected at 10 min intervals.

2.4. Air and soil microclimate

Profiles of air temperature (T_{Air}) were obtained from measurements on a 35 m tall tower at 2, 10, 20, 25 and 35 m above ground. Six soil temperature sensors (T703, Yellow Springs Inst. Co., USA) were buried at depths of 0.05, 0.15 and 0.25 m between A and F.

2.5. Freezing experiments in the laboratory

P. abies saplings (8–10 years old) were grown outdoors in a nursery in circular pots (volume: 13 l; substrate: 30% (by weight) peat, 70% Toresa; fertilizer: Osmocote plus 3 g l^{-1} , horn meal 3 g l^{-1} , $\text{pH} \approx 4.5$), their stems were used for the freezing experiments in the laboratory. The trees were between 1.0 and 1.5 m tall, their stems were between 35 and 50 mm in diameter, and the thickness of the elastic tissues of the bark (cambium, phloem, and parenchyma) was between 2.1 and 3.3 mm. Fifteen of the 50 cut stem segments were separated into bark and wood and used to measure the respective actual water contents at the time of cutting. The water contents are expressed as percentage of the respective dry weight. Another 15 stem segments were put into a freezing chamber at -18°C for 15 h. Ten of these segments were split into bark and wood in the frozen state and used to measure the respective water contents. The other five frozen segments were thawed at 20°C and then split into bark and wood. We used an electronic, precision balance (BP3100 P, Sartorius, Germany) to weigh the samples. The tissues were dried for 48 h in an oven at 65°C .

Another 20 stem segments of approximately the same size and age were used to measure the radius change of the bark before and after freezing (-18°C). Ten of these stem segments were used as intact pieces

and the others were separated into bark and wood. The thickness of bark, wood, and entire segments were measured with a precision micrometer.

3. Results

3.1. Frost shrinkage and thaw expansion of roots and stems

The courses of stem and root radius fluctuations of a mature *P. abies* (Tree A) are shown for a period of 2 years in Fig. 1, representative for all eight investigated trees. Rectangles mark three characteristic phases within this time: the sharp radius changes in winter (Fig. 2a), the fluctuations during a cold period (Fig. 2b), and diurnal stem radius fluctuations in summer (Fig. 2c). The radial changes over the winter months differ in both amplitude and temporal course from those in summer. The stem shrinkage in winter (1–1.5 mm) is 5–10 times larger than in summer and the typical summer day pattern — shrinkage in the morning and expansion during the night — was not observed during cold periods. As in summer, though, the stem radius fluctuations occur mainly in the elastic bark tissue (cambium, phloem, and parenchyma), independent of the season (Fig. 3).

We distinguish between two stem or root states — the physiologically ‘active state’ and the ‘cold state’ — and three radius fluctuation processes: ‘frost shrinkage’, ‘thaw expansion’, and ‘diurnal stem radius changes’ (Fig. 4).

‘Active state’ specifies the range of stem or root size that allows physiological activities of the tree as water transport in the xylem, and transpiration and photosynthesis in the crown. The active states mainly occur during the growing season, but sporadically they are also observed in winter at temperatures $> -4^\circ\text{C}$.

‘Diurnal stem radius changes’ refer to the characteristic stem shrinkage and expansion in summer, occurring exclusively during the active state (Fig. 2c). This process is closely related to xylem water potential through diurnal transpiration course. Thus, the diurnal stem radius changes depend on physiological activities and are not directly sensitive to the temperature course.

‘Cold state’ defines the contracted status of stems or roots. In this state, all radius changes are

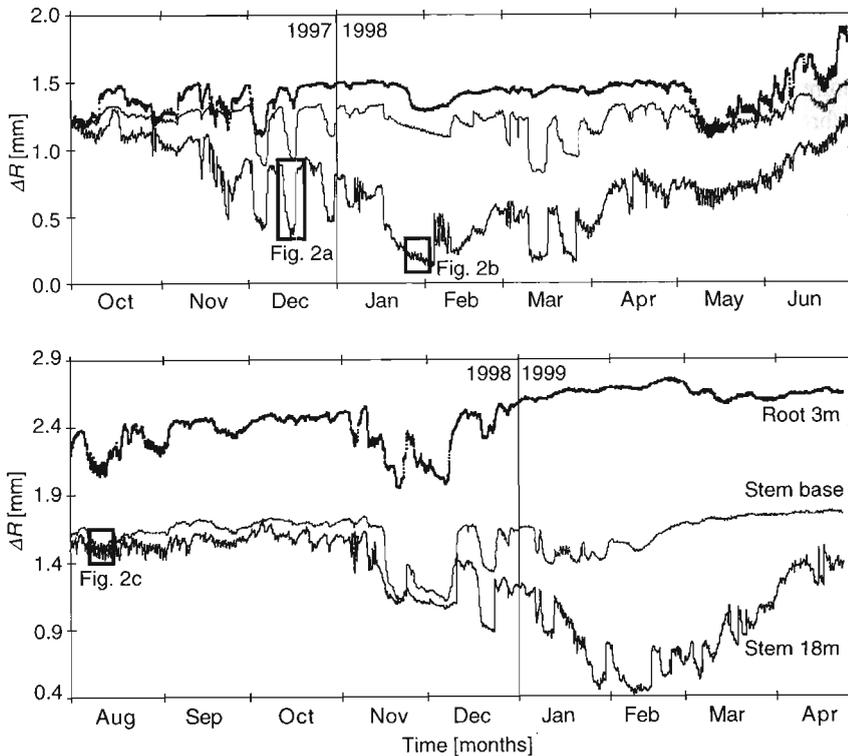


Fig. 1. Representative course of radius changes (ΔR) measured on Tree A over 2 years: root section at 3 m distance from the trunk, stem base, and stem section at 18 m above ground. The rectangular insets refer to Fig. 2.

temperature-induced (Fig. 2a) and the physiological activities of the respective tree sections are thought to cease.

'Frost shrinkage' describes the sudden reduction of the radius initiated by low temperatures. It includes both the transition from the active state to the cold state with a large radius contraction (up to 1.5 mm) (Fig. 2a) and the small radius shrinkage events within the cold state itself (Fig. 2b). Frost shrinkage is not related to particular times of day and occurs when T_{Air} drops below -5°C .

'Thaw expansion' reverses the frost shrinkage at times of increasing T_{Air} above a minimum temperature of approximately -12°C . Similarly to frost shrinkage, this process is temperature-induced and comprises a small radius expansion in the cold state (Fig. 2b) as well as the transition from the cold to the active state (Fig. 2a). At first sight, the small thaw and frost induced radius fluctuations, illustrated in Fig. 2b, resemble the diurnal stem radius changes,

depicted in Fig. 2c. In contrast to the diurnal stem radius changes, however, the thaw and frost dynamics are temperature induced and have, therefore, an inverse day/night-time-pattern: the radius expands during the day when the temperature is increasing and contracts during the night. The radius increases very fast during thaw expansion and reaches rates three times as high as the expansion rates measured in the active state.

3.2. Relationship between radius fluctuations and temperature

The relationship between stem or root radius fluctuations and (bark and air) temperature was investigated by splitting the course of ΔR into the three defined processes: frost shrinkage, thaw expansion, and diurnal stem radius changes. The number of events of the respective processes was correlated to the daily minimum temperature (frost shrinkage and diurnal stem

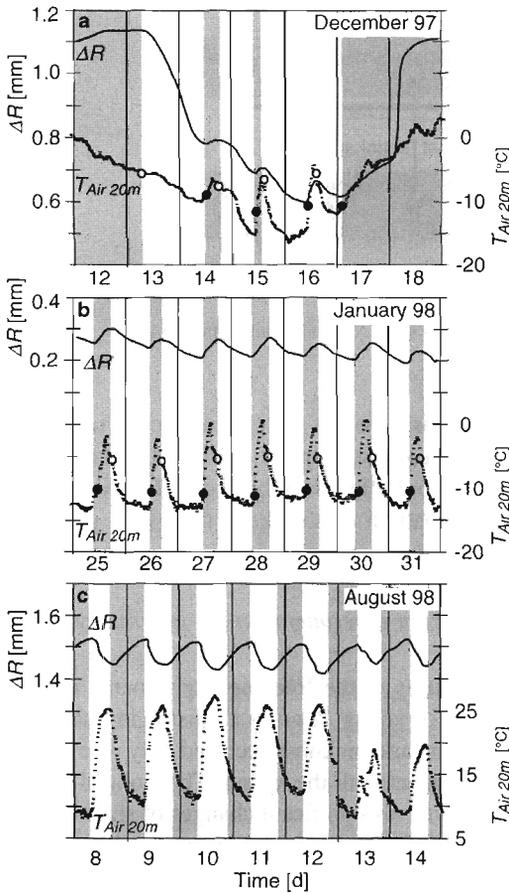


Fig. 2. Stem radius changes ΔR (Tree A, level 18 m) and the corresponding air temperature (T_{Air}) for selected periods in winter (a) and (b) and in summer (c). The gray areas mark a period of radius increase, the white areas a period of radius decrease. The full circles indicate the temperature of initial radius increase, the open circles indicate the temperature of initial radius decrease.

radius changes) or to the daily maximum temperature (thaw expansion). The results are shown in Fig. 5. For $T_{Air} > +10^\circ\text{C}$ (bark temperature $T_{Bark} > +5^\circ\text{C}$), only diurnal stem radius changes occur, and these disappear quickly when the temperature drops below the freezing point. Only approximately 10% of the days which reach a daily temperature minimum of -2°C ($T_{Bark}: 0^\circ\text{C}$), still show temperature insensitive stem radius changes. Frost shrinkage occurs at temperatures $< -5^\circ\text{C}$ (-0.5°C), and the bark tissue is always in the cold state for temperatures $< -12^\circ\text{C}$ (-9°C). Thaw expansion occurs between -12 and $+10^\circ\text{C}$

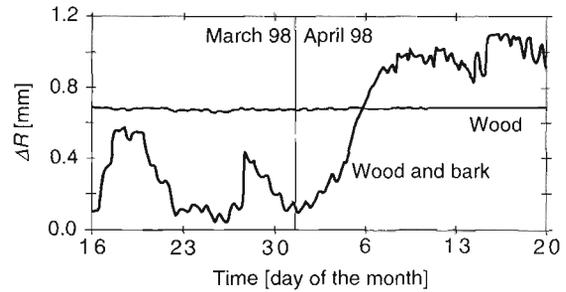


Fig. 3. Comparison between the radius fluctuations ΔR of wood and bark over 5 weeks. One point dendrometer sensor was placed on the bark, the other one directly onto the xylem.

(-10 and $+5^\circ\text{C}$) when the temperature is increasing. As a consequence, in the temperature range between -12 and -5°C (-9 and -0.5°C), both frost and thaw processes were observed, depending on increasing or decreasing temperature. In periods with a changing course of temperature, frost shrinkage as well as thaw expansion occurred on the same day (Fig. 2b).

More than 100 events of frost shrinkage and thaw expansion were counted per winter on every single measurement point. Approximately 25% of these temperature induced stem radius fluctuations were larger than 0.2 mm. Such great stem size changes are measured more frequently in the upper stem part than in the lower part or on roots.

3.3. Spatial patterns of frost shrinkage and thaw expansion

Each stem and root section responds individually to temperature. Strongest distinctions of T_{Air} were measured within the crown and the temperature was, on average, lowest just above the snow pack. Moderate temperatures with small radius variations occurred in the soil and within the snow layer. A vertical profile of the average T_{Air} is shown in Fig. 6b for December 1998. The corresponding stem radius fluctuations are depicted in Fig. 6a. In the crown section, thawing temperatures are reached more often than in the lower stem section. Therefore, the lower stem sections above the snow layer are in the active state for shorter periods than the stem sections in the upper part of the tree. The stem sections covered by snow and the roots in the soil are less exposed to freezing conditions and show significantly longer periods in the active state

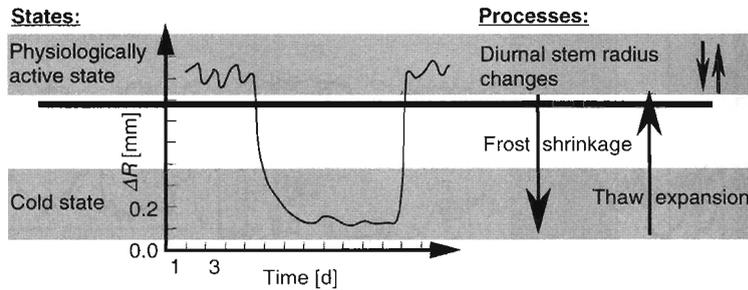


Fig. 4. Schematic diagram of states and processes of the stem (root) size. ΔR =stem radius fluctuation.

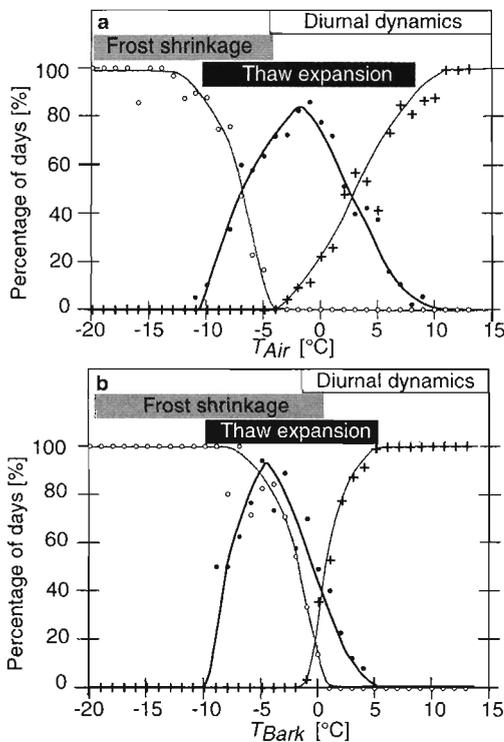


Fig. 5. Relative number of days showing frost shrinkage (open circles), thaw expansion (closed circles), and diurnal stem radius changes (crosses) related to (a) air and (b) bark temperature (T_{Air} and T_{Bark} , respectively).

(>50% of the winter) than the other parts (<40% of the winter).

Variations in temperature within the canopy occur not only in the vertical direction but also horizontally, depending on the azimuth of the respective measurement location on the stem. Frost shrinkage, as well as

thaw expansion varies with the respective temperature, and thus sunny stem parts exposed toward south and east are more effectively heated and show a different temporal pattern of shrinkage than stem parts facing north.

3.4. Freezing experiments in the laboratory

The results of the freezing experiments with stem segments of young *P. abies* are listed in Table 1. The changes in bark thickness occurred only when the bark was in contact with the xylem. The isolated pieces of bark showed no significant changes of size. The water content of the frozen bark was reduced by 10% (by weight) relative to that of the fresh bark. The frozen and thawed stem segments showed a re-hydrated bark, with water content similar to those of fresh samples.

4. Discussion

The 2-year investigations on mature *P. abies* in a subalpine forest enabled us to postulate mechanism of the frost-induced stem and root bark shrinkage known to occur in winter (Bryan and Doolittle, 1950; McCracken and Kozłowski, 1965; Pook and Hall, 1977; Larcher et al., 1985) in comparison with diurnal stem radius changes in summer (Herzog et al., 1995; Zweifel, 1999). Our results provide evidence that the sharp stem radius changes in winter (frost shrinkage and thaw expansion) are caused by changes of the turgor in the elastic bark cells (cambium, phloem, and parenchyma) in the same way as the diurnal radius fluctuations in summer. In other words, the bark thickness is proportional to the bark water content (Zweifel,

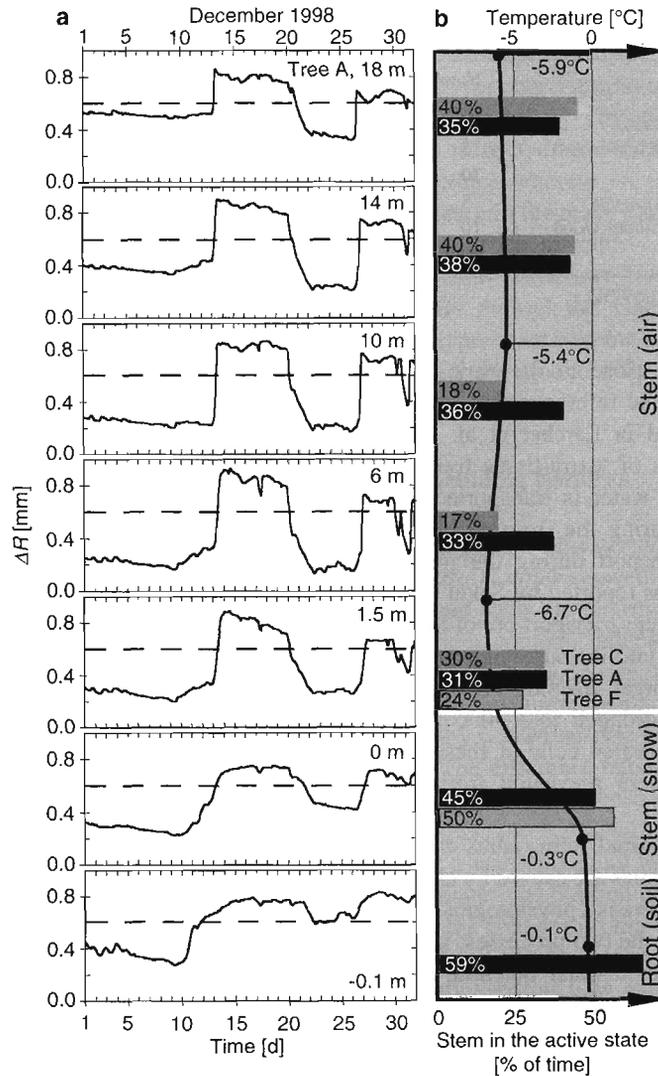


Fig. 6. (a) Course of stem radius changes ΔR in different root and stem sections of Tree A in December 1998 (solid line). The dotted lines mark the transition between active and cold state of the respective bark sections. (b) Profile of bark size state and profile of temperature. The bars indicate the relative number of days with the respective bark section in the active state (dark gray: Tree C, black: Tree A, light gray: Tree F). The black circles indicate the average temperature in December 1998.

1999). In contrast to the bark, the wood shows only small volume fluctuations during freezing and thawing periods (Fig. 3). This result is in accordance with the findings of Dobbs and Scott (1971), Molz and Klepper (1973), and Siau (1984), who reported only small fluctuations in wood size at moderate temperatures. In freezing experiments, it was detected that the bark radius only changes when the bark is in

contact with the xylem. Therefore we conclude, that not only are the protoplasts dehydrated, but the whole bark tissue is emptied and that, therefore, the water is moved from the bark into the neighboring xylem. The alternative route for water transport through the bark to the air seems not to be plausible to us because of the hydrophobic bark epidermis and the quick re-hydration during thawing periods. We suggest that

Table 1
Freezing experiment with stem segments of young *Picea abies*

Sample treatment	Number of replicates	Change of bark size (% of initial volume)	Change of bark water content (water content in % of the control samples)
Freezing of stem segments (bark and wood)	15	–6 to –10*	–7 to –12*
Freezing of bark without wood	10	+2 to –2	Not measured
Freezing and thawing of stem segments	5	+1 to –3	+4 to –2
Freezing and thawing of bark without wood	10	+2 to –3	Not measured
No treatment	10	Control samples	Control samples

* Significant (Wilcoxon-test: $p > 97\%$).

the water stays relatively close to the bark and is not lost by evaporation. One reference that supports this conclusion was found in Larcher et al. (1985, p. 362). The authors speak of ‘extra-tissue freezing’, by which they mean that water is transported from one tissue into another during the freezing process. A similar inter-tissue transport during the freezing process in conifer buds was reported by Sakai (1979, 1982). He described the water transport out of the primordial shoot of the buds into the surrounding tissue with the expression ‘extraorgan freezing’. Despite the fact that the temperature dropped to -30°C during his observations, the dehydrated cells of these trees remained unfrozen and were prevented from frost damage.

Even though both the diurnal stem radius changes and the frost-induced dynamics are caused by changes of the bark water content, there is a physiologically important difference between the two processes: namely the mechanism that initiates a water potential gradient. Hydraulic gradients in the active state are mainly caused by the daily transpiration course, which forces water to move between different compartments of the plant. This concept has been used in several models (Edwards et al., 1986; Tyree, 1988) and verified with measurements on young *P. abies* (Zweifel, 1999). In contrast to the diurnal stem radius changes in summer, the 10-fold larger stem radius changes during frost shrinkage and thaw expansion are not an expression of transpiration-induced water potential gradients. During these periods, the transpiration rate and the photosynthetic activity are always strongly reduced or non-existent. The corresponding amount of water which disappears from the bark during a single event of frost shrinkage was estimated at approximately 20 l (stem diameter: 0.5 m, tree height: 25 m, ΔR : 1 mm) by Zweifel (1999).

4.1. A proposed mechanism of frost shrinkage

Based on our results and on findings reported in literature, we suggest the following mechanism of frost-induced bark shrinkage:

The initial ice crystallization: exposed twigs of the crown periphery freeze first when the temperature drops below the freezing point. Asahina (1956) and Kitaura (1967) argued that the initial freezing in the large vessels of leaves is to be expected since their large diameter does not favor super-cooling, and their dilute sap probably has the highest freezing point of any water in the plant.

Formation of ice along the vessels: once ice forms in the tracheids, the freezing proceeds along the stem from a few nucleation points and reaches all parts of the tree relatively quickly (Single (1964): 0.76 m min^{-1} , Levitt (1980): 0.34 m min^{-1}).

Water transport from the unfrozen bark to the frozen xylem: due to the high velocity of ice formation in the xylem, the water in the xylem is frozen whereas the sap in the bark remains liquid (Larcher et al., 1985). In frozen tissue, the liquid water content is extremely small and the water potential exceedingly negative. This situation leads to steep hydraulic gradients between frozen and unfrozen tissue compartments, as observed by Olien (1966), Sakai (1982), and Jeffree et al. (1987). In the case of frost shrinkage (inter-tissue water transport), the compartments consist not only of a protoplast, separated by a membrane from the intercellular space, but comprise two different tissues (bark and wood). Nevertheless, we suggest that the water potential gradient between partially frozen tissue (wood) and unfrozen tissue (bark) withdraws water from the bark in the same way as known from extracellular freezing, which describes the water movement out of protoplasts into the frozen, intercellular space.

Ice forms in the intercellular spaces of the xylem: the additional space for ice formation in the tracheids (ice needs approximately 9% more volume than water) and the additional water from the bark might find place in air-filled intercellular spaces of the xylem (Kübler, 1983; Jeffree et al., 1987; Robson et al., 1988). We estimate the volume of additional water, transported from the bark into the xylem, at a maximum of 0.5% of the entire stem volume, which corresponds to the intercellular space in the xylem of conifers reported by Larson (1994).

Replenishment of the bark: during thawing periods, the ice in the xylem melts and the water potential gradient becomes abruptly reversed. Additionally, the increased osmotic and matric potential in the dehydrated bark accelerates the water transport back into the phloem and the bark re-expands.

The proposed mechanism of frost shrinkage is mainly based on physical processes (initial ice crystallization in the xylem and water transport along an osmotic potential gradient) and does not depend on active transport energy or a biochemical temperature sensor. As long as ice is initially formed in the xylem and not in the bark, this mechanism of bark dehydration comes into play and protects the living cells from frost damage. The reversibility of the mechanism supports the finding that frost shrinkage and thaw expansion occur more than 100 times a winter without obvious disadvantage for the mature trees. The loss of hydraulic conductivity due to freeze-thaw cycles, reported by Lemoine et al. (1999), seem not essentially to disturb the vitality of these trees. Also, the intra-annual radial cracks in wood of *P. abies* (Cherubini et al., 1997) have not been clearly related to frost periods in winter so far. However, damage in stem tissues due to frost is possible when the temperature drops too fast for a regular dehydration of the frost-sensitive tissues. We suggest that the morphological structure of the xylem plays an important role for an efficient radial water transport during freezing periods in winter. The ideal morphological stem structure enables an initial ice formation in the wood and also a high velocity of ice expansion along the flow path. Both depend on the size of the tracheids. It would be interesting to investigate the differences in the morphological xylem structure between trees adapted and not adapted to cold and to compare these results with our hypothesis.

The ability to switch very quickly between the cold and active states enables *P. abies* to reactivate photosynthesis for only a few hours even in winter (Zweifel, 1999). On a sunny day, the crown gathers enough warmth to re-hydrate the bark in the upper tree part (active state), whereas the lower stem remains frozen (cold state). In the reactivated part of the crown, small amounts of photosynthesis and transpiration occur and water is withdrawn from internal reserves. Consequently, through the winter, the crown and the bark of the upper stem become more dehydrated than stem parts near the ground (Fig. 1).

5. Concluding remarks

Investigations of water storage dynamics in the bark of mature *P. abies* showed that radius fluctuations of stems and roots are closely related to changes of the bark water content, independent of the season. The sudden frost-induced radius fluctuations in winter — as well as the diurnal radius changes in summer — are caused by water transport processes between bark and wood. The difference between warm and cold season lies only in the mechanism that initiates a water potential gradient for this radial water transport. In the warm season, a water potential gradient is strongly coupled to the daily transpiration course, whereas in the cold season the gradient is built by freezing processes. The proposed mechanism of frost-induced water transport plausibly explains how plants switch between the inactive cold state (dehydrated living tissues) and the physiologically active state (hydrated living tissues) within only 1 day, and how they save their living tissues from frost damage.

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