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# The Ecological Significance of Thickness Changes in Stem, Branches and Twigs of *Pinus cembra* L. during Winter

By

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## Summary

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During winter various types of thickness changes in the cortex of twigs, branches and the stem of cembran pine (*Pinus cembra* L.) were established, caused by direct and indirect effects of frost. Direct effects of freezing are the shrinking of the living cortex and its expansion during the following thaw. The mechanism behind this is the transfer of water from the cells into the intercellular space during ice formation, which is accompanied by a loss of cell volume, and the resorption of water by the cells during a thaw.

Thickness changes caused indirectly by frost are due to dehydration and hydration of the cortex tissue. As long as the soil was frozen cumulative dehydration of the cortex resulted in considerable shrinking, which was stronger in the stem than in branches and twigs. After soil water was available again, cortex tissues re-expanded and indicated water resaturation of the tree. We conclude that thickness changes measured with dendrometers are a suitable indicator for water relations of trees during winter.

## Introduction

Since the investigations by FRIEDRICHS 1897 it has been known that frost causes considerable changes in the thickness of tree stems in winter, i.e. shrinking during freezing and expansion during the following thawing ("frost changes").

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Frost leads to pronounced shrinking of the living bark due to the formation of extracellular ice, whereas no or only minor changes in dimension are reported for the wooden cylinder, i.e. expansion in water saturated wood (POOK & HALL 1977) or shrinking in rather dry wood (KÜBLER 1983). These findings correspond with our results in *P. cembra* and *Pinus sylvestris* where frost caused shrinking solely in the living cortex, while a minor expansion was observed in the wood, amounting to less than 10% of the fluctuation of the cortex (LORIS, unpublished). Apart from these "frost changes" other, so far unknown, short and long-term changes of thickness were observed during continuous measurements of the radial thickness in stems of *Pinus cembra, Larix decidua,* and *Picea abies* trees at the subalpine timberline at Mt. Patscherkofel near Innsbruck (LORIS 1981). In laboratory experiments (LORIS, in preparation) they could be proved to be due to changes in the water content of the living cortex, as well as to radial and longitudinal water transfer in the bole. Their ecological importance became particularly apparent in spring, when a period of severe frost was immediately followed by fine warm weather during which the cortex shrank considerably due to dehydration. As a consequence the start of the cambium activity was delayed and the growth period shortened. These results demonstrated that thickness changes during winter may be of similar ecological significance as they are in summer. However, the above results were obtained from measurements at breast height only. Therefore a re-examination for the whole tree seemed to be of great interest, especially at the alpine timberline where water stress and frost drought injuries occur mainly in winter (TRANQUILLINI 1979, SAKAI & LARCHER 1987).

## Material and Methods

Measurements were performed on a cembran pine tree (*Pinus cembra* L.) during the winter of 1993/94. This tree (10m high, bhd 0.3m) stands on a SW-slope below the Klimahaus research station (1,950m a.s.l.) at Mt. Patscherkofel near Innsbruck. It is open to the E and S but borders closed forest in the W and NW. The positions of the sensors in, and diameters of, stem, branches and twigs are given in Table 1. Thermocouples were placed close to each dendrometer to measure temperatures in the living cortex, in 10mm and, where possible, in 50mm xylem depth.

Table 1. Position of dendrometers and thermocouples installed in the experimental tree.

| Dendrometer position | Tree height (m) | Stem, branch, twig diameter (mm) | Thermocouple position |
|---|---|---|---|
| stem south | 7.0 | 50 | cortex & xylem 10mm |
| stem south | 4.0 | 140 | cortex & xylem 10mm, 50mm |
| stem south | 1.7 | 300 | cortex & xylem 10mm, 50mm |
| stem north | 1.7 | 300 | cortex & xylem 10mm, 50mm |
| twig south | 4.2 | 15 | cortex & xylem |
| branch south | 4.2 | 40 | cortex & xylem 10mm |
| twig south | 2.5 | 15 | cortex & xylem |
| branch south | 2.5 | 45 | cortex & xylem 10mm |

Specification of dendrometers has been described in LORIS 1981, 1995. Radial changes of the cortex were measured in the stem, and diameter changes in branches and twigs. Sensor resolution was 2µm. Temperatures and dendrometer values were recorded every 10 minutes with a Campbell CR10 datalogger.

## Results and Discussion

Earlier results indicating that tree stems shrink during frost and expand again during a thaw (frost change) were confirmed by the present investigations for the main stem and for branches and twigs. Furthermore we found additional thickness changes which are interpreted as water content changes. As an example the thickness changes of the stem at breast height together with cortex temperature and soil temperature in 0.15m soil depth are presented in Figure 1 for the period 01 December 1993 to 30 April 1994. Since the records of the other measuring locations are similar, only these results are interpreted.

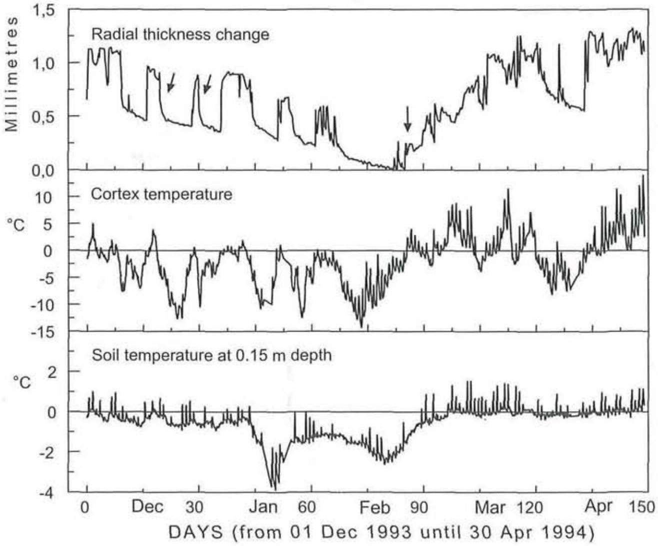

Fig. 1. Seasonal course of radial thickness change and cortex temperature of the stem at breast height, and of soil temperature at 0.15m soil depth.

The large and partly long lasting shrinkage (see slanting arrows) followed by expansions are typical of diameter fluctuations in winter. They are directly related to the frost periods as can be seen in Fig. 1. The shrinkage commenced when the cortex temperature reached subzero temperatures between –0.4 and –2.3° C. The course of the temperature decrease indicated more or less continuous freezing, which is typical of tissues with fairly uniform structure (SAKAI & LARCHER 1987). In *P. cembra* the tissue shrank rapidly at first regardless of the freezing conditions, but the shrinking rate decreased to a fairly constant low rate when the cortex temperature dropped below approximately –6°C.

The seasonal variations in the onset of the extracellular ice formation can partly be explained by different water contents and osmotic potentials of the cortex cells, as was found for needles in *P. cembra* by TRANQUILLINI & HOLZER 1958. There ice formation in the needles started at lower temperatures and resulted in smaller amounts of ice formed in the needles, the lower the water content of the needles was at the beginning of the freezing. Ice formation in needles reached its maximum already at –8°C when about 50 percent of the total water were frozen while the rest remained as bound water in the needles, regardless of a further temperature decrease down to –40°C. This bears a resemblance to the curves of the cortex shrinking where the rate below ca.–6°C indicates that ice formation has come to an end. This also explains why there was no strong correlation between the amount of shrinkage and the intensity of frost.

During subsequent thawing periods the cortex dimensions recovered only after the rising cortex temperature had passed a certain threshold which was also not constant throughout the measuring period but varied between –1°C and –3°C. Expansions were completed when the cortex temperature approached 0°C.

Although the interpretation of the mechanisms controlling the fluctuations in consideration may not be completely satisfactory yet, the basic processes can be deduced on the basis of current knowledge of extracellular freezing in freezing-tolerant plant tissues. What freezes first are either small droplets of water (PEARCE & BECKETT 1985) or water vapour condensed on the cell walls in the course of cooling (LEVITT 1972). Ice nucleation starts here, either due to ice-seeding from vessels or from ice nucleators present in the extracellular space, and because this almost pure water has a lower solute concentration than the intracellular vacuolar and cytoplasmic water. Once the temperature sinks below the freezing point of the cell contents, their vapour pressure will be higher than that of the intercellular ice at the same temperature. Consequently water diffuses from the cells through the semipermeable lipid plasma membranes to the ice in the intercellular space where it accumulates as ice on the external surface of the cell walls. As a consequence of this water loss, the cells shrink and with it the whole tissue.

The expansions are driven by the same mechanism because the vapour pressure gradient becomes inverted with increasing temperature and water returns into the cells (KÜBLER 1962). On the basis of this mechanism a correlation between the rate of cooling and the outflow of water, which the dimension loss depends on, and the reverse, should be expected. This holds true for cereals (GUSTA & FOWLER 1975) and *Eucalyptus pauciflora* (POOK & HALL 1976, 1977) but not for the cortex of *P. cembra,* as mentioned above. More investigations are needed to answer this question.

Further studies are also needed to explain the long term trend of decrease of the radial diameter until the end of February and the following increase (vertical arrow, Figure 1). The magnitude of the total radial shrinkage amounted to 1,2 mm which is about 27 % of the thickness of the cortex. Contractions of that magnitude have so far been known only in stems in the Mediterranean climate during drought periods in summer (LORIS 1995). At the end of February the shrinkage reversed to a progressing expansion until the end of April, interrupted only for the first two weeks in April due to frost. Finally at the end of April the cortex reached its initial thickness of December. This remarkable long-term shrinkage and expansion seems to be controlled by the changing water balance of the whole tree. It is well known that during winter low soil temperature impedes the water uptake by roots and water uptake ceases completely when frost penetrates the soil down to the root horizon. On the other hand the transpiration demand can be high. (TRANQUILLINI 1979). As a consequence, the water loss due to cuticular and peridermal transpiration cannot be replaced during the periods of frozen soil, and high water deficits develop (PISEK & LARCHER 1954). This holds true for the whole tree including the cortex, which therefore shrinks. During severe winter drought shrinkage of the bark of twigs can even be observed visually. A comparison of the curves of the thickness change and the soil temperature (Fig. 1) confirms this interpretation. As long as soil temperature was below 0°C and declining further until the end of February the thickness decreased more or less gradually. Only after the soil temperature rose and remained above zero the radial expansion progressed indicating a water re-saturation of the whole tree. Unfortunately we measured needle water relations only during the next winter (1994/95), when almost no long-term cortex shrinkage occurred (data not shown here) and when needle water potential and water content remained high throughout winter. From comparison of the dendrometer curves of the two years one may conclude that the long-trem decrease during the winter 1993/94 is evidence of some water stress in the tree.

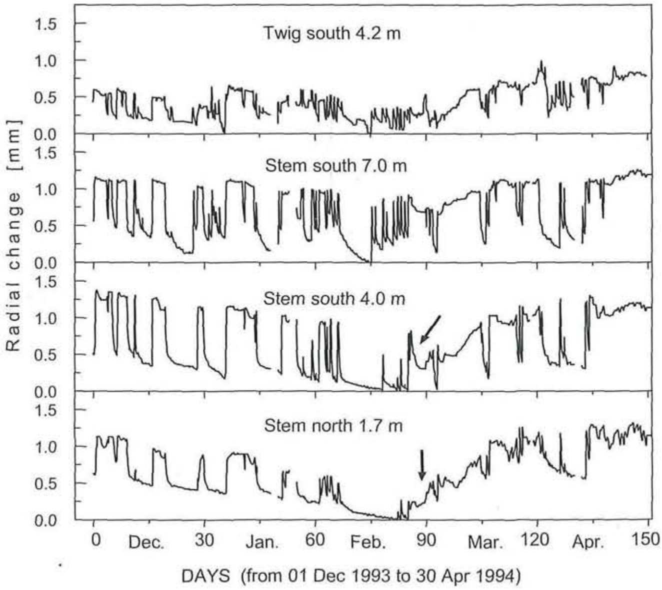

Fig. 2. Selected thickness changes at different positions along the stem, and of a twig.

The results presented above and the discussion apply in general also to the other measuring locations (Fig. 2). But there are some differences. Frost changes occurred more often in twigs and branches than in the lower stem. This is due to the faster freezing and thawing of the smaller mass and to the greater exposure of twigs to radiation. There are also differences in the amplitude of the frost fluctuations which to a certain extent are caused by the different cortex thickness which on average was 4.5 mm in stems, 2.5 mm in branches and only 1.5mm in twigs.

What is of ecological importance is the observation that the average threshold temperature for the onset of shrinkage sank from –1.2° C in the lower part of the stem to –1.8°C in the middle stem and to –2.2 and –3.1°C in the twigs. Although these temperatures are not exactly equal to the lowering of the freezing point of the cell sap, the gradient focuses attention on the influence of the osmotic gradients in trees. Another indication for a water transfer along an osmotic gradient from the stem to the needles could be the different percentages of long term shrinkage occurring between December and the end of February. They amounted to maximally 27% of the cortex thickness in the stem at breast height, and only to 16% in twigs. However, further measurements in the field are needed to quantify water transfer within the tree during freeze-thaw cycles, which has been established in laboratory experiments (LORIS, in preparation).

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