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Electrical resistivity tomography: patterns in *Betula pendula*, *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris*

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Title

“Electrical resistivity tomography: patterns in *Betula pendula*, *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris*”

Running title

“Electrical resistivity patterns in four European tree species”

Highlight

Electrical resistivity patterns in tree stems are closely linked to wood properties. Here, we provide specific information on wood parameters influencing the electrical resistivity distribution in four species.

Summary

Electrical resistivity (ER) tomography is a promising technique to minimal-invasively study stems of living trees. It allows insights into xylem properties based on the cross-sectional distribution of ER which is governed by the wood’s electrical conductance.

In this study, ER measurements were carried out on four forest tree species, *Betula pendula*, *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris* to demonstrate interspecific, intraspecific and within-tree variation of ER tomograms. Further, ER patterns were linked to xylem moisture content, electrolyte content and density, obtained from wood core analyses.

ER patterns of both coniferous species, *P. abies* and *P. sylvestris* were found to be more homogenous and concentric compared to the complex tomograms of angiosperms. However, the ER range of coniferous trees showed considerably intraspecific variation. Measurements near ground level showed pronounced effects on ER tomograms, highlighting the importance of the chosen measurement height. A strong relation between ER and wood density was found in *F. sylvatica* while ER patterns of conifers were mainly influenced by moisture content.

Results demonstrate a high species-specificity of ER tomograms and of respective influencing xylem traits. They underline the importance of reference measurements for a correct interpretation of ER studies.

Key words: *Betula pendula*, *Fagus sylvatica*, electrical resistivity tomography, electrolyte content, moisture content, *Picea abies*, *Pinus sylvestris*, wood density

Introduction

Imaging of organs, for example by X-ray or nuclear spin tomography, is an essential diagnostic tool in medicine. For trees, due to their dense tissues (and inability to visit hospitals) comparable non- or minimal-invasive methods are widely lacking. Though, electrical resistivity (ER) tomography may offer detailed insights into tree stems *in situ*. Analysis of electrical currents to obtain physical properties of objects was first established in the field of geophysical sciences, where ER meanwhile is a widely used method for measurements and imaging of subsoil structures and hydrogeology (Revil *et al.*, 2012; Perrone *et al.*, 2014). Methodical adaptations (e.g. Tattar *et al.*, 1972; Shigo and Shigo, 1974; Shortle, 1982; Just and Jacobs, 1998; al Hagrey, 2007) allowed the introduction of ER techniques into plant sciences and provided the opportunity to assess living trees without compromising their health. The generation of an electrical field and the subsequent measurement of the electrical conductivity (and ER as its reciprocal) enables the *in vivo* visualization of the cross-sectional resistivity distribution of tree stems and to draw conclusions about the structural composition (e.g. heartwood-sapwood patterns) of the xylem (Bieker and Rust, 2010a; Wang *et al.*, 2016). Exact knowledge on heartwood-sapwood boundaries and amounts is not only of great interest to the wood and paper industry (Barnett and Jeronimidis, 2003), but also a necessary prerequisite to quantify ecohydrological processes such as the sap flow in tree stems. Sapwood area estimations obtained by ER measurements can add valuable information to the upscaling process of sap flow data from tree to stand level (Bieker and Rust, 2010a; Guyot *et al.*, 2013; Pfausch and Macfarlane, 2016; Wang *et al.*, 2016) as well as to the analysis of flow pathways in the hydraulic system. Further, ER tomography is a promising technique to identify conspicuous alterations of internal xylem structures. Abnormalities in ER patterns have been successfully used for the assessment of fungal infections and internal wood decay in both angiosperm (Nicolotti *et al.*, 2003; Bieker *et al.*, 2010; Brazee *et al.*, 2011; Martin and Günther, 2013) and coniferous tree species (Larsson *et al.*, 2004; Humplík *et al.*, 2016), as well as for the detection of red heartwood formation in European beech (*Fagus sylvatica*; Goncz *et al.*, 2018). ER tomograms can visualize the heterogeneous distribution of resistivities in stems, which is caused by the varying physical characteristics of wood and can strongly differ between species in both ER magnitudes and patterns. The wood's electrical properties are mainly influenced by moisture content, electrolyte concentration and wood density (al Hagrey, 2007; Bieker and Rust, 2010b; Bieker *et al.*, 2010; Rowell, 2012; Guyot *et al.*, 2013). However, it has been shown that the impact of these factors on ER patterns can strongly vary between species. For example, the ER distribution in *Pinus elliotti* (Guyot *et al.*, 2013) is hardly related to electrolyte content

but strongly depends on wood moisture and density. In contrast, resistivity patterns in *Quercus robur* stems were strongly influenced by electrolytes (Bieker and Rust, 2010b). Thus, it is difficult to draw any conclusion from ER tomograms on wood characteristics, unless information on species-specific patterns and correlation with mentioned influencing factors are known. Unfortunately, information on variation across species is scarce, and little is also known about the intraspecific variation of ER patterns and potential seasonal or age-related changes. Further, detailed information on ER variation in relation to stem height are lacking, although soil and roots might substantially influence measurements.

In the present study, we focused on the variation of ER within stem cross sections of four European tree species (*Betula pendula*, *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris*) at interspecific and intraspecific levels. Additionally, within-tree variation was analyzed by conducting ER measurements at several heights along the stem. Besides ER measurements, wood cores from study trees were taken to analyze the corresponding wood moisture content, electrolyte content (measured via electrical conductivity of wood extracts) and wood density.

We hypothesized that (i) ER tomograms vary in range and patterns across species with overall more complex patterns in angiosperms due to their more complex wood structure. We also expected (ii) species-specific correlations between wood moisture content, electrolyte content and density and ER patterns, and (iii) relevant variation with measurement height. Analyses should create a solid base for interpretation of future ER measurements on trees of the study species and a respective template for studies on other tree species. Information on the intraspecific and within-tree variability may help to efficiently use ER tomography in further studies.

Material and Methods

Selection of trees and study sites

The study was performed on four European forest tree species, *Fagus sylvatica* L., *Betula pendula* Roth., *Picea abies* (L.) Karsten and *Pinus sylvestris* L., growing in a mixed forest stand situated north and northwest of Innsbruck, Austria (47°17'N, 11°24'E, 940 m asl; slope gradient: 0-20°; exposition: southeast to southwest; mean annual temperature: 9.72 °C; mean annual precipitation: 910.03 mm; climate data 1988 to 2017 from nearby weather stations of Central Institute for Meteorology and Geodynamics, ZAMG). Five healthy and straight-grown mature trees of each species were selected, on which measurements were conducted between April and August 2015 to address hypotheses (i) and (ii). One additional representative tree of

each species was selected for the within-tree comparison of ER patterns (hypothesis (iii)), on which measurements were carried out in September 2018.

Electrical resistivity (ER) tomography

For each tomogram, nail probes were installed at 24 measuring points (MP) at breast height (130 cm) equally distributed around the tree circumference (Fig.1; see Table S1 for detailed information on single trees). Nails were inserted into the trunk counterclockwise, starting with a northward orientation (MP 1), until contact to the sapwood was established. Tree geometry and positions of MP were determined with an electronic caliper (PiCUS Calliper Standard Version, Argus Electronic GmbH, Rostock, DE) and processed using the PiCUS Software (PiCUS Q73, Argus Electronic GmbH, Rostock, DE). All nails were then connected via electrodes to a 24-channel resistivity system (PiCUS: TreeTronic, Argus Electronic GmbH, Rostock, DE) and electrical voltages were applied step by step to all MP. Several voltage levels were applied prior to the measurement to test for sufficient amperage input and voltage at the MP. Measurements were then carried out at voltages between level 3 and 5. Data on the electrical field were sent to the software on a laptop, with which the cross-sectional distribution of ER was calculated for each tree and the respective tomogram generated. The reconstruction of the spatial distribution of resistivities is based on an inversion scheme that uses a finite element simulation operating with regularly arranged tetrahedrons (Günther, 2004; Günther *et al.*, 2006; Rücker *et al.*, 2006). The software then includes the source data into a two-dimensional model and provides a planar triangular-based mesh at the measurement level. Each triangle is colored according to its resistivity for a better visualization of the patterns and information about triangle size, position and respective ER value can be exported for further analyses. As triangle areas vary in dependence on their radial position, the weighted electrical resistivity (ER_w , Ωm) was calculated for each triangle:

$$ER_w = (ER * A) / A_{mean} \quad \text{Eqn. 1}$$

where A (cm²) is the individual triangle area and A_{mean} (cm²) the mean area of all triangles. The average ER of each entire cross section was then calculated as the mean of ER_w of all triangles. ER profiles were created for each tomogram by excerpting ER values along sectors spanning the entire tomogram (width = 1 cm). ER values of all triangles, whose center were located within the sector, were used for the calculation of ER profiles. As ER tomograms of angiosperms revealed pronounced reaction wood zones - indicated by high ER values - in the periphery, ER profile sectors of angiosperms were manually orientated along opposite wood

(rectangular to the direction of peripheral reaction wood zones). This procedure allowed a better interspecific comparison by providing ER profiles which only consider normal wood. Studied conifers hardly showed reaction wood and thus ER profile sectors were generally aligned along the west-east axis (see Fig. 1C).

For correlation between ER and properties of extracted wood cores (moisture content, electrolyte content, wood density), the west to center oriented radius of stems was used in all species (see Fig. 1B). Again, ER values of all triangles, whose center points were located within the sector, were selected. After determining their relative position along the length of the radial sector, ER values of each tree were pooled in 10 percentage classes of 10% and averaged. Mean values for each percentage class were then calculated from the average data of all five specimens. This enabled to account for variation in stem diameter and respective statistical analysis of data from several specimens.

For the within-tree comparison of ER patterns, tomography measurements were conducted at heights of 10, 40, 70, 100 and 130 cm above ground level.

Analyses of wood cores: Moisture content, electrolyte content and wood density

Wood cores were taken subsequently after each ER tomography measurement with a 5 mm increment borer (Haglöf Sweden AB, Langsele, SE) from the west side of the trunk directed towards its center. Core sampling was performed at the same height as ER tomography measurements. Cores were immediately sealed with plastic film and brought to the laboratory under airtight conditions. After bark removal, the cores were cut into samples of 5 mm (outermost 0 to 10 cm of the trunk) or 10 mm (inner section) length and immediately put in vials (Safe-Lock Tubes 2.0 ml, Eppendorf AG, Hamburg, DE) to avoid moisture loss. Weight of vials including fresh samples were determined, before vials were opened and samples dried for 12 hours at 80 °C. Then sample dry weight (DW; µg) and weight of the vial were measured to calculate sample fresh weight (FW; µg) and determine wood moisture content (MC; %):

$$MC = ((FW - DW) / DW) * 100 \quad \text{Eqn. 2}$$

Further, wood density (kg m⁻³) of samples was calculated by dividing DW by sample volume (V; m³), which was derived from sample dimensions:

$$V = \pi * r^2 * l \quad \text{Eqn. 3}$$

where r is the sample radius and l the sample length.

Following MC analysis and wood density calculation, dry samples were cut into small slices (8 and 16 slices for 5 and 10 mm samples, respectively) to increase the surface for electrolyte leakage. Sample slices were returned into the vials, which were filled with distilled water (1 and 2 ml for 5 and 10 mm samples, respectively), and shaken for 6 h on a horizontal shaker (ST5 Bidimensional Shaker, CAT, Staufen, DE) at room temperature. The electrical conductivity ($\mu\text{S cm}^{-1}$) of sample solutions was then measured with a conductivity meter (B-173, Twin Cond, Horiba JP) as a proxy for the electrolyte content.

For the alignment of results on MC, electrical conductivity and wood density with the corresponding resistivity values from ER tomography analyses, the relative position of each core sample was calculated based on its absolute position along the length of the wood core. Depending on their relative position, samples and the according wood property data of single trees were pooled in classes of 10% and averaged. Mean values for each percentage class were then calculated from the average data of all five specimens.

Statistics

Data were tested for Gaussian distribution (Shapiro-Wilk test) and variance homogeneity (Levene test). Means were compared using a one-way analysis of variance followed by a post-hoc Tukey test. NonGaussian-distributed data were tested with the Mann-Whitney test. Data were tested for correlations using Spearman's' ranks correlation coefficient to account for non-normality of data. All tests were performed at a probability level of 5% using R version 3.4.2 (R Core Team, 2017).

Results

Electrical resistivity tomography patterns

Measured resistivities in tree stem cross-sections ranged from 9.5 to above 13000 Ωm , and highest maximal resistivities were found in *P. sylvestris* (up to 13581.20 Ωm ; see also Table S1). The two conifers exhibited higher mean resistivity than the studied angiosperms *B. pendula* and *F. sylvatica* (Fig. 2A). In all species, ER tomograms and profiles (Fig. 3) revealed lowest resistivities in the outer sapwood regions of stems. Note that tomograms of both *B. pendula* and *F. sylvatica* also showed peripheral arcs with high resistivity, which were related to reaction wood, probably formed due to ground slope. Therefore, angiosperm ER profiles were always aligned rectangular to the direction of maximum resistivities in the periphery of ER tomograms and thus along opposite wood (see methods). All profiles showed a pronounced increase in resistivity from the sapwood towards the center indicating a transition from sap- to heartwood

(*P. abies*, *P. sylvestris*) or from sap- to ripewood (*B. pendula*, *F. sylvatica*). Following the transition zone, resistivity within all *B. pendula* and *F. sylvatica* specimens decreased. In most *F. sylvatica* trees, another peak in resistivity was observed in the stem center. In *B. pendula*, like in studied conifers, the stem center showed a lower resistivity compared to peak resistivity in the transition zone, whereby this resistivity drop showed some variation across specimens (Fig. 3A, C, D). Sapwood, transition zone and central heartwood led to very homogenous, concentric patterns in conifer ER tomograms, while angiosperms showed overall higher variability with several patches of high and low resistivity in the stem center. Despite overall similar ER tomogram patterns, conifers showed higher variability in average absolute resistivity across specimens than angiosperms (see profiles and respective scales in Fig. 3).

Moisture content, electrolyte content and wood density

Average moisture was found to be around 60% in all species and only slightly lower in conifers than in angiosperms (Fig. 2B). In contrast, electrolyte content and wood density widely differed across species with overall higher electrolyte content and wood densities in angiosperms (Fig. 2C, D). MC, electrolyte content and wood density of core samples and the respective ER along the radial stem position (10-percent steps) are shown in Fig. 4. Increasing ER towards the stem center (transition zone, see above) corresponded to decreasing wood MC and electrolyte content in *P. abies* and *P. sylvestris*, while no pronounced trend was found in angiosperms. An increase in wood density (corresponding to slightly increasing ER) towards the stem center was only observed in *F. sylvatica*. Correlation analysis (Fig. 5) revealed an influence of MC on ER in three out of four species and of electrolyte content in two species, while a correlation of density and ER was only found in *F. sylvatica*. The latter was thus the only species, where ER was correlated with all three wood parameters and where all correlations were positive. In contrast, observed correlation of ER *versus* moisture and electrolyte content in *P. abies* and *P. sylvestris* were negative.

Within-tree variation of electrical resistivity

Variation in ER patterns with increasing height from the ground are shown in Fig 6. Tomograms at different levels demonstrated relevant changes in ER patterns within the same tree. In all species, measurements near the ground differed from measurements at higher stem positions. Average cross-sectional ER_w of all species was found to be 20.5 ± 4.4 % lower at 10 cm height compared to measurements at 40 cm, while differences between 70 and 130 cm height (8.0 ± 3.7 %) as well as between 100 and 130 cm height (3.6 ± 1.3 %) were comparatively small.

Discussion

The present study demonstrated (i) a broad variation in ER ranges and patterns across tree species with complex tomograms in studied angiosperms and comparable homogenous and concentric patterns in conifer tomograms. Our data also (ii) revealed species-specific relations between ER and wood traits and (iii) showed a clear height dependency of ER measurements.

In general, average resistivity was substantially higher in studied conifers than in angiosperms (Fig. 2A). Similar results were reported by Gora & Yanoviak (2015), who suggested variations in ER to be related to phylogenetic differences in wood structure and physiology. The authors also suggested that factors others than wood MC may explain resistivity variation between taxa. Our data indicate an important role of the wood electrolyte content as angiosperm wood cores showed more than two times higher electrolyte contents and respective lower mean ER than conifers (Fig. 2A, C), while the higher wood density seemed not to affect mean ER of angiosperms. The high electric conductivity of angiosperm wood is likely attributed to their higher proportion of living parenchyma, containing more mineral nutrients than gymnosperm wood (Meerts, 2002). In both studied coniferous species, lower wood MC (Fig. 2B) may further contribute to high average ER. However, it is known that effects of MC on ER above the fiber saturation point (~ 30 % w/w of most wood tissues) are small (Tattar *et al.*, 1972; Shigo and Shigo, 1974). It should be noted that low ranging ER values as obtained from both angiosperms (Fig. 3A, 3B) can be critical for the inversion process. Cell sizes during modelling are influenced by spatial ER gradients and low ER variability can lead to limitations of the resolution by increasing cell sizes (Günther, 2004; Günther *et al.*, 2006). In order to achieve the highest resolution possible, we used 24 electrodes – the maximum of our ER system – to minimize electrode spacing and increase tomogram resolutions (al Hagrey, 2007).

Tomograms of *P. abies* and *P. sylvestris* (Fig. 3C, D) displayed comparably clearly structured ER patterns, which seem to be characteristic for members of the Pinaceae family (Bieker and Rust, 2010a; Guyot *et al.*, 2013). Typically, these tomograms show a clear peripheral ring of low ER reflecting sapwood and a steep ER increase towards the central heartwood area (with considerably higher ER). While sap- and heartwood could be easily distinguished in *P. abies* and *P. sylvestris*, the interpretation of ER tomograms in studied angiosperms was more difficult. The sapwood of *B. pendula* and *F. sylvatica* usually showed parts with high ER indicating the presence of reaction wood, while the ripewood often included patches of lower ER, which complicates the clear identification of boundaries. The presence of high ER zones in the

periphery of *B. pendula* and *F. sylvatica* stems at the study sites with only moderate slopes indicate that these species form reaction wood already at moderate mechanical growth stress intensities (Jullien *et al.*, 2013; Groover, 2016).

Areas of low ER in the stem center of *B. pendula* and *F. sylvatica* can indicate the formation of red heartwood, a facultative stress-triggered coloration of ripewood, which can predominantly be found in older trees and is often associated with enhanced MC (Knoke, 2003; Hörnfeldt *et al.*, 2010). The detection of red heartwood based on its changed electrical properties has successfully been demonstrated in *F. sylvatica* by Goncz *et al.* (2018). On an intraspecific level, tomograms of *B. pendula* and *F. sylvatica* showed a high variability of ER patterns, while the homogenous and concentric patterns in conifers were similar across studied specimens (Fig. 3). However, in both *P. abies* and *P. sylvestris*, absolute ER varied considerably (see ER profiles in Fig. 3C, D).

But what are the underlying wood properties causing observed ER patterns? Studies on the impact of wood properties on ER tomography are scarce and a direct relation between wood MC and density *versus* ER patterns in conifers has been reported only for subtropical pine trees (Guyot *et al.*, 2013). In the same study, no radial changes in electrolyte content were found. Links between ER patterns and wood properties for angiosperm species have previously been demonstrated only by Bieker & Rust (2010b), who attributed the cross-sectional variation of ER in *Q. robur* to radial changes in electrolyte content. The present study indicated ER patterns in conifers to be mainly governed by MC (Fig. 5). In *P. abies* and *P. sylvestris*, wood moisture showed a sharp decrease from about 100% and 75%, respectively, in the sapwood to about 25% in the stem center, with a parallel strong ER increase (Fig. 4A, B). Additionally, electrolyte content influenced ER patterns of *P. sylvestris*, while for *P. abies* this relationship was less pronounced (Fig. 5). Wood density, in contrast, was relatively constant along the radial transect, and thus not associated with ER changes in conifers. Our results did not reveal clear relations between ER and single wood properties for *B. pendula*, making an appropriate interpretation of the obtained ER patterns difficult. In contrast, wood density seems to be a major factor influencing ER in *F. sylvatica*. The wood of *F. sylvatica* tended to become denser towards the stem center (Fig. 4D; Bouriaud *et al.*, 2004), which correlated well with concurrently increasing ER values in our study (Fig. 5). Surprisingly, in *F. sylvatica* positive correlations were found between ER and MC, and between ER and electrolyte content. As high MC and electrolyte content causally reduce ER (Tattar and Blanchard, 1976; Shortle, 1982), these phenomena are probably spurious relationships caused by wood density as an intervening variable, which dominates the effects on ER. This may explain why an electrolyte increase towards the center

(Fig. 4C), eventually caused by the accumulation of secondary metabolites in the heartwood (Meerts, 2002), induced no decrease of ER in *F. sylvatica*. It should be also be noted that our data do not consider variation due to different growth conditions or age (e.g. Pichler and Oberhuber, 2007; Martinez-Vilalta *et al.*, 2012), due to different phenological stages or to potential seasonal changes in wood properties, which might influence ER patterns. For instance, it is known that xylem sap composition and chemistry can change with seasonality in both angiosperms (Glavac *et al.*, 1990) and gymnosperms (Losso *et al.*, 2018), altering the sap's electric conductivity over the year. Further research is needed to understand the exact impact of these factors on the ER distribution in tree stems.

Present ER analyses also demonstrated that the measurement height can substantially affect ER tomography (Fig. 6). Pronounced effects of soil and/or roots on ER patterns were clearly visibly in measurements near ground level. Lowered ER at the stem base may result from an overall increase of moisture and/or electrolytes within tissues. Additionally, the close connection to the soil could lead to an external bypass movement of electrons, causing low ER measurements. Thus, we suggest to conduct reliable ER measurements above 50 cm height, and measurements performed about breast height (100 - 130 cm) may be most suitable for obtaining representative, species-specific tomograms.

Conclusion

ER tomography is a promising, minimal-invasive technique with versatile fields of application. Our study emphasizes the complexity of underlying wood properties and respective difficulties in interpretation of ER tomograms. Several representative tomograms for each species under study are thus a prerequisite to draw correct and meaningful conclusions. The testing of relevant wood parameters, such as density, moisture or electrolyte content can help to unravel the underlying influences. Further research and respective measurements on more species are needed to obtain a broader understanding of the ER variation among species.

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Figures

Fig. 1. Procedure of (A) electrical resistivity (ER) measurements and wood core sampling, and (B, C) ER data extraction. (A1) ER measurements were carried out via a 24-channel resistivity system, which was connected to 24 equally distributed measuring points (inserted nail probes) around the tree circumference. After ER data were sent to a laptop, (A2) a wood core was taken from each tree with an increment borer from the west side of the trunk directed towards the center. (A3) Consequently, moisture content (MC), electrolyte content (via electric conductivity; σ) and wood density (ρ) were analyzed in the laboratory. From ER data, the cross-sectional ER distribution of each tree was calculated and the respective tomogram generated. (B) For correlation analyses between ER data and wood properties (MC, σ , ρ), ER sectors were defined (black bars; width = 1cm) according to the position of the extracted wood cores and ER values within these sectors were excerpted. (C) For ER profiles, an additional sector was defined spanning the entire tomogram (white dashed line; width = 1cm). ER profile sectors in angiosperms were chosen rectangular to the direction of reaction wood (red colored peripheral arcs of high resistivities), while values for ER profiles of conifers were always excerpted from west-east oriented sectors.

Fig. 2. Boxplots of average electrical resistivity and wood properties for *Betula pendula*, *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris*. (A) Weighted electrical resistivity (Ωm) was calculated from averaged values of each of entire cross-section ($n = 5$). (B) Moisture content (%), (C) electrolyte content (measured by via electrical conductivity; $\mu\text{S cm}^{-1}$) and (D) wood density (kg m^{-3}) were obtained from wood core ($n = 5$) analysis. Boxplots indicate the median (thick central line), interquartile range (box), minimum and maximum (whiskers), and outliers (circles). Different letters indicate significant differences.

Fig. 3. Electrical resistivity (ER) tomograms and profiles of five individuals for (A) *Betula pendula*, (B) *Fagus sylvatica*, (C) *Picea abies* and (D) *Pinus sylvestris*, respectively. Areas of high resistivity in tomograms are indicated by red colors while areas of low resistivity are indicated by blue colors. Note that the limits of the displayed resistivity ranges were set manually to optimize visualization, and minimum/maximum ER values may exceed these limits. Vertical black scale bars on the left side of each tomogram represent 10 cm. For each tomogram, ER values were excerpted along a chosen diameter (dashed white line) to generate the corresponding profile. Absolute resistivity values in ER profiles are displayed in accordance to their relative position (0 % = stem center, $\pm 100\%$ = youngest annual growth ring).

Fig. 4. Analysis of wood properties. Mean values ($\pm$ SE) for (A) electrical resistivity (Ωm), (B) moisture content (%), (C) electrolyte content (measured by via electrical conductivity; $\mu\text{S cm}^{-1}$) and (D) wood density (kg m^{-3}) *versus* their relative position. The relative position refers to the distance between the cambium and the stem center (0% = youngest annual growth ring, 100 % = stem center).

Fig. 5. Spearman's' rank correlations between electrical resistivity (Ωm) and individual wood properties (moisture content (%), electrolyte content (measured by via electrical conductivity; $\mu\text{S cm}^{-1}$) and wood density (kg m^{-3})) for *Betula pendula*, *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris*. Correlation coefficients are reported. Linear trend lines were fitted to datasets with significant correlations between variables ($P \leq 0.05$). Mean $\pm$ SE.

Fig. 6. Within-tree variation of electrical resistivities (ER) for *Betula pendula*, *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris*. Tomograms at five different measurement heights (10, 40, 70, 100 and 130 cm) are displayed for each species. Red colors indicate high ER, blue colors indicate low ER. Note that the limits of the displayed resistivity ranges were set manually to optimize visualization, and minimum/maximum ER values may exceed these limits. Vertical black scale bars on the left side of each tomogram represent 10 cm.