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Study on the wood anatomy, annual wood increment and intra-annual growth dynamics of *Podocarpus oleifolius* var. *macrostachyus* from Costa Rica

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Summary

Tropical countries in the future will have an increasing demand for softwoods which favours mixed plantations possibly with minor portions of native conifer species. In this context numerous tropical species of the Podocarpaceae can be of ecological and economical interest. In Costa Rica the native species *Podocarpus oleifolius* var. *macrostachyus* (Parl.) Buchholz & Gray could be attractive for the establishment of manmade forests. However, profound knowledge on growth characteristics and wood properties is missing. In particular, information on the annual wood increment and intra-annual growth dynamics under natural site conditions at higher altitudes where *P. oleifolius* var. *macrostachyus* competes with hardwood species is not available and therefore the objective of this study. At the Cordillera de Talamanca (approx. 2,700 m a.s.l.), Costa Rica, an old-growth stand was chosen from which in total 5 trees (40 to 80 cm diameter at DBH) were sampled by taking stem sections and discs (2 trees)or increment cores (3 trees). During the period from October 1998 to December 2000, two trees of the site were pinned monthly for exact determination of the annual wood increment and the intra-annual growth dynamics in relationship to climate. The results of one of these pinned trees are demonstrated. It turned out that at high altitude the annual wood increment of old growth trees amounts to 1-2 mm (diameter) only. The tracheids show a rather constant cell wall thickness (2.5-4.5 µm) throughout the year, but a very variable radial cell diameter from 29 to 61 µm. The exact age of the tree cannot be determined anatomically, as there are no distinct tree-ring boundaries, but only very moderately developed terminal bands of flattened tracheids which do not circle the entire circumference of the stem. The monthly pin-labelling documents that during the dry season from about January until March in 1999 and 2000, virtually no cells were formed. However, with the beginning of the rainy season, about 59 % of the wood increment resulted from the months April to June. This increment rate already decreased from July to September to 32 %. Due to a distinct decrease in precipitation towards the end of the year, only 9 % of the wood increment were formed in the last quarter of the year, mainly consisting of the hardly visible terminal and flattened tracheids. The wood of this species is of very homogeneous structure and certainly attractive for high-quality wood production.

Introduction

In the tropical country Costa Rica the demand for commercially important softwoods will increase in the future, whereas in former decades the limited portion of native conifer species was considerably exploited already (ARIAS and DOHRENBUSCH, 2001). In particular, species of the Podocarpaceae family would be of interest for their cultivation, for which they are also estimated in other tropical countries (e.g. GÜNTER et al., 2004). However, preliminary results indicate that natural regeneration does not guarantee fertilized female cones due to increased distance between the individual trees. The establishment of mixed plantations enables the cultivation of minor portions of the native species *Podocarpus oleifolius* var. *macrostachyus* (Parl.) Buchholz & Gray, which reaches a height of up to 30 m and a diameter of more than 1 m in old-growth sites (BUCHHOLZ and GRAY, 1948; LAUBENFELS, 1990) and with good wood properties (MALAVASSI, 1995; BAUCH et al., 2006). Unfortunately, there is hardly any documentation (BLASER and CAMACHO, 1991; OROZCO, 1991) on the annual wood increment for this native species in Costa Rica and in particular no data exist on the intra-annual growth dynamics in relation to exogenous influences such as precipitation and day/night temperature gradients at high altitudes.
In the subsequent study an old-growth site of *Podocarpus oleifolius* var. *macrostachyus* of the Cordillera de Talamanca was chosen for a preliminary investigation on wood characteristics, annual wood increment and intra-annual growth dynamics. This qualitative and quantitative wood characterization will further allow us to evaluate the potential of this species for mixed plantations at high altitudes.

Material and methods

Site and tree selection of a natural forest

In order to obtain information on wood structure and growth characteristics of the native species *Podocarpus oleifolius* var. *macrostachyus* (Parl.) Buchholz & Gray in a natural forest (Fig. 1a) at high altitude stem sections, discs and increment cores of in total 5 old growth trees were selected at the Cordillera de Talamanca, approx. 2,700 m a.s.l. (9°33´ north, 83°40´ west), Costa Rica. In former years, this species was studied taxonomically (e.g. LAUBENFELS, 1990; HAMMEL et al., 2003) and finally determined as a var. of *Podocarpus oleifolius* and thus no longer as a separate species (Fig. 1b).
Podocarpus oleifolius var. *macrostachyus* (Parl.) Buchholz & Gray only contributes a few per cent portion (~7%, QUIROS unpubl.) to the mixed hardwood species (e.g. predominantly *Quercus costaricencis*, *Quercus copeyensis*, *Drimys winteri*, *Weinmannia pinnata*), attainable heights of about 30 m and a diameter of more than 1 m. In October 1997 discs of one tree (DBH approx. 60 cm) were collected for wood structural studies. At October 16, 1998 we started with the cambial analysis by 26 monthly executed pin-markers (December 1999 left out) ending in December 2000 on two trees of the same site (DBH approx. 40 cm). Due to a complete prohibition for tree felling at that site only one tree of both could be felled on April 26, 2001 and the pinned stem sections collected (1m - 4m tree height).
For additional microscopic observations and confirmations of the anatomical results, six increment cores from three other trees at the same site were collected in July 2003.
The annual precipitation at that site amounts to about 2,500 mm, exhibiting high variation during the rainy season from April to about November/December and the dry months from January to March (BLASER, 1987; ANONYMUS, 2001, Fig. 2, Tab. 1). These intra-annual dynamics of the water supply with distinct dry months leads to a drastical water deficit in the soil (comp. BLASER, 1987). The average monthly temperatures are fairly constant ranging between 10.0 and 11.8° C (Fig. 2), however, the day/night temperature gradient is

Fig. 1: Experimental site. a. Old growth trees of *Podocarpus oleifolius* var. *macrostachyus* (Parl.) Buchholz & Gray. b. Leaves and female cones of an investigated tree.

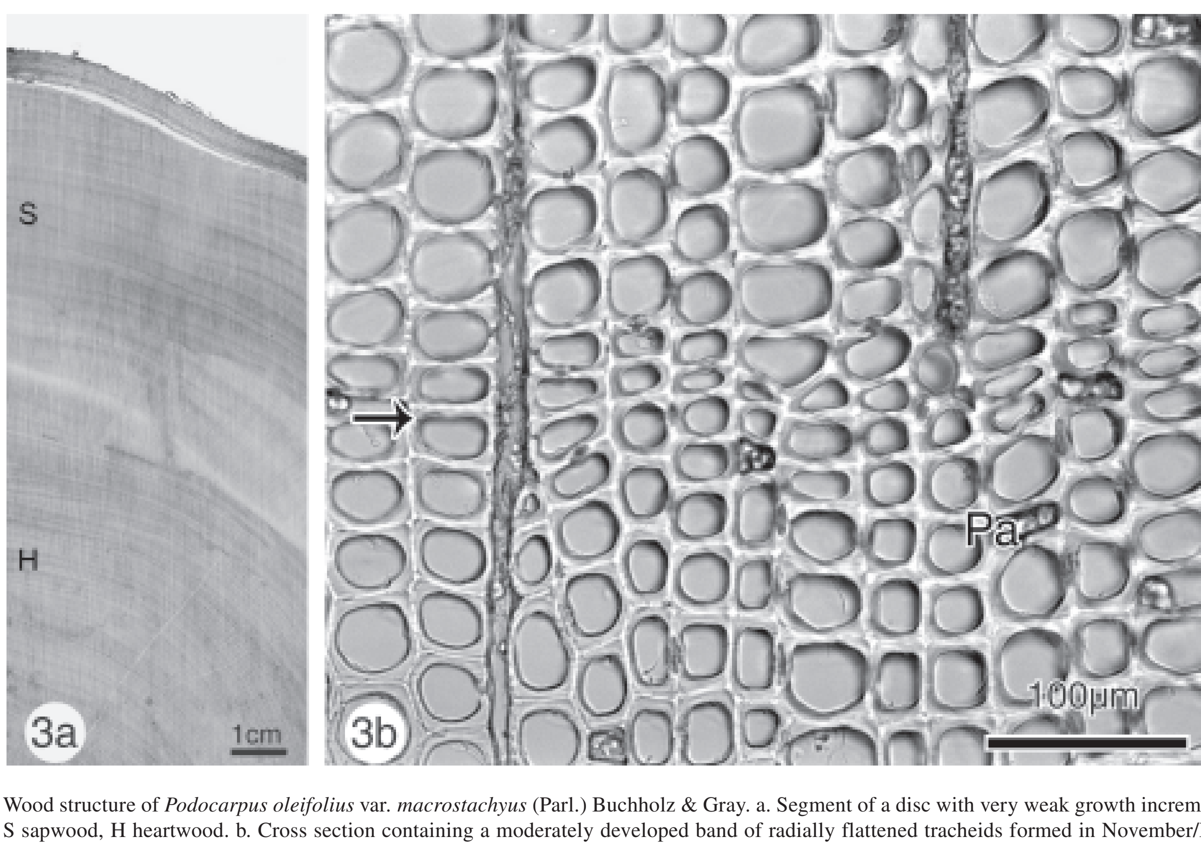

Fig. 3: Wood structure of *Podocarpus oleifolius* var. *macrostachyus* (Parl.) Buchholz & Gray. a. Segment of a disc with very weak growth increment zones. S sapwood, H heartwood. b. Cross section containing a moderately developed band of radially flattened tracheids formed in November/December (→ border of an increment zone). All tracheids exhibit more or less constant wall thickness. Diffuse distributed axial parenchyma (Pa).

considerable and moreover, also varies significantly from day to day with measured minima of almost 0°C during the night (BLASER, 1987). The duration of daily sunshine differs remarkably from 7.5 hours (monthly average) in February to 3.0 hours in September (SEGURA and VENEGAS, 1999). The soil consists of a moderately fertile humus layer with a deficit in nitrogen and phosphorus (GRUBB, 1976). According to NUHN (1978) this soil type is classified as Litosole.

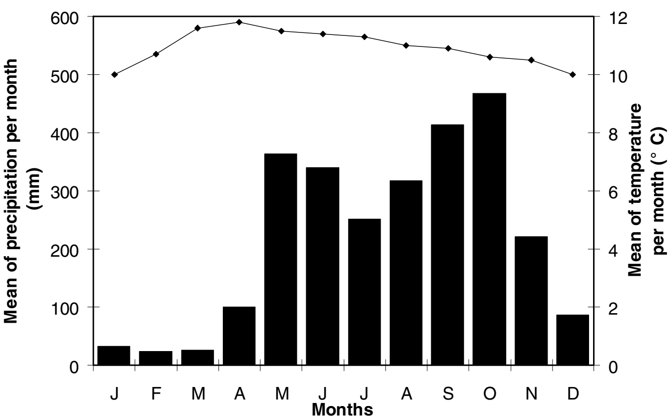

Fig. 2: Mean of precipitation and air temperature per month for the neighbourhood of the selected forest site at the Cordillera de Talamanca for the years 1942-1985 (BLASER, 1987).

Tab. 1: Mean of precipitation [mm] per month available from the neighbourhood of the selected forest site at the Cordillera de Talamanca for the years 1999 and 2000 (ANONYMUS, 2001).

Month	1999	2000
January	9.4	26.7
February	129.8	25.6
March	25.0	14.7
April	175.8	50.6
May	450.2	368.1
June	437.4	395.4
July	94.8	186.3
August	448.8	110.8
September	377.7	572.6
October	529.5	423.8
November	264.9	162.4
December	207.1	46.0

Microscopical observations of the structural characteristics of the wood

Cross-sectioned slides from the sapwood and heartwood of the discs and cores of the five selected trees, treated with safranin-astrablue, were used to determine variation in percentage of tracheids and longitudinal and ray parenchyma. The individual tracheid characteristics were determined histometrically such as radial tracheid diameter, cell wall thickness and tracheid length on sections and on macerated tissue by a digitized image analysis system (analySIS®, Olympus Hamburg), adjusted on a AX 70 microscope.

Determination of annual growth increment and intra-annual growth dynamics

Referring to former pinning experiences (KURODA and KIYONO, 1997; BAUCH and DÜNISCH, 2000) small pieces of razor blades were put into the cambial tissue of the selected trees monthly to verify the start of the wound response exactly to the date of treatment even after more than two years. The consistent monthly treatment allowed to determine the intra-annual growth dynamics triggered at the cambial zone. Despite of the low annual increment, the wound response caused by the pin-marks immediately led to an abrupt and drastical reduction of tracheid length and tracheid cross area as well as to an accumulation of longitudinal parenchyma at the wound spot. The structurally recognizable increment zones, the intra-annual growth dynamics and the variation of the radial cell diameter of the tracheids were also recorded with the digitized image analysis system.

Results

Anatomical structure of the woody tissue

The structure of wood with special reference to growth increment zones (Fig. 3a) was studied on cross, radial and tangential wood sections from sapwood and heartwood from discs and cores of the five selected trees. In dry condition the brownish wood colour does not remarkably differ between sapwood and heartwood. It is striking that only weakly formed bands of radially flattened tracheids indicate wood increment zones (Fig. 3b). However, they are not continuously formed circularly within the stem which means that they do not automatically indicate the exact age of the tree. Due to relatively equal cell wall thickness (2.5-4.5 µm) of the tracheids (Fig. 3b) across the woody tissue including thin walled longitudinal and ray parenchyma, the wood reveals a homogeneous appearance (comp. Tab. 2). The tracheid length ranges from 3.1 to 4.9 mm. However, the radial diameters of the tracheids vary considerably from cell to cell with a maximum of 61 µm and a minimum of 29 µm (unpinned sapwood), measured on macerated tracheids and confirmed by means of cross sections. But the flattened tracheids, which occur at the border of an annual increment show radial cell diameters of less than 20 µm (comp. Fig. 3b). The anatomical and histometrical results do not allow any precise conclusion with reference to annual wood increment and intra-annual growth dynamics. Consequently, pinning studies were chosen for a profound determination of wood formation.

Annual wood increment

By means of 26 monthly executed pins from October 16, 1998 to December 18, 2000, it could be proven that radially flattened tracheids – often only a few tangentially oriented series – are formed during

Tab. 2: Histometrical results for the adult wood of *Podocarpus oleifolius* var. *macrostachyus*

Tracheids proportion [%]	Axial parenchyma proportion [%]	Rays proportion [%]	Tracheid	
			length [mm]	wall thickness tang [µm]
91.8 - 92.9 - 94.2	1.7 - 2.2 - 2.8	4.1 - 4.9 - 5.5	3.1 - 4.0 - 4.9	2.5 - 4.5 (→6.5)

November and December (Figs. 3b, 4). This is the period when the monthly amount of precipitation usually decreases. Fig. 4 illustrates that the cells 6 and 7 were formed in November - December 2000, and the cells 28 and 29 were identified as being formed in November - December 1999. For the years 1999 and 2000 from January to March no cells were formed. The annual growth rate can be determined as 0.86 mm for both years. This means an average of only about 1.7 mm increase in wood diameter (DBH) per year based on nine months cambial cell formation.

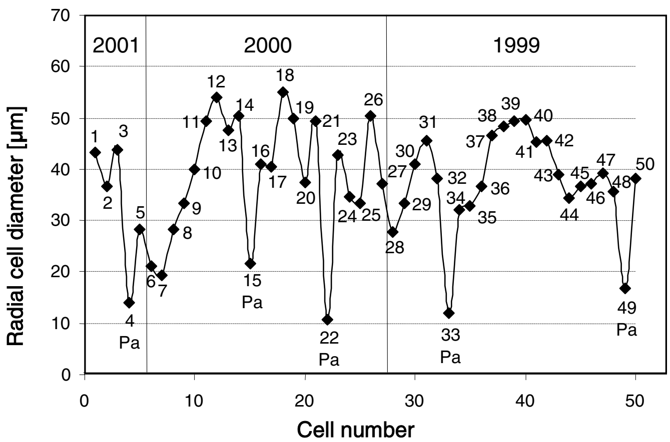

Fig. 4: Variation of radial cell diameter of an individual continuous series of radially oriented cells from April 26, 2001 (felling date) to April 1999 (Pa axial parenchyma cell).

Intra-annual growth dynamics

In addition to the determination of the annual wood increment, the study of the intra-annual growth dynamics might indicate to which extent environmental parameters such as monthly amount of precipitation, average temperature, sharp gradients of day and night temperature and hours of sunshine will influence the quality and quantity of wood formation. The cross sections with the 26 pin-marks in total give precise information on the number and radial diameter of the monthly formed tracheids and longitudinal parenchyma cells as shown in the selected example (Fig. 4). The measurements for the years 1999 and 2000 were averaged and the data grouped in 3 months (Fig. 5). It could be demonstrated that during January to March the cambium apparently does not produce any cells. This is in accordance with the dry months with 4.2 % mm precipitation refered to the amount of the whole year (Fig. 5). The cambial activity begins at the period with a high amount of precipitation starting in April (April - June 33.9 % mm). The corresponding increment from April to June shows the highest values with 58.4 % of the radial increment of the entire year. In July and August, the amount of precipitation (Tab. 1) is retrogressive (in several years even significantly lower, comp. Fig. 2), but increases again in September and October (Tab. 1). The individual meteorological measurements for these months in 1999 and 2000 (ANONYMUS, 2001) were in accordance with the average values of 1942-1985 (BLASER, 1987). The wood increment from July to September equals 32.4 % of the entire year. Apparently from July onwards also other parameters such as limited duration of sunshine (SEGURA and VENEGAS, 1999) may contribute to a retardant cambial cell division. From October to December, the amount of precipitation (29.5 %) significantly decreases (Tab. 1). The few cell series formed from October to December correspond to an increment rate of only 9.2 % of the entire annual increment (Fig. 5), which is ecophysiologically an interesting fact. Moreover, these tracheids do not differ in cell wall thickness from others, but some show reduced radial cell diameters (comp. Fig. 3b). Under temperate climate this special „latewood"-phenomenon is visible in species of *Juniperus* and *Pinus strobus* which obviously is strongly genetically controlled (LARSON, 1995).

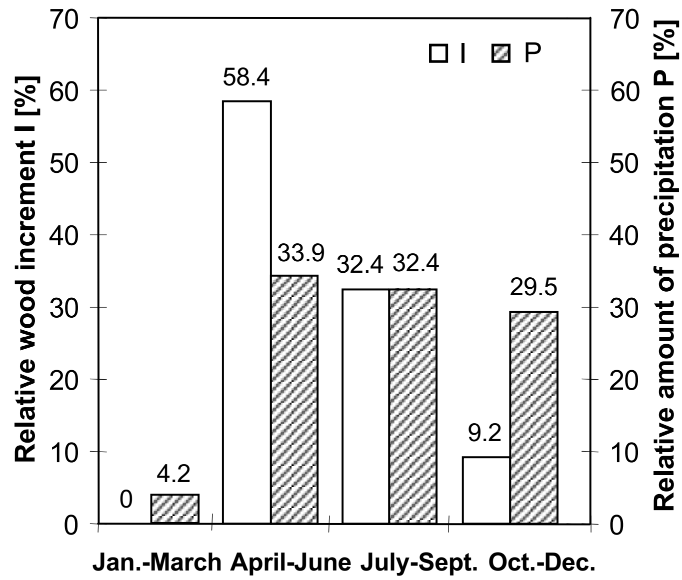

Fig. 5: Intra-annual growth dynamics, monthly determined by pinning examplified for one tree. Wood increment (I) illustrated as relative average values every three months for the years 1999 and 2000 in comparison to the distribution of precipation (P).

Discussion

This preliminary study of the wood anatomical characteristics, the annual wood increment and the intra-annual growth dynamics of *Podocarpus oleifolius* var. *macrostachyus* offers hints on wood characteristics and growth potential at high altitude conditions.

The investigated trees show only faint growth ring boundaries with mostly incomplete series of radially flattened tracheids, which do not allow to determine the exact age of the tree. This finding corresponds to the growth characteristics of the long-lived *Podocarpus neriifolius* and other tropical Asian species of this genus (BUCKLEY et al., 1995) which also do not permit a dendrochronological dating. However, other species of the genus *Podocarpus* from outside of the tropics develop distinct annual growth boundaries, such as *Podocarpus nubigens* in Chilean Patagonia (SWED and INOUE, 1987).

The histometrical data reveal that *Podocarpus oleifolius* var. *macrostachyus* is superior in qualitative aspects (such as fiber characteristics)to the wood of the commercially important species *Podocarpus salignus* from Chile and Argentina (BAUCH et al., 2006).

The pinning experiments allowed investigations of the annual growth increment and the intra-annual growth dynamics triggered in the cambium as documented in detail by FRITTS (1976) and LARSON (1995) for trees grown under temperate climate. For tropical softwood species, hardly any data for annual wood increment and intra-annual growth dynamics are available (JACOBY, 1989), whereas for tropical hardwoods numerous case studies were published in recent years (e.g. BREITSPRECHER and BETHEL, 1990; WORBES, 1999; WORBES and JUNK, 1999; DÜNISCH et al., 2003).

The monthly and annually determined growth rates of a dominant tree of *Podocarpus oleifolius* var. *macrostachyus* exhibit full accordance throughout the years 1999 and 2000. The total annual increase in wood diameter is about 1.7 mm, which corresponds to some individual dendrometer measurements of the same site with about 1.9 mm total increase in diameter (DBH) per year (QUIROS, unpubl.). Comparative studies on *P. oleifolius* in montane forests (2,000 m a.s.l.) in Ecuador reveal an even lower annual increment (HOMEIER, 2004). Individual dendrometer measurements in a secondary managed forest of Costa Rica show that under climatically more moderate conditions this softwood species can compete with commercially important native hardwoods reaching an increase of up to about 4-5 mm diameter increase per year (QUIROS, unpubl.). Nevertheless, it should be also evaluated in how far this conifer species can cope sociologically with hardwoods under mixed plantation condition. There are studies for the species *Podocarpus nubigena* as a shade-tolerant species (LUSK, 1996; GUTIERREZ et al., 2004). For *Podocarpus oleifolius* var. *macrostachyus* corresponding experiences do not exist.

The monthly determined growth rates reveal some relationship to exogenous influences at the experimental site. The wood formation is triggered by the begin of the rainy season in April and it ends in December with the onset of dry season.

In contrast to the genetically controlled relatively uniform cell wall thickness of the tracheids (comp. LARSON, 1995) throughout the entire year, the considerable variability of the lumen area from tracheid to tracheid depends obviously on short term influences, which have an direct impact on the primary cell wall phase. With adequate water supply this period of primary cell wall formation with radial tracheid enlargement lasts for *Picea abies* only 7-14 hours and is mainly induced during night time (DÜNISCH and BAUCH, 1994). During the night the water content in the sapwood tracheids can be increased via the fine roots and supply subsequently the cambium. Ongoing experiments under controlled conditions with temperature variation also indicate an influence of the existing air temperature during night time (DÜNISCH unpubl.). At the Cordillera de Talamanca at about 2,700 m a.s.l., the annual growth increment and the intra-annual growth dynamics will primarily depend on the distribution of the annual precipitation, but also the variation of day/night temperature has to be considered.

Conclusion

The preliminary investigation on wood anatomical characteristics of *Podocarpus oleifolius* var. *macrostachyus* (Parl.) Buchholz & Gray demonstrates a tropical conifer with considerable intra-annual dynamics in wood production, obviously controlled mainly by climatic conditions.

The data of our study suggest that high altitudes are most likely not suitable for plantations due to the limited annual wood increment of the trees. However, with regard to the ecological amplitude and the potential for sociological competition this species can be recommended for regeneration concepts in mountainous humid regions of more moderate altitude levels (e.g. RÄBER, 1991; QUIROS unpubl.). This conclusion is underlined by some investigations of the wood properties (comp. MALAVASSI, 1995; BAUCH et al., 2006). Without doubt, this wood species can be recommended for its high-quality homogeneous raw material with reference to lumber with decorative value for furniture.

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