INTRODUCTION

Comparative and quantitative wood anatomy combined with dendrochronology may provide information regarding wood anatomy related to species, provenance, as well as the time and conditions in which the wood was formed.

Research into wood anatomy allows the analysis of anatomical traits, which can reflect important environmental signals (Verheyden et al., 2004; García-González & Fonti, 2006; Campelo et al., 2010). Wood quality also depends on wood anatomy, which varies between and within species, individual trees and even growth layers.

Dendrochronology, as the study of tree rings (growth layers), is based on cross-dating, which helps to assign every tree ring to the calendar year when it was formed. This principle can be applied in trees from temperate environments, where the tree rings are generally annual. They usually contain early- and late-wood, and are demarcated by tree-ring boundaries.
However, in Mediterranean and tropical environments it is often challenging to define tree rings and the boundaries between them, as their formation is not necessarily synchronised with calendar years (Cherubini et al., 2003; De Luis et al., 2011; Balzano et al., 2018, 2019a, b). Such growth layers typically contain numerous anomalies associated with intra-annual density fluctuations (IADFs) (Campelo et al., 2007; De Micco et al., 2016a) sometimes called false rings (e.g. Kaennel & Schweingruber, 1995).

To help with the identification of tree rings we often apply quantitative wood anatomy (QWA), which is based on the measurement of anatomical traits (for instance shape, dimensions and frequency of xylem elements, thickness of cell walls etc.) in relation to time (position in the growth layer). This is used to characterise the relationships between plant growth and various environmental factors.

Studying anatomical features requires time-consuming sample preparation for microscopy, i.e. the cutting of thin microscopic slides. Therefore, there is a search for methodologies which enable observation and analyses of microscopic structures without special specimen preparation (e.g., Fioravanti et al., 2016, 2017). One such method could be confocal microscopy, which has already been successfully applied in material and surface science, although to date there are few studies in the field of life sciences and wood anatomy or dendrochronology (e.g., Haag et al., 2018).

The objective of the present study is thus to evaluate the possibilities of applying a Confocal Laser Scanning Microscope (CLSM) Olympus LEXT OLS5000 for different case studies in dendrochronology and quantitative wood anatomy, and to evaluate its suitability in replacing classical methods based on the time-consuming preparation of thin sections and light microscopy.

2 MATERIALS AND METHODS

2.1 MATERIAL

We studied wood structure on cores (5 mm in diameter) collected from trees with an increment borer. The cores were smoothed by sanding (with sandpaper grits from 80 to 280) to observe the cross-sections of the wood to identify the growth layers and observe their wood-anatomical characteristics.

The investigated species were:
1) temperate European beech (*Fagus sylvatica* L.) from a site in Croatia ca. 45.42°, Longitude: 16.28°, Altitude: ca. 100 m) (Lukić, 2018),
2) Mediterranean Aleppo pine (*Pinus halepensis* Mill.) from Alicante in southern Spain (Latitude: 38.40°, Longitude: -0.44°, Altitude: ca. 70 m),
3) octe pine (*Pinus oocarpa* Schiede ex Schlt-l.) from Siguatepeque in Honduras (Latitude: 14.60°, Longitude: -87.83°, Altitude: ca. 1100 m), from high elevation in the tropical zone, collected by Jean Pierre Veillon in 1970 (Lu-na-Lugo, & Marciano-Berti, 2011),
4) Tropical true mahogany (*Swietenia macrophylla* King) from Ticoporo in Venezuela (Latitude 8.15°, Longitude -70.84°, Altitude: ca. 200 m) collected by Jean Pierre Veillon in 1969 and
5) cedrela (*Cedrela odorata* L.) from Turrialba in Costa Rica (Latitude 9.90°, Longitude -83.69°, Altitude ca. 700 m) collected by Jean Pierre Veillon in 1966.

2.3 CONFOCAL LASER SCANNING MICROSCOPY

The objects were observed with a Confocal Laser Scanning Microscope (CLSM) Olympus LEXT OLS5000 (Olympus Corporation Tokyo 163-0914, Japan) (Figure 1) with the following objectives: MPLFLN5x (numerical aperture 0.15, working distance 20 mm), MPLFLN10xLEXT (numerical aperture 0.3, working distance 10.4 mm), and LM-PFLFN20xLEXT (numerical aperture 0.45, working distance 6.5mm). The microscope is equipped with a 405 nm violet laser, which enables the best lateral resolution in range (0.12 μm), and allows the microscope to capture fine patterns and defects that conventional optical microscopes, white-light interferometers, or red laser-based microscopes are unable to detect.

First, we used optical systems for colour observation. The system acquired microscope colour images by illuminating the sample with the white light-emitting diode (LED) light source and imaging the reflected light with the complementary metal-oxide-semiconductor (CMOS) image sensor.
The objects were placed on the stage. By moving the stage, we used the system to create a panoramic macro map based on stitching images on the moving trace in real-time for an overview of the sample. Colour digital images obtained using the stitching function covered the entire length of the cores in order to identify the growth layers and perform tree-ring width measurements for dendrochronology. As the focal depth was relatively deep, we could use the colour images to observe some details or define the positions for detailed observations using the confocal laser scan.

High resolution laser confocal images were acquired at different focus positions to identify the minute structures and measure anatomical parameters. All the measurements were performed with the OLS5000 image analysis software.

3 RESULTS AND DISCUSSION

3.1 DENDROCHRONOLOGY – GROWTH LAYERS AND ANOMALIES IN WOOD

The presented examples show the potential of use of LEXT OLS5000 3D in different wood species, *Fagus sylvatica*, *Pinus halepensis*, *Pinus oocarpa*, *Swietenia macrophylla* and *Cedrela odorata*, with different wood anatomies and structures of the growth layers addressed for different research purposes.

The stitched images of polished increment cores based on combining the live observations (Figure 2) with the analysis of an acquired image enabled us to study the growth layers and growth ring boundaries at different magnifications.
At higher magnifications and resolutions, we could observe structural variations in the wood and apply image analysis. The detailed results for different wood species are shown in the next chapters.

### 3.2 TREE-RING ANOMALIES IN EUROPEAN BEECH

**3.2 ANOMALIJE BRANIK V LESU BUKVE**

European beech (*Fagus sylvatica*), as a typical temperate species, normally contains clear growth rings formed due to interruption of cambium activity during the cold period of the year (e.g., Prislan et al., 2013a, b). The investigated cores of *Fagus sylvatica* from a site near Petrinja in Croatia contained tree rings with numerous anomalies. This caused difficulties to correctly perform tree-ring width measurement and cross-dating (Lukić, personal communication). In 2013 numerous beech trees suffered an attack of gipsy moth (*Lymantria dispar*), which typically attacks oaks. In 2013 it caused also defoliation of beech (Lukić, 2018), and consequently an extremely narrow tree ring was formed (Figure 3). On the pictures observed under the stereomicroscope and on those obtained by flat-bed scanner, the tools usually applied in dendrochronology, the 2013 ring appeared pale and sometimes could not be recognised (Figure 3a). At higher magnification and resolution of CLSM, the tree ring and its structure could be identified. The 2013 ring showed early- and latewood and clear growth ring boundary (Figure 3d). Another extremely narrow tree ring was formed in 1966 (Figure 3c). It contains earlywood and narrow latewood and a clear growth ring boundary, which could indicate that cambial production was possibly interrupted at the end of June (Prislan et al., 2013a). The same species also had some very wide tree rings with intra-annual density fluctuations, like the 1984 tree ring, which at lower magnifications were erroneously interpreted as tree rings (Figure 3a, b), whereas higher magnification showed no growth ring boundary (Figure 3e).

The questions raised can as a rule be solved by dendrochronological cross-dating, while the application of CLSM enables better interpretation of the anomaly.

**Figure 3.** European beech (*Fagus sylvatica*): (a) a core scanned with a flat-bed scanner at 1200 dpi resolution with potentially very narrow rings (arrows), and (b) the same core after tree-ring width measurement in CooRecorder and with cross-dating; (c, d, e) detailed views of individual rings captured by CLSM with tree ring 1966 at two magnifications (c), tree ring 2013 (d) and intra-annual density fluctuation in the 1984 ring (e). **Slika 3. Bukev (Fagus sylvatica):** (a) izvrtek posnet s skenerjem z ločljivostjo 1200 dpi, z označenimi potencialno zelo ozkimi branikami (puščice) in (b) isti izvrtek po merjenju širin branik s pomočjo programa CooRecorder in datiranju, (c, d, e) podrobna zgradba posameznih branik posnetih s CLSM: branik 1966 pri dveh povečavah (c), branik 2013 (d) in gostotna variacija v braniki 1984 (e).  

Balzano, A., Novak, K., Humar, M., & Čufar, K.: Uporaba konfokalne laserske vrstične mikroskopije v dendrokronologiji
3.3 GROWTH RING ANOMALIES IN ALEPPO PINE

Growth layers of Aleppo pine (Pinus halepensis) from Alicante in south-eastern Spain are often not annual and often contain numerous anomalies with intra-annual density fluctuations (IADFs) (Figure 4). They are characterised by latewood-like cells in earlywood (E-IADF), and earlywood like cells in different portions of latewood (L-IADF) (Figure 4). The species often have unclear growth ring boundaries (Figure 4b) which are a consequence of uninterrupted cambial production in winter (De Luis et al., 2007, 2011; De Micco et al., 2016a; Novak et al., 2016a; Balzano et al., 2018, 2019a, b), and lack of cambial dormancy in winter (Prislan et al., 2016). The species can also contain dark rings (Figure 4b), i.e. rings which contain only latewood (Novak et al., 2016a). Furthermore, the species contains numerous missing rings (Novak et al., 2011, 2016b). All these anomalies can only be detected with dendrochronological cross-dating.

IADFs are usually first defined visually; however, their characteristics can be more precisely defined only by measuring the dimensions of tracheids or tracheid lumina, and the cell walls along the same radial in terms of tracheidogram (Vaganov, 1990). Such measurements are usually performed on thin cross-sections observed under a light microscope, after a time-consuming sample preparation. The presented case study shows that it is possible to use CLSM and the associated image analysis system to obtain sufficient magnifications and resolutions, and thus to measure the tracheid parameters (Figure 5).
Figure 5. Wood of *Pinus halepensis* and measurement of cell wall thickness and dimensions of lumina (tracheids) of a radial row using Lext CLSM and image analysis software OLS5000. The laser system provides the intensity, colour and height of the image of the same object. Using the measurement option “profile” we can get the intensity, colour and height profiles in a chosen linear row and measure on it different parameters (here the diameter measurement of tracheids). The colour profile is also shown.

Slika 5. Les alepskega bora (*Pinus halepensis*): merjenje debelin celičnih sten in dimenzij lumnov (traheid) vzdolž radialnega niza traheid z uporabo CLSM Lext in programske opreme za analizo slike OLS5000. Laserski sistem zagotavlja intenzivnost, barvo in sliko po višini istega predmeta. Z možnostjo merjenja „profila“ lahko dobimo profile intenzitete, barve in višine v izbrani linearni vrstici in na njej izmerimo različne parametre (tukaj je prikazano merjenje premerov traheid). Prikazan je tudi barvni profil.

### 3.4 GROWTH LAYERS IN (*Pinus oocarpa*) FROM HONDURAS

**3.4 PRIRASTNE PLASTI V BORU (*Pinus oocarpa*) IZ HONDURASA**

Ocote pine (*Pinus oocarpa*), native to Central America, is poorly known in Europe. We inspected the wood structure of this species on cross-sections of the cores to evaluate the suitability for tree-ring analysis. Images at larger magnifications showed that the species has tree rings with typical early- and latewood and clear tree-ring boundaries. Many rings contain E- or L- types of IADFs (Figure 6).
The first impression is that the structure of ocote pine tree rings is similar to that of tree rings of conifers (pines) growing in temperate environments. The investigated samples originated from the trees growing in Honduras, near Siguatepeque, ca. 1100 m above sea level, where the climate is characterised by three seasons: a wet and relatively cool season (between May and November) with sufficient rain to ensure vegetation, a colder interlude (November to February) with temperatures occasionally down to 8 °C, and a dry season (February to May), with temperatures of up to 32 °C (Wikipedia, 2019, El clima promedio en Siguatepeque, Honduras, 2019).

Although November to February temperatures are not very low, the clear growth ring boundaries could be a consequence of the interruption of cambial activity in winter. The change of seasons could explain the IADFs in the rings. Dendrochronological cross-dating supported by detailed anatomy studied with CLSM could help to explain the processes affecting IADF formation and interruption of cambial activity resulting in clear tree-ring boundaries.

3.5 GROWTH LAYERS IN TROPICAL TRUE MAHOGANY

3.5 PRIRASTNE PLASTI V TROPSKEM SREDNJEAMERIŠKEM MAHAGONIJU

True mahogany (Swietenia macrophylla) is a tropical hardwood species of the family Meliaceae that grows in Mexico, Central America, and tropical South America (except the Amazon basin). The species is also planted outside its natural range. It is listed in CITES, Annex II (Richter et al., 2017).

The wood of Swietenia contains heartwood which is brown to red-brown and can be differentiated from the sapwood. The air-dry density is 400–500–650 kg/m³ (Richter & Dallwitz, 2000). The species is characterised by interlocked grain and ribbon figures. The wood is diffuse-porous, vessels are of medium size with a tangential diameter in the range of 90–160–255 µm. The vessels regularly contain dark reddish-brown deposits. The fibres are as a rule septate and have medium-thick cell walls. The rays are multiseriate, mainly 1–2–4(–5) cells wide. Rays, axial parenchyma and vessel elements are storied, although storied rays cannot be observed in all specimens. Axial parenchyma is mainly banded. The bands are marginal (or seemingly marginal), mainly 4–8 cells wide and present growth ring boundaries. The wood also contains paratracheal axial parenchyma which is scanty to vasicentric.

The material presented in this study originates from Ticoporo near Barinas in Venezuela, which is characterised by a tropical climate with dry seasons (average annual temperature 27.6 °C, average temperature variation between the hottest and the coldest month less than 3 °C, average annual rainfall ca. 2500 mm) (Pereyra et al., 2005). The wood contains marginal parenchyma demarcating growth layers. It was found that the optimal technique and magnification should be used to recognise the growth layers (Figure 7). The dimensions of the vessels varied in the radial direction, as shown by image analysis of the CLSM system. This could be of help with defining the growth layers.
Figure 7. True mahogany Swietenia macrophylla: (a) stitched image of increment core acquired with CLSM with 5x objective at the resolution of 96 dpi, and (b) detail of the same image; (c) thin cross-section under the light microscope, and (d) wood at the same magnification observed with CLSM. Arrows show bands of marginal axial parenchyma. Scale bars 500 µm.

Slika 7. Pravi mahagoni Swietenia macrophylla: (a) spojena slika posnetkov prečnega prereza lesa iz izvrtka, pridobljena s CLSM, objektiv 5x povečave pri ločljivosti 96 dpi, in (b) podrobnosti iste slike; (c) prečni prerez tanke rezine pod svetlobnim mikroskopom in (d) les pri isti povečavi, posnet s CLSM. Puščice kažejo pasove marginalnega aksialnega parenhima. Merilne doljice 500 µm.

Figure 8. Measurement of vessel lumen diameter and area in Swietenia macrophylla in a linear row. Here are shown the colour profile and height profile obtained with a confocal laser scan.

Slika 8. Merjenje premerov in površine lumnov trahej v lesu mahagonija Swietenia macrophylla. Tu sta prikazana barvni profil in profil po višini objekta, pridobljena s konfokalnim laserskim skeniranjem.
Several studies have shown that dendrochronological methods might be possible for Swietenia macrophylla as the growth increments in the adult xylem are marked by terminal parenchyma bands and are annual (Dünisch et al., 2002, 2003). The same studies in Swietenia macrophylla in Brazil also showed that besides annual rings there are also non-annual increment zones, and false rings may occur. Furthermore, cambium showed dormant phases during the dry period in Brazil. Studies also indicated that the seasonal pattern of cambial growth of Swietenia and tropical tree species in general has to be analysed separately on each site before tree-ring chronologies can be established (Dünisch et al., 2002, 2003).

3.6 GROWTH LAYERS IN TROPICAL CEDRELA
3.6 PRIRASTNE PLASTI V TROPSKI CEDRELI

Cedrela, or Central American cedar (Cedrela odorata), is a hardwood from the Meliaceae family. The wood of Cedrela resembles that of Swietenia (from the same family) and is of similar colour and density. The identification keys list only a few wood anatomical differences between the two taxa. Cedrela is generally semi-ring porous, has larger vessels, does not have storied structures and has a pleasant aromatic odour, whereas Swietenia is diffuse-porous, has medium-sized pores, storied structures and is odourless (Richter & Dallwitz, 2000).

The geographic distribution of Cedrela is Mexico and Central America, the Caribbean, and tropical South America. Cedrela odorata is on the CITES list of protected species, Appendix III (Richter et al., 2017).

Cedrela generally has distinct growth rings demarcated by marginal (or seemingly marginal) axial parenchyma bands, which are usually more than three cells wide (Richter & Dallwitz, 2000).

Detailed studies proved that also cedrela has growth layers which can be studied by dendrochronological methods (Dünisch et al., 2002, 2003). It was shown that the formation of increment zones

Figure 9. Cedrela (Cedrela odorata): (a) stitched image of increment core acquired with CLSM with 5x objective at the resolution of 96 dpi, and (b) details of the same image, arrows show growth ring boundaries; (c) detailed view of wood structure with bands of marginal axial parenchyma (double arrow) and fibres (arrow). Scale bars 500 µm.

Slika 9. Cedrela (Cedrela odorata): (a) spojena slika posnetkov prečnega prereza lesa izvrtka, pridobljenih s CLSM, objektiv 5x povečave pri ločljivosti 96 dpi, in (b) podrobnosti iste slike, kjer puščice kažejo meje med prirastnimi plastmi; (c) prečni prerez lesa pri večji povečavi, kjer dvojna puščica kaže pas marginalneg aksialnega parenhima, enojna puščica pa vlakna. Merilne daljice 500 µm.
in cedrela was annual, and that annual growth increments are indicated by alternating fibre and vessel bands embedded in paratracheal parenchyma (Dünisch et al., 2002). Like in Swietenia, the cambium showed dormant phases during the dry period in Brazil (Dünisch et al., 2002, 2003).

The material presented in this study are the cores from trees from Turrialba in Costa Rica, at an altitude of ca. 700 m. We had an impression that the growth layers are less distinct than in Swietenia (Figure 9). Surface preparation of the cores was a possible reason that we could not find the alternating fibre and vessel bands embedded in paratracheal parenchyma reported by Dünisch and co-workers (2002).

In addition, less clear growth layers could be a consequence of climatic conditions in the area around Turrialba, which is characterised by significant rainfall, abundant even in the driest period. In Turrialba, the average annual temperature is 22.9 °C, and the average total annual rainfall is 2854 mm (Climate Turrialba, 2019).

4 CONCLUSIONS

Other advantages of CLSM are the possibility to work at ambient conditions on polished cross-sections under different magnifications, the ability to control the depth of field and collect serial optical sections from thick specimens.

The observation of the such details can significantly improve the recognition of growth layers and the boundaries between them, as well as help to study growth anomalies. This can vastly enhance the quality of dendrochronological studies.

The study presented here, which to the best of our knowledge is one of the first to apply this technique in the field of wood science comprehensively, helped us to evaluate the potential and the advantages of CLSM in comparison with classical wood anatomy and dendrochronology techniques.

5 SUMMARY

5 P OVZETEK

Primerjalna in kvantitativna anatomija lesa v kombinaciji z dendrokronologijo lahko poda informacije o zgradbi lesa, ki so povezane z genetiko, zemljevidnim območjem, pa tudi s časom in razmerami, v katerih je les nastal. Raziskave anatomije lesa omogočajo analizo anatomskih znakov, ki lahko odražajo pomembne okoljske signale (Verheyden et al., 2004; García-González & Fonti, 2006; Campelo et al., 2010). Za proučevanje anatomskih znakov je običajno potrebna priprava in uporaba tankih mikroskopskih rezin za svetlobno mikroskopijo, kar pa je zelo zamudno. Zaradi tega iščemo metodologije, ki omogočajo opazovanje in analize mikroskopskih struktur brez posebne priprave vzorcev.

Cilj te študije je oceniti možnosti uporabe konfokalne laserske vrstične mikroskopije (CLSM) za različne študije v dendrokronologiji in oceniti primernost CLSM za nadomeščanje klasičnih metod, ki temeljijo na zamudni pripravi mikroskopskih rezin in svetlobni mikroskopiji.

Zgradbo lesa smo proučevali na izvrtnih premere 5 mm, odvzetih iz dreves s prirodstoslovnim svedrom. Prečne površine na izvrtnih smo gladko zbrušili. V lesu različnih vrst iz različnih okolij smo proučevali prirastne plasti (branike), meje med njimi (letnice) (Torelli, 1990) in druge lesno-anatomsko posebnosti.

Raziskali smo les naslednjih vrst: 1) navadna bukev (Fagus sylvatica L.) z rastišča na Hrvaškem
kasnega lesa) in je na splošno težko ugotoviti, kaj je branika in ali je nastala znotraj istega koledarskega leta (De Luis et al., 2011; Novak et al., 2016a; Balzno et al., 2018, 2019). Vrsta ima pogosto nejasne meje med prirastnimi plastmi (slika 4b), ki so posledica neprekinjenega delovanja kambija tudi pozimi (Prislan et al., 2016). Pojavljajo se tudi »temne branike«, ki predstavljajo prirastne plasti, ki v osnovi vsebujejo le kasni les (Novak et al., 2016a) (slika 4c). Predstavljena študija kaže, da je mogoče uporabiti CLMS in pripadajoči sistem za analizo slike, za opazovanje lesa pri veliki povečavi in ločljivosti ter za merjenje dimenzij celic in celičnih sten (slika 5). Slednje omogoča izdelavo traeidograma (Vaganov, 1990), kar pripomobre k prepoznavanju gostotnih varijacij in rastnih anomalij.

Na posnetkih prečnih prerezov lesa bora (Pinus oocarpa) iz Hondurasa, z rastšča na visoki nadmorski višini 1100 m, ki se sicer nahaja v tropskem pasu, smo ob večjih povečavah lahko videli razločne prirastne plasti. Te so imele zgradbo, tipično za branike lesnih vrst iz zmernega podnebja, ki vsebujejo rani in kasni les ter jasne letnice. Številne prirastne plasti vsebujejo tudi tipične gostotne varijacije tipa E- in L-IADF (slika 6). Slednje so verjetno posledica menjava treh letnih časov na območju Sigueatepeque v Hokudu rasu, z zelo različnimi temperaturami in padavinami. Dendrochronološko sinhroniziranje, podprto s podrobnim analizom anatomske zgradbe s pomočjo CLSM, bi lahko pomagalo razložiti procese, ki vplivajo na nastajanje IADF in na prekinitve aktivnosti kambija, kar ima za posledico jasne meje med prirastnimi plastmi.

Predstavljamo tudi dendrochronološki potencial pravega mahagonija (Swietenia macrophylla) (Torelli, 1997, 2006), ki v našem primeru izvir iz tropskega območja v Venezueli. Prirastne plasti pri tem mahagoniju razmeju jasni pasovi marginalnega aksialnega parenhma. Posnetki s CLSM kažejo, da je za prepoznavanje prirastnih plast ter izbriati optimalno (in ne nujno največje) povečavo (slika 7). Slike kažejo, da premere trajee od začetka do zaključka plasti upadajo in da jih je mogoče izmeriti s sistemom za analizo slike. Tudi spremljanje dimenzij trajee je v pomoč pri določanju prirastnih plast.

Les cedrele (Cedrela odorata), iz družine Meliaceae, kamor spadajo tudi mahagoniji (Torelli, Les/Wood, Vol. 68, No. 2, December 2019
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