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SEASONAL CAMBIAL ACTIVITY OF SPRUCE (*PICEA ABIES* KARST.) WITH INDENTED RINGS IN THE PANEVEGGIO FOREST (TRENTO, ITALY)

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Wood with indented rings has long been of interest because it was believed to have special acoustic characteristics and was preferred by the most famous lute and violin makers of the past. In recent years its biological, technical and physical features have become the subject of research. The indentations, which are anatomical anomalies, can be explained by abnormal cambial growth but it is still unclear why and how they are produced. The pinning technique has been used to study the duration and intensity of wood formation of spruce with indented rings grown in the Paneveggio Forest, Italy. The present work describes and discusses the kinetics of cambial activity of trees examined in 2002. Comparison of normal wood and indented xylem showed very similar cambial activity dynamics, characterized by contemporaneous onset and cessation, and by similar trends. Growth rate and final width were the same in each part of the ring. The main differences were not in the timing of xylogenetic processes, but in the morphology of the new cells formed.

Key words: Pinning technique, cambium, indentation, intra-annual wood formation, *Picea abies*, Hazel growth.

INTRODUCTION

Spruce wood with indented rings was often preferred in the past by famous lute and violin makers, such as Amati, Guarneri, Stradivarius, Gabrielli and Gagliano, though today the presence of indentations is not generally considered a necessary characteristic for high quality musical instruments (Corona, 1990).

The biological, technical and physical features of wood with indented rings have been variously investigated in recent years, particularly phenotype traits and aspects of wood anatomy (Ziegler and Merz, 1961; Ohtani et al., 1987; Bonamini et al., 1991; Lev-Yadun and Aloni, 1991; Bucur et al., 1999; Treu and Hapla, 2000; Paoletti, 2002; Romagnoli et al., 2003). Wood containing indentations is characterized by certain modifications as compared with normal wood, such as tracheid disorientation and irregular shape, reduced tracheid length, and increased ray number and ray size (Ziegler and Merz, 1961; Ohtani et al., 1987). As a consequence of these anatomical features, the elastic anisotropy and the propagation of energy in the form of vibrations are modified in the wood (Bonamini et al., 1991).

These anatomical anomalies can be explained by abnormal cambial growth, but it is still unclear why and how indented rings are produced. Indentations are generated by a dysfunction of some cambial derivatives during a given growing season, but the cause of this phenomenon is still unknown. It is also unknown whether the development of cells during the growing season is synchronous in modified (indented) and unmodified (normal) cambial areas. The present work analyzes wood formation with high time resolution, in order to contribute to a better understanding of wood formation dynamics in stems with indented rings.

Different methods can be used to investigate cambium activity (Rossi et al., 2006a), one of which is the pinning technique. It was introduced by Wolter (1968), and has been used for various applications in recent years (Yoshimura et al., 1981; Kuroda and Shimaji, 1984a,b; Kuroda and Shimaji, 1985; Nobuchi et al., 1995; Schmitt et al., 2000; Schmitt et al., 2004; Gričar et al., 2007a; Seo et al., 2007). It consists in inserting a pin at regular intervals during the growing season, through the bark and the cambium into the outer xylem. The wound reactions of the cambium along the pinning canal,

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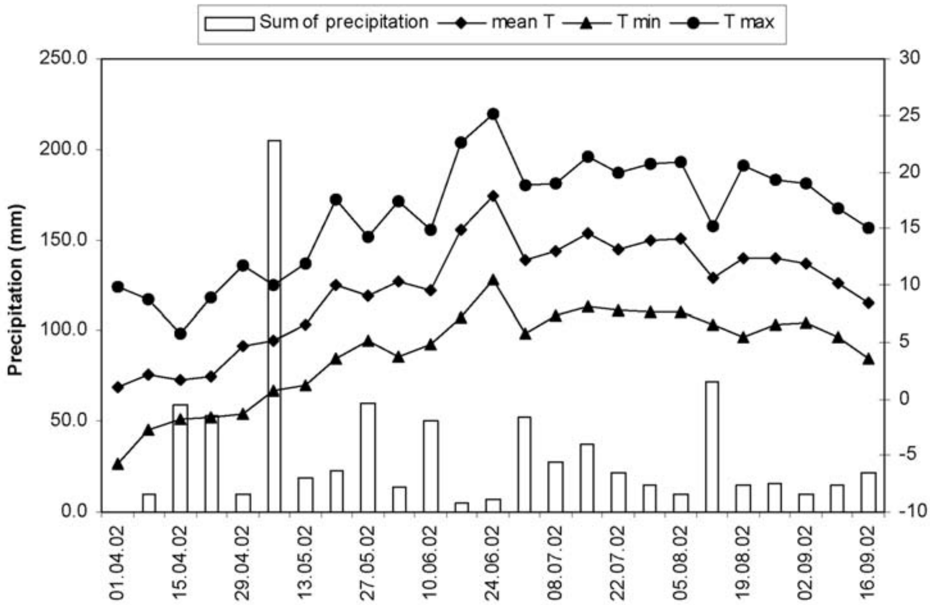

Fig. 1. Climate data for the 2002 growing season. Precipitation is shown as weekly sums, temperature as weekly average.

that is, the immediate degeneration of woody tissues due to pinning, are then used to determine the course of wood formation by means of light microscopy.

The duration and intensity of wood formation of three spruce trees with indented rings was analyzed for the year 2002 by means of the pinning technique.

MATERIALS AND METHODS

SITE DESCRIPTION

Three spruce trees with indented rings were selected in the Paneveggio Forest, a public area situated in the Dolomites, Italy (46°17'N, 11°44'E). The area has an alpine climate, characterized by cold and dry winters and cool summers. The annual mean temperature is 3–4°C and the mean of maximum temperature during July and August is 19°C; precipitation is 1,100–1,200 mm annually, concentrated mainly in spring and autumn (Fig. 1) (data from http://217.222.71.209/meteo/index.php).

Phenotype characteristics were used to ensure the presence of indentations in wood (Paoletti and Viola, 1994); special attention was given to the presence of axial marks, which can be distinguished on the trunk surface just below the bark.

Tree 1 was located at the highest site (1,830 m a.s.l.), while the other two trees were at a lower location, not far from each other. Table 1 summarizes the characteristics of the sites and trees.

WOOD SAMPLES

The investigation was carried out between April and September 2002. The pinning experiments were started in Paneveggio on April 3. The trees were pinned weekly until the middle of May, in order to reduce the temporal interval of uncertainty; cambial activity onset was expected at this time. In the following months the trees were pinned bi-weekly until mid-September.

Four wounds were made on each tree on each pinning date: two on the north side of the stem and two on the south. Tree 2 was growing on a steep slope, so to avoid complications due to compression wood, this tree was pinned laterally, on the east and west sides of the stem. The pins used for the experiments were 2 mm in diameter and were inserted in the stem at breast height in a geometrical pattern, about 10 cm apart on both the vertical and horizontal planes, to avoid wound reactions between neighboring pins.

ANATOMY

For microscopy, small cubic samples of wood, ~1 cm on a side, were chiseled from the area surrounding each pinning canal. The samples were fixed for 1–3 days in phosphate-buffered solution of 37% formaldehyde (Schmitt et al., 2000) and then embedded in polyethylene glycol (PEG 2000). Next, sections 20 μm thick were prepared with a sliding microtome, double-stained with safranin and Astra blue, and finally mounted on glass slides. The sections were then examined under a light microscope. Using an image analyzer, the width of the newly formed xylem was

TABLE 1. Site and tree description. DBH – diameter at breast height

Tree	Site	Elevation (m a.s.l.)	Slope (%)	Exposure	DBH (cm)	Height (m)
1	Rolle	1830	20	SSW	83	28
2	Campedelotti	1540	58	S	47	34
3	Val dei Buoi	1550	20	S	62	34

measured and the number of current-year cells along the pinning canal was counted. The measurements – four measurements on each side (two samples per side and two measurements per sample) – were made for each pinning date. Finally, graphs were plotted using the mean values of ring width and cell number.

RESULTS

The location of the pins could not be programmed to coincide precisely with the indentations, as it would have been impossible to identify their exact position without removing the bark and thereby damaging the cambium. Fortunately, however, many samples from Tree 1 showed indentations, allowing comparisons between the microsection specimens taken from the indentations and those from normal wood. We found no differences in the onset of cambial activity, the pattern of radial growth rate, or the end of the cambial activity between normal and indented wood. Comparison of normal wood and indented xylem of Tree 1 showed very similar ring width and cell number for every pinning date, meaning that growth rate and final width were the same in each part of the ring. The main differences were not in the timing of xylogenesis but in the morphology of the new cells formed. In particular, chaotic cell row layout and irregular cell shape were noted in the boundary zone between indented and normal wood (Fig. 2).

The kinetics of cambial activity in the three spruces examined are described below. Microscopic examination of slides showed dormant cambium until the end of April (April 24) in the 3 trees examined, as no histological reaction to the pinning was noted in the samples taken up to and including that date (Fig. 3a). It can be inferred that cambial activity must have begun between the pinnings of April 24 and May 1 (Fig. 3b), because a wounding reaction to pinning was noted on the latter occasion. Nevertheless, no new xylem cells were observed in any of the following samples until the pinning date of June 26 (Fig. 3c), in which already thickened wall cells were found. In the samples of this date, it was possible to carry out the first measurements of ring width and to count the number of tracheids formed, which already showed a thickened secondary wall.

The onset of cambial activity was synchronous in the two sampled sides of the trunks in all the trees (north and south sides of Trees 1 and 3; east and west sides of Tree 2). Reactivation of cambial activity was also synchronous in all the examined trees, and the observations were very similar up to June 26. After this date the trees showed different growth rates and the end of the growing season occurred at different times. Trees 1 and 3 showed a gradual increase in the number of newly formed cells from June 16 to the end of the season. However, the corresponding ring width showed a different pattern: the radial growth rate (in terms of ring width) appeared to be slow at the beginning, until the middle of July. In the second half of July there was a sudden increase, followed by a decrease from July 24 to August 21. Finally there was a great increase in radial growth lasting to the end of the growing season (Fig. 4).

Dormant cambium was observed in Tree 3 on September 5 (Fig. 3g) and in Tree 1 on September 18. The end of cambial activity can be dated at the end of August for Tree 3 and at the beginning of September for Tree 1.

In contrast, the growth rate of Tree 2 was high until August 7, when the whole ring had already formed. By this date the cambium was dormant; cambial activity must have ended in the previous week, considerably earlier than in the other two trees (Fig. 5).

The final radial growth of the three plants differed: ring width was on average 3.08 mm in Tree 1 and 0.5 mm in Tree 2; Tree 3, with ring width of 2 mm, showed intermediate growth in comparison.

DISCUSSION

Some information on the indentations in spruce can be deduced from xylogenesis. The normal and the indented parts of the ring showed very similar cambial activity dynamics, characterized by contemporaneous onset and ending, and similarity of trends. The final ring width in 2002 was the same along the indentation and in the normal part of the trunk. This result agrees with the findings of Romagnoli et al. (2003). Cell morphology showed the main differences, particularly in the boundary zone between the middle of the

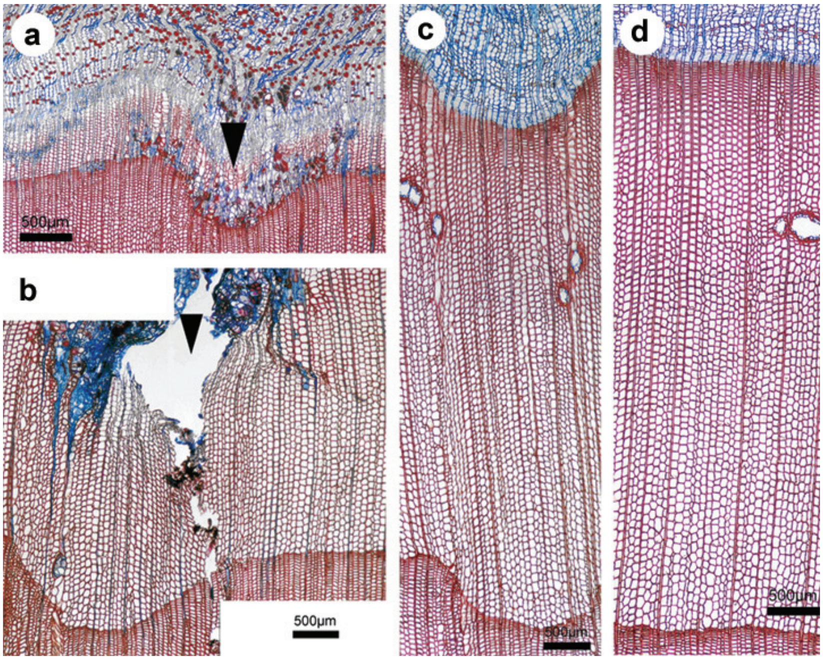

Fig. 2. Tree 1. (**a**) Pinning performed on May 16, wood reaction to wound inside the indentation, (**b**) Pinning performed on July 24 in the indentation border, indented ring and normal wood show almost the same ring width and cell number; September 18: indented ring (**c**) and normal wood (**d**) at the end of growing season. Arrowhead indicates the pinning canal.

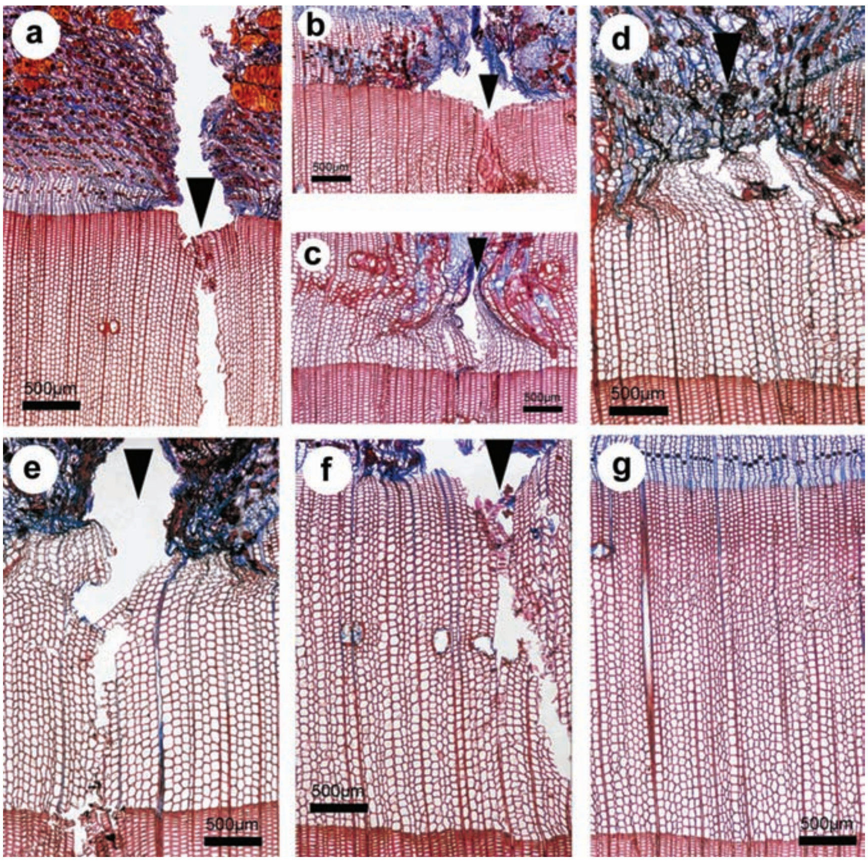

Fig. 3. Tree 3. Pinning performed on April 24, no wound reaction (**a**), on June 16 wound reaction is evident but new cells are not visible (**b**), on June 26 (**c**), on July 24 (**d**), on August 8 (**e**), on August 21 (**f**), on September 5 (**g**). Arrowhead indicates pinning canal.

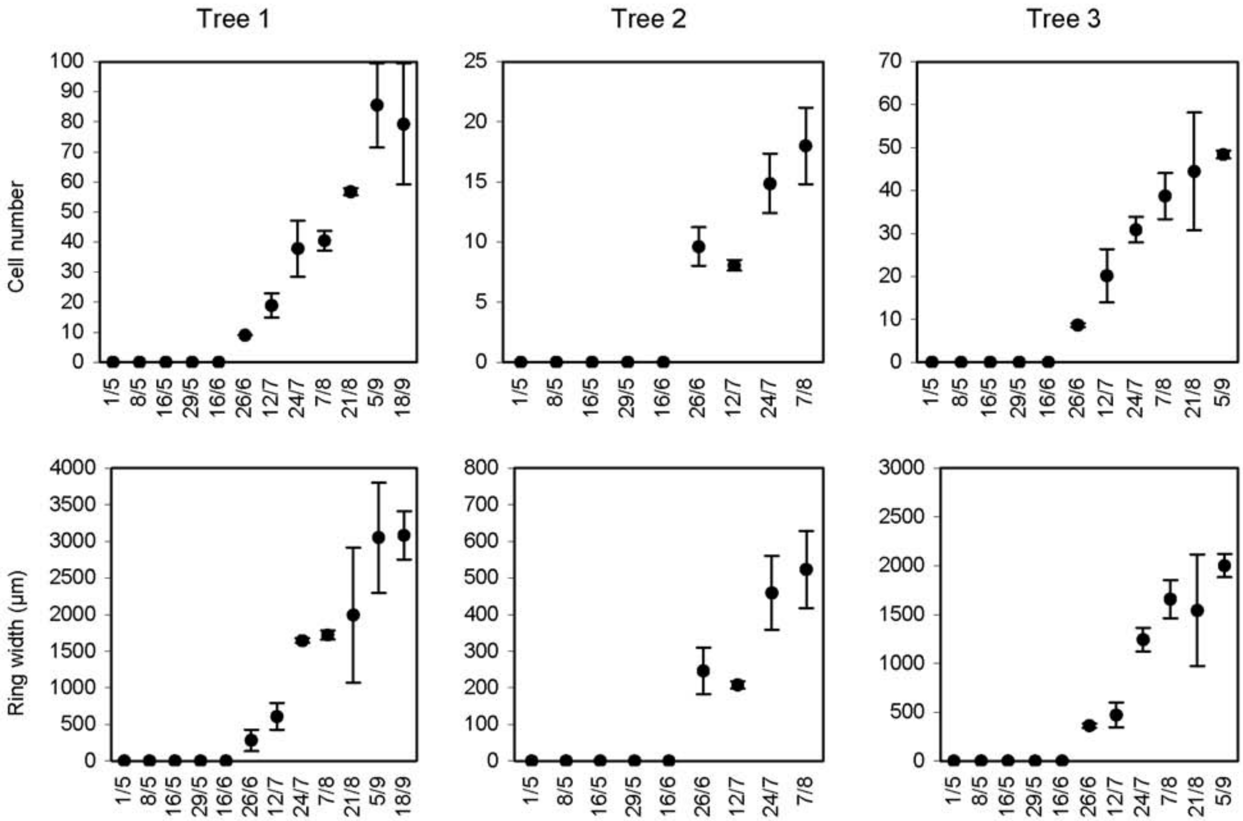

Fig. 4. Number of cells containing the secondary wall and ring width observed in Trees 1, 2 and 3 on all pinning dates. Dots and bars represent respectively average values and standard deviations among the samples collected from the two sides of the trees (north and south sides of Trees 1 and 3; east and west sides of Tree 2).

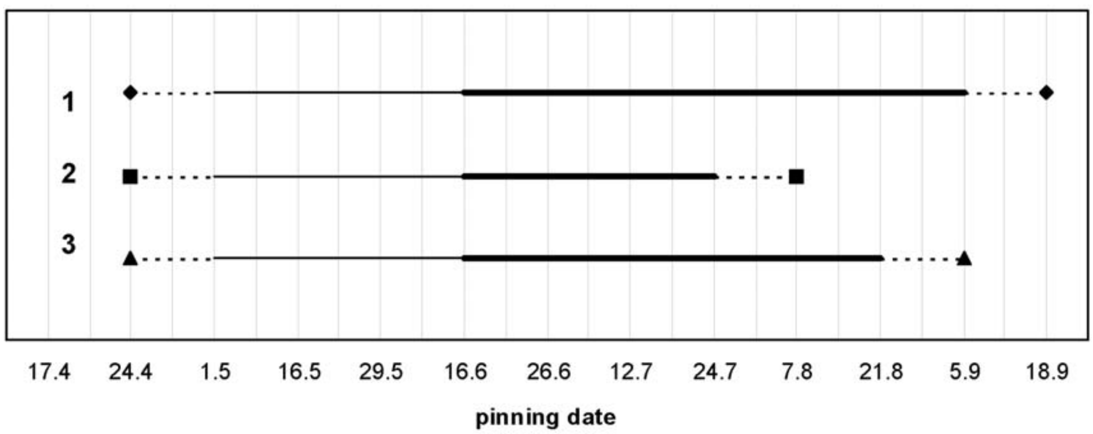

Fig. 5. Duration of cambial activity during 2002. At the beginning and end of cambial activity there is a period of uncertainty due to the pinning interval (– – –). Thin line indicates the period in which only the cambial reaction to pinning was discernible; thick line indicates the period in which wall-thickened cells were discernible.

indentation and the surrounding normal wood, where radial rows of tracheids were considerably disordered and irregular in shape and size.

The typical curvature that annual rings show, corresponding to the indentations, is not due to differences in the timing of cell division and maturation, at least when the indentation is developing after the first year in which it appears (origin). The year of origin of a new anomaly is the most important for understanding the causes of this phenomenon (Paoletti, 2002). The malfunctioning of the cambium that is believed to generate indentations probably starts with qualitative and quantitative alterations, but in the following years the same timing of cell formation and the same growth rate are re-established throughout the whole circumference. The anomalies of cell shape and morphology are maintained until unknown events restore the normal functioning of the cambium and the indentation cannot be detected in the new rings. Then we can state that the cambium response to exogenous or endogenous factors is the same, both inside and outside the indentations.

The greatest difficulty in comparing data on wood formation is the high variation of growth rhythm data in the literature. The main causes of this include species characteristics (different species can have dissimilar behavior) and site characteristics (geographical location and climatic factors). The methodologies used to study cambial activity also vary, and sometimes the results are not comparable (Kuroda and Kiyono, 1997; Bäucker et al., 1998; Mäkinen et al., 2003); terminology and the criteria used to establish cambium reactivation are often ambiguous and may cause misinterpretation of results (Frankenstein et al., 2005).

Nevertheless, the observations regarding the onset of cambium activity reported here are in general agreement with the findings of earlier work on *Picea abies*. Rossi et al. (2006b) investigated spruce growth at the Alpine timberline (above 2,000 m a.s.l.) and found that the onset of the growing season took place in the second half of May. At a lower altitude (1,020 m a.s.l.) the first enlarging cells was observed in the first week of May (Tedoldi, 2003/2004). In a study of spruce ring formation in the Czech Republic, Horacek et al. (1999) observed the presence of new enlarging tracheids from the end of April.

Amongst the many studies carried out in various species and in different countries, temperature appears to be the most important climatic factor at the beginning of the growing season (Antonova and Stasova, 1993, 1997; Horacek et al., 1999; Kirdyanov et al., 2003; Mäkinen et al., 2003; Schmitt et al., 2004; Gričar et al., 2006; Rossi and Deslauriers, 2007; Rossi et al., 2007; Gričar et al., 2007b). In Norway spruce, Horacek et al. (1999) found the critical mean daily temperature for onset of growth at 5 ± 1°C. In agreement with Horacek's results, the onset of cambial activity in the trees of the Paneveggio forest was noted during the week of April 24 to May 1, when the diurnal temperature reached 5°C (Fig. 1).

After the onset of cambial activity, a gap of about 6 weeks was noted between the observation of the first cambial reaction (May 1) and the discernible presence of intact (and already wall-thickened) new cells (June 16–26). It should be remembered that inserting a pin may cause deformation or destruction of enlarged cells characterized by a thin wall. On the other hand, although cells in the phase of cell wall thickening may be distorted or separated from each other along the pinning canal, they are usually visible in sections (Wolter, 1968; Yoshimura et al., 1981; Kuroda and Shimaji, 1984a; Schmitt et al., 2000).

As regards the duration of cell development phases, in timberline alpine spruce at the beginning of the growing season Rossi et al. (2006b) found the duration of the enlargement phase to be 14–25 days, and for the maturation phase it was 5–15 days. For *Picea abies*, Horacek et al. (1999) reported a longer period for the entire maturation process, from a minimum of 36 to a maximum of 79 days: 9–45 days for enlargement and 13–60 days for wall thickening. In conifers of Central Europe, the enlargement phase varies from 2 to 4 weeks; the time cells spend in the wall thickening phase averages 4 to 5 weeks, with a maximum of 8 weeks (Wodzicki, 1971, in Horacek et al., 1999). Therefore the 6-week gap noted here seems realistic, and can be explained by cell development processes: new cells were developing and were probably destroyed when the pin was inserted. Of course this is only a probable explanation, requiring additional observations and confirmation.

A number of authors have described a sigmoid trend of wood formation dynamics (Rossi et al., 2003; Smith et al., 2000; Schmitt et al., 2004; Mäkinen et al., 2003); in any case, growth rate does sometimes show a slight decline in the middle of the season (Wilson and Howard, 1968). We observed a sigmoid trend for ring width development of spruce in the Paneveggio Forest, with a slight pause in August. Looking at the graphs of cell number and ring width (Fig. 4), the patterns of cell division seem similar. Variations in ring width during the growing period can be ascribed to cell number and cell dimensions.

Cell dimensions are closely connected to the enlargement process, which is the process most influenced by climatic factors (Horacek et al., 1999; Vaganov, 1994). Dendroclimatological investigations of Alpine spruce showed a positive correlation between April-May temperature and ring width (Brandini et al., 1994; Brunetti et al., 1996). According to our findings, this relationship can be partially explained by the timing of ring formation: in May the cells seem to be mostly in the enlargement phase, highly influenced by external factors; this is also the most important period for determining the final width of at least the earlywood. High temperatures in May can have a positive effect on cell enlargement. This suggestion requires further study and specific analysis.

We observed some differences in the behavior of the examined trees. Their cambial activity lasted from the end of April to the first half of September, except for Tree 2, which ended wood production at the beginning of August, about a month before the other two plants. This tree showed some symptoms of decline, such as reduced wood formation, needle loss, and small and stunted foliage. In previous studies on fir in Slovenia, Schmitt et al. (2003) concluded that healthy trees ended wood formation and cell differentiation later than diseased firs. The unhealthy state of Tree 2 could explain its extremely narrow rings and the early end of its cambial activity. In a recent study of silver fir, Gričar et al. (2005) reported a delay of the end of cambium activity in the more productive trees, which produced more cells and therefore wider rings. Supporting that finding, Tree 1 in our study formed the most cells and the widest ring, and it ended cambial activity later then the others (Fig. 5), while Tree 2, which had the lowest radial growth, was the first plant to stop cambial activity.

CONCLUSION

The present investigation originated from a desire to increase our knowledge of the special trees growing in Paneveggio. Different aspects of the Paneveggio Forest and its trees have been studied for some time, and the singular "anomaly" of indented rings has drawn the interest of many researchers. The origin of the indentations seems related to cambial dynamics. Many aspects of the problem are still unexplained, but it is now clear that the timing of the development of an indentation, measured in terms of the number of cells formed and the ring width at the time of each pinning, is similar to that of normal wood at the same height on the stem. Also, this more detailed knowledge of the growing period and cambial activity of Paneveggio spruce may be of use in further studies.

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