Holzforschung
54 (2000) 9–11

Short Note

Characteristics of Spruce [*Picea abies* (L.) Karst] Latewood Formed under Abnormally Low Temperatures

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Keywords: Lignification · *Picea abies* (L.) Karst · Low temperature latewood · Tracheid · UV-Absorption · Wood formation · Latewood · Low density wood

Introduction

Timberline spruce [*Picea abies* (L.) Karst] frequently forms rings with light latewood (LW) (Fig. 1). Since the growth of trees near their altitudinal limit in Alpine areas is primarily limited by the temperature and the length of the growing season (Tranquillini 1979), the formation of light LW is attributed to low temperatures during its production (Yamaguchi *et al.* 1993). In the year 1912 low density LW was formed in conifers in large parts of Europe (Schweingruber 1989; Kyncl *et al.* 1990). This year was characterized by particularly adverse growing conditions in Austria: from August to October, the monthly mean temperatures were well below the long term mean, and September 1912, with a mean temperature 5,2 °C below the 1796–1992 mean, was the coldest in the history of instrumental temperature records in Austria (Böhm 1992). It is generally assumed, that these outstanding meteorological conditions were at least in part caused by the eruption of Novarupta (Mt. Katmai) in southwestern Alaska, USA, in June 1912 (Bradley and Jones 1995). The aim of this study was to determine, whether the cell properties, particularly the lignin content of LW tracheids were affected in a similar way by the prevailing low temperatures, as it is known for density.

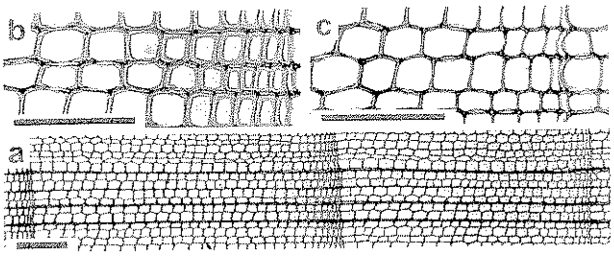

Fig. 1. Microphotographs of a cross section showing the 1911 reference and the 1912 increment with light latewood: a) entire 1911 and 1912 increments (bar = 200 μm), b) latewood of 1911 (bar = 100 μm), c) latewood of 1912 (bar = 100 μm).

Material and Methods

A stem disc was taken from an approx. 250 years old timberline spruce [*Picea abies* (L.) Karst] at an altitude of 1750 m at the Blaseneck mountain in the Austrian Eastern Alps. Samples for image analysis, radiodensitometry and UV spectroscopy were taken from immediately adjacent locations on the disc. Special care was taken to select a non eccentric disc, free of compression wood, to exclude mechanical stress as a potential cause for variations in lignin content (Okuyama *et al.* 1998).

Cross sections 20 μm thick were taken on a sliding microtome, stained with Methylene Blue and mounted permanently in Malinol (Chroma-Ges., Köngen, Germany). Radial cell wall thickness, radial lumen diameter and total cell wall area without rays and resin ducts were measured using a digital camera attached to a microscope and the image analysis software NIH-Image. Measurements were taken in 20 radial files from the 8th to the 12th earlywood (EW) cell and in the last 5 cells (representing LW) of the 1911 and 1912 ring. Tracheid diameter was calculated by adding 2× cell wall thickness to the respective lumen diameter.

A cross section 1,2 mm thick was taken with a double bladed circular saw, placed on an x-ray sensitive film and exposed to an x-ray source. The x-ray micrograph was analysed on a microdensitometer (WALESCH DENDRO 2003, WSL Birmensdorf, Switzerland) and density was determined in reference to a cellulose acetate calibration wedge (Lenz *et al.* 1976).

A small block 0,5 mm wide in tangential direction containing the entire 1911 and 1912 increment was embedded in Spurrs resin (Spurr 1969). Cross sections 1 μm thick were taken on an ultramicrotome using glass knives. The sections were mounted on quartz slides and embedded in glycerol. UV absorption spectra were determined using the microspectrophotometer ZEISS MPM800. The diameter of the measuring spot was 1 μm, monochromator bandwidth was set to 5 nm, magnification was 1000×. Two measurements were taken in the S2 layers of 12 adjacent cells in the 10th (EW) and the last but 2nd (LW) tangential cell file of the 1911 and 1912 ring. Lignin concentration was estimated according to Fergus *et al.* (1969) using the Beer-Lambert law:

$$A = \varepsilon \times C \times d$$

where A is the logarithmic absorption at 280 nm, ε is the extinction coefficient, C is the lignin concentration and d is the section thickness.

Results

Mean values of all investigated tracheid properties are compiled in Table 1. All analysed EW properties do not vary

Table 1. Selected properties of spruce tracheids formed in 1911 and 1912

	1911		1912	
	Earlywood	Latewood	Earlywood	Latewood
Radial cell wall thickness (μm)	3,7 ± 0,4	5,6 ± 0,5	3,8 ± 0,4	1,8 ± 0,5
Radial tracheid diameter (μm)	52,7 ± 3,2	10,4 ± 4,1	55,5 ± 3,5	9,3 ± 5,7
Cell wall area (%)	36,5 ± 3,7	85,4 ± 3,4	37,6 ± 4,1	41,8 ± 3,8
Density (g cm^{-3})	0,30	0,81	0,31	0,24
UV absorption of S2 at 280 nm	0,35 ± 0,04	0,54 ± 0,04	0,37 ± 0,03	0,31 ± 0,03
Mean lignin concentration in S2 (g g^{-1})	0,23	0,35	0,24	0,21

much between the 1911 and the 1912 ring. Contrarily, all LW properties, with the exception of radial tracheid diameter, differ greatly. Radial cell wall thickness in 1912 is reduced to one third of the 1911 reference and cell wall area is reduced to the half. The radiodensitometric density curve (Fig. 2) reveals a high LW density in 1911, and a drastically reduced LW density in 1912. Its minimum is even lower than the EW density of the respective year.

Examples for UV absorption spectra of the S2 layer of LW tracheids are displayed in Figure 3. Absorption shows a distinct peak at 280 nm and approaches near zero values at approx. 400 nm. The estimated lignin content is reduced in LW tracheids formed in 1912 compared to the 1911 LW.

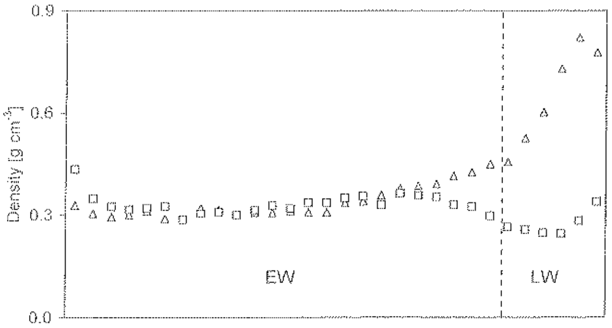

Fig. 2. Density profiles of the 1911 (triangles) and 1912 (squares) tree rings. EW = earlywood, LW = latewood.

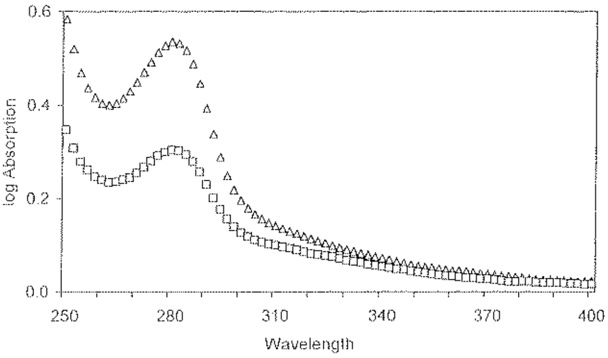

Fig. 3. UV absorption spectra of S2 layers of latewood tracheids formed in 1911 (triangles) and 1912 (squares).

Discussion

Cell wall thickness, tracheid diameter, cell wall area and density of the 1911 increment are in the magnitude expected for spruce (Trendelenburg 1939; Wagenführ and Scheiber 1985). Therefore it is reasonable to choose this year as a reference. While EW properties of both years do not differ, cell wall synthesis was obviously slowed down to a great extent by the low temperatures during LW production in 1912, as indicated by the greatly reduced cell wall thickness, cell wall area and density. Regarding lignification, lignin content of the S2 of EW tracheids of both years is comparable to values from 0,22 to 0,24 g g^{-1} for spruce given by other authors (Fergus *et al.* 1969; Takano *et al.* 1983). The intra-annual pattern of lignin distribution in conifers consists of a decrease from the first EW cell to the EW-LW boundary and a rise towards the end of the annual increment, with high values and variation in the last LW cells (Fukazawa and Imagawa 1981; Takano *et al.* 1983). Mean lignin concentrations in conifers are slightly higher in EW than in LW (Fukazawa and Imagawa 1981; Takano *et al.* 1983), which does not exclude the possibility of highly lignified cells in the terminal LW as indicated by the estimated concentration of 0,35 g g^{-1} in the last but 3rd cell of the 1911 ring. While radial growth at the timberline is completed at the end of August (Müller 1981), photosynthesis (and as a consequence lignin biosynthesis) can operate at high rates into late autumn (Pisek and Winkler 1958). Thus, lignin concentration in the last few cells of an annual increment in timberline spruce should depend on the late season temperatures, when mechanical stress can be excluded as a potential cause for variations. Because September to October temperatures were above the long term mean in 1911 and well below in 1912, it is concluded, that the prevailing late season temperatures in the respective years caused the difference in lignin content between the last but 2nd LW tracheids of the 1911 and 1912 increment.

Acknowledgement

A part of this work was funded by the Austrian National Bank, project number 6019.

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Received November 24th 1998

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