

# Altered growth with blue rings: comparison of radial growth and wood anatomy between trampled and non-trampled Scots pine roots

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## Abstract

Our understanding of wood anatomy and radial growth in tree roots remains very incomplete, particularly with respect to how ecological factors affect root growth at a relatively small spatial scale, i.e., within a single root system. Here, we compared root growth with and without trampling exposure on a hiking trail. We conducted a quantitative analysis of radial growth and wood anatomical changes, including compression wood (CW) and blue rings (BRs), of two adjacent Scots pine roots in high resolution. A total of 32

cross sections from two roots sampled every 25 cm at the same distance from the respective stem were compared. The buried root (B) was completely buried and had an unexposed segment on a hiking trail. In contrast, the exposed root (E) had an exposed segment that was trampled. 1,706 growth rings were analysed for the common period 1954-2015.

We found that the volume of the E root in the trampling zone exceeded ten times the volume of the B root. The root surface area of the exposed sections of the E root was on average 14 times larger than that of the unexposed B root section in the trampling zone. The highest number of missing rings was found in the B root. Root sections sampled at the shortest distance from the stem showed the highest coherence in radial growth pattern, which decreased with increasing distance from the stem.

BRs were recognized for the first time in tree roots. In total 25 tree rings contained BRs, and their occurrence was restricted to cross sections of the exposed root. BRs were formed over the course of 25 calendar years, i.e., in 40% of tree rings from the common period 1954-2015. Mean monthly temperatures for the years with and without BRs formation showed that colder November ( $p = 0.012$ ) and, albeit only slightly, colder September ( $p = 0.051$ ) temperatures favoured formation of BRs in Scots pine roots. In addition, mean monthly precipitation in July ( $p = 0.017$ ) was significantly higher for BR years, suggesting an impact of moisture availability on the formation of BRs in Scots pine roots. The study highlights a high rate of growth discrepancies within a single root system. Further, altered growth of trampled roots with high proportions of BRs opens a new challenge for future dendroecological studies on tree roots.

**Keywords:** tree roots, cross-dating, *Pinus sylvestris* L., wood anatomy, compression wood, blue ring

Abbreviations: B, the buried root; E, the exposed root; R1-R16, ID of root sections; PRES, the trees subjected to trampling pressure on a hiking trail; EX, the broader exposed root pool; REF root, the broader

reference root pool; ZZST, Zig-Zag Segment Tracing; RGC, radial growth coherency; MRW, mean ring width, PRDs, pronounced resin ducts; CW, compression wood; BR, blue ring

## 1. Introduction

Radial growth of roots and stems serves as a unique source of information on ecological changes in the natural environment (Cook and Kairiukstis, 1990; Schweingruber, 1996), however tree-ring chronologies from roots are exceptionally rare. Traditionally, studies of radial growth focused mainly on the tree stem (Schulman, 1945; Fayle 1968; Krause and Eckstein, 1993; Krause and Morin, 1995) and few analyses have been carried out on root chronologies, mainly because sampling of the belowground tree parts is difficult. In addition, analyses of roots differ from analyses of stem growth, because the radial growth and the anatomy of the root is potentially altered by other environmental factors than stem growth, such as soil conditions. This results in differences in ring-width development as well as in the anatomical structure of roots, which often differs significantly from the structure of stem wood (Glock et al., 1937; Fayle, 1968; Krause and Eckstein, 1993). Compared to the annual rings of a stem, the annual ring boundaries in roots are generally less distinct at both macroscopic and microscopic levels (Rybniček et al., 2007). However, the importance of the root system for tree growth becomes clear when considering its main functions: stabilization, absorption of water and minerals, their transport to the photosynthetic part of the tree, and storage of biochemical compounds (Coutts, 1983; Drexhage et al., 1999; Pagès, 2002; Karliński et al., 2014; Zadworny et al., 2015). There is a need for comprehensive knowledge of the complex root systems of trees, that would help to develop a better understanding of important aspects of root behaviour related to mechanical stress, water and nutrient transport, carbohydrate storage, and also biomass allocation (Pagès, 2002; Danjon et al., 2013; Jagodziński et al., 2016; Terzaghi et al., 2016).

Various above- and belowground factors affect the growth of roots and stems (Fayle, 1968; Bohm, 1979; McMichael and Burke, 1998; Pregitzer et al., 2000). Root growth pattern is known to be affected by soil properties such as soil compaction, bulk density and organic matter content (Bohm, 1979). Root orientation, aeration, light availability, and soil moisture and temperature have important influences on root growth. In addition, root growth is known to be affected by insect defoliation (Krause and Morin, 2005), biomechanical weathering of rocks (Malik et al., 2019), gully and sheet erosion (Vandekerckhove et al., 2001; Hitz et al., 2008; Malik, 2008b; Lopez Saez et al., 2011; Morawska, 2012), windthrows (Nicoll and Ray, 1996; Danjon et al., 2005; Montagnoli et al., 2019b) and trampling (Bodoque et al., 2005; Pelfini and Santili, 2006; Rubiales et al., 2008; Matulewski et al., 2021).

Changes in root morphology indicate the effect of ecological factors (Bohm, 1979; Coutts, 1987). In ecological studies, assessment of root morphological parameters, including root architecture, provides data on ecological conditions of root growth (Chiatante et al., 2002; Ostonen et al., 2007; Jagodziński and Kałucka, 2011; Jagodziński et al., 2016; Wagner et al., 2010, 2011). An understanding of root diameter growth provides insight into the relationship between soil pore size and the ability of roots to penetrate the soil (Wiersum, 1957; Bohm, 1979). Root surface area and volume are the most important parameters for determining water and nutrient absorption (Ran et al., 1992; Dunbabin et al., 2002; Jagodzinski and Kałucka, 2010), while tree root biomass plays an important role in the circulation of matter and energy (Waring, Schlesinger, 1985; Vogt et al., 1995; Cairns et al., 1997; Jagodziński and Kałucka, 2010).

Furthermore, root parameters indicating the influence of ecological factors are radial growth and wood anatomical changes. Variations in root growth caused by external factors can lead to changes in growth patterns (Pelfini and Santili, 2006). Annual ring-widths in roots change substantially over the years and vary greatly between different parts of the

same root (Fayle, 1968; Krause, 1992). Several authors report the occurrence of irregular annual growth rings indicative of discontinuous wood production (Bodoque et al., 2005; Pelfini and Santili, 2006; Rubiales et al., 2008; Wrońska-Wałach et al., 2016). Missing, false and wedged rings represent a considerable problem for root dating by dendrochronology (Rybniček et al., 2007). Radial variations of growth irregularities are common in roots due to differences in cambial activity between years. They also vary along the horizontal profiles of the roots (Wagenführ 1999; Schweingruber 1996; Wrońska-Wałach et al., 2016).

Wood anatomical changes in roots have rarely been analysed, in contrast to those in stems and branches (Gärtner, 2007; de Zio et al., 2020). Based on the work of Fayle (1968), a number of exposure related anatomical changes within the annual rings of roots have been identified (Gärtner et al., 2001; Gärtner, 2003) and applied to dendrogeomorphology (Bodoque et al., 2005). The occurrence of scars and traumatic resin ducts in exposed roots have been described as markers for ecological and geomorphical process activities (Carrara and Carroll, 1979; Malik 2008a; Gärtner 2007; Wrońska-Wałach et al., 2016). Another possible marker in tree roots could be compression wood, which is developed due to mechanical stress (Panshin and de Zeeuw, 1970; Carrara and Carroll, 1979; Timell, 1986). The qualitative features of compression wood differ from those of normal wood in terms of tracheid form (i.e. they are round in cross section, forming intercellular spaces), tracheid cell wall thickness, ultrastructure and chemical composition (Lee and Eom, 1988; Ruelle, 2014). Occurrence of compression wood in roots is probably the result of auxin redistribution caused by the action of gravity (e.g., Yamaguchi et al., 1983). However, to our knowledge, quantitative studies considering compression wood in tree roots have not been performed.

Another wood anatomical feature related to radial growth constraints of trees is the occurrence of blue rings (Piermattei et al., 2015; Matisons et al., 2020; Tardif et al., 2020).

Blue rings are tree-rings with some layers of cells with incompletely lignified cell walls that appear blue after double-staining wood sections by Astra blue and Safranin (Piermattei et al., 2015). Studies of blue rings occurring in tree stems indicate that their formation is related to years of extreme (i.e., cold) climatic and/or ecological events resulting in a sudden stopping of cell formation before lignification of the last cells is finished or even started (Piermattei et al., 2015; Tardif et al., 2020). To date, there is no study published on the occurrence of blue rings in roots.

Our current understanding of radial growth patterns and wood anatomical irregularities in roots remains incomplete (Wrońska-Wałach et al., 2016; Matulewski et al., 2021). The mechanism responsible for growth irregularities in tree roots remains largely unknown (Montagnoli et al., 2019b). The lack of a comprehensive approach in root studies that could reveal growth discrepancies and wood anatomical changes limits our ability to describe the temporal and spatial effects of ecological factors on tree root growth. Moreover, the changing growth requirements within a single root system remain poorly understood. The ability to accurately track changes in radial growth and wood anatomy of roots can be facilitated by high resolution studies that examine the effects of different environmental conditions within the same root system.

The goal of the present study was to investigate radial growth and wood anatomical changes in roots of Scots pine (*Pinus sylvestris* L.), subjected to direct and indirect impacts of trampling, at a relatively small spatial scale. For this purpose, we compared root morphology, radial growth and wood anatomical changes of two adjacent roots from the same Scots pine tree in high resolution. These roots were selected because of their unique, i.e. parallel position, from a bigger set of samples (204 roots from 97 trees) analysed for the common period 1970-2015 (Matulewski et al., 2021). The first root was naturally buried in the soil and was not exposed on the hiking trail, whereas the second root was partially exposed on the same hiking trail and was directly subjected to trampling.

Our main objectives were: i) to compare root morphology and biomass between the two roots; ii) to compare radial growth between the roots and the respective stem; iii) to characterize wood anatomical changes in the studied roots, specifically the occurrence of compression wood and blue rings. We hypothesized that the two adjacent roots represented a coherent radial growth pattern, but that the changes in wood anatomy would be more pronounced in the root exposed to direct impacts of trampling due to mechanical pressure and more diverse climatic conditions.

## **2. Materials and methods**

### **2.1. Site description**

The study was conducted in the Brodnica Landscape Park located within the Brodnica Lakeland in the north-eastern Poland (Fig. 1a). The study area represents a typical lowland landscape with morainic hills and a high number of postglacial lakes (Niewiarowski and Wysota, 1986). The climate of this region is diversified depending on landforms, proximity to lakes and forest areas (Kondracki, 2000). According to the Köppen-Geiger Climate Classification, the region is located in the warm temperate, fully humid zone with warm summers (Kottek et al., 2006). The mean annual air temperature (as assessed for the period 1971-2015) was 8.2 °C (Fig. 1d), and the warmest month was July with a mean air temperature around 18 °C, while the coldest was February with a mean of -4.1 °C. The R package 'climatol' (Guijarro, 2019) was used to produce the Walter and Lieth (1960) climate diagram for the study area (1971-2015) using E-OBS 20.0e climate data. The growing season usually lasts less than 170 days. The mean annual precipitation amounted to 543 mm and the number of days with precipitation ranged from 150 to 160 annually. July was the wettest month with average precipitation around 80 mm (Wójcik and Marciniak, 1993).

The vicinity of the sampling site represents a mixed forest mainly composed of Scots pine (*Pinus sylvestris* L.), silver birch (*Betula pendula* Roth), English oak (*Quercus robur* L.), black alder (*Alnus glutinosa* (L.) Gaertn.) and sporadic Norway maple (*Acer platanoides* L.). Scots pine is the dominant species and covers ca. 84% of the study area. The mean age of Scots pine trees is ca. 70 years, with some individuals over 130 years old (Bank Danych o Lasach, 2020). The studied trees are located in a protected stand in naturally regenerated forest of the Brodnica Landscape Park.

The sampling site in the vicinity of Bachotek Lake (53°31' N, 19°45' E, Fig. 1b), represents a section of a hiking trail excluded from vehicle traffic. This trail was officially marked in 1976 and is one of the most frequently used trails in the Brodnica Lakeland (Matulewski et al., 2019). The tourist season in the study area usually lasts 140 days, i.e., from May to mid-September. The average tourist load is up to 10,000 hikers per summer season, peaking from June to August (Matulewski, 2018).

## 2.2. Root and stem sampling

Root sampling was performed within the frame of a bigger study in June 2015 (Matulewski et al., 2021). For the detailed study presented here, we selected an atypical Scots pine tree that was growing at a relatively short distance (ca. 3.0 m) from a hiking trail with two parallel roots crossing the trail, one buried (unexposed) and one partially exposed root within the trail (Fig. 1c). By excavating both roots, we confirmed that they emerged from the same tree. These two second-order roots, that sprouted from a main lateral root (i.e., first-order root) at a distance of 1.2 m from the stem, were named as the buried (B) and the exposed (E) root. The B root grew completely buried in the soil, whereas the E root had an exposed part on the hiking trail in the trampling zone (Fig. 1c). Sampling of the B and E roots was performed by applying serial sectioning (Kolishchuk, 1990; Krause and Morin, 1995, 1999; Wrońska-Wałach et al., 2016). For this purpose, a root disc sample



(i.e., individual root cross section) was taken every 25 cm along the length of the root. In total 32 cross sections, i.e. 16 cross sections per root sampled from exactly the same distances from the stem, were analysed. In each root, cross sections were labelled in the same way, i.e., from R1 (located closest to the stem) to R16 (positioned in the outermost location from the tree stem) (Fig. 1c). Cross sections from R13 to R16 were located in the trampling zone (Fig. 1c, Fig. 3b). The R13 to R16 parts of the B root were buried naturally in the soil (and excavated only for the purpose of sampling) while those parts of the E root were exposed due to trampling on a hiking trail.

Each root was sampled at a minimum distance of 1.0 m from the base of the tree stem (R1 sections) and up to 4.11 m apart from the stem, i.e., as far as the outer edge of the trampling zone (R16 sections). The minimum distance of 1.0 m from the stem was chosen for two reasons: (i) the movement of the stem base pulling roots upwards, and (ii) roots close to the stem base often experience bending stress due to stem displacement (LaMarche, 1968; Gärtner et al., 2001; Scuderi, 2017). Complete root discs were collected using a hand saw, avoiding bent root parts or spurs.

The B and the E root tree-ring series were cross-dated with the corresponding stem (STEM) chronology and compared with a site chronology (PRES). The PRES chronology was constructed as an arithmetic mean using tree-ring series of 18 trees sampled within the hiking trail, i.e. subjected to trampling. Two to four cores were taken at breast height (1.3 m) from each tree stem using a Pressler incremental corer.

Additionally, to compare the calendar years of both CW and BR occurrences in the B and E roots with other trees, we randomly sampled 18 buried (REF root) and 18 exposed roots (EX). 18 buried roots were sampled from 9 trees growing outside of the hiking trail, i.e., reference site. Both the buried and exposed roots were sampled at maximum distance of 150 m away from the E and B roots. Based on these roots a reference root chronology (REF root) was established and compared with the B and E root chronologies.

### 2.3. Root characteristics

For each root cross section of both roots a description of the root morphology was made, which included an assessment of the mean root diameter, root circularity, root eccentricity, and root surface area (Supplementary Material, Table S1). The depth of the unexposed roots, i.e., the distance between the upper side of the root and the soil surface or the distance between the upper side of the exposed root and the current soil surface were determined. Root circularity  $C$  was obtained following the equation by Kojima et al. (1971),

$$C = 4\pi A/P^2$$

where:  $A$  - root surface area, and  $P$  - root surface perimeter.

Root eccentricity was calculated as a difference between the geometric centre and the actual centre of the root, presented as a percentage of the radius of a circle having the same area as the root cross section (Wrońska-Wałach et al., 2015).

Root surface area was vectorized using a scanned image of each root and then calculated using ImageJ software (Rasband and ImageJ, 1997-2018). To calculate the root volume, the B and the E roots were divided into 15 segments. The average length of a root segment was  $27.4 \pm 6.3$  cm. The volume of each root segment, expressed in cubic centimetres, was measured using the Cylindrical Huber Formula (Grochowski 1973; Pazdrowski et al., 2009),

$$V = \pi l r^2$$

where:  $l$  - length of root segment,  $r$  - Huber radius.

Huber radius is the arithmetic mean of the two radii measured at the beginning and end of the root segment. Cumulative root volume was calculated by summing the volume of all segments for the B and the E roots separately.

## **2.4. Laboratory work**

To ensure an accurate examination of annual growth rings in roots, microscopic analyses were conducted on thin sections. Each root disc was sectioned according to standard protocol (Gärtner and Schweingruber, 2013). In total, 104 thin sections were prepared including multiple sequential cuts taken from root discs of large size. Each 15-20 µm thick section was prepared using a GSL1 sledge microtome (Gärtner et al., 2014). We immersed all the thin sections in sodium hypochlorite (NaOCl) and then stained them with a mixture of Safranin and Astra blue, which enhanced the contrast between the lignified (stained red by Safranin) and non-lignified (stained blue by Astra blue) components of the roots' anatomical structure. After staining, the thin sections were gradually dehydrated with ethanol (50%, 75%, 96%) and rinsed with xylene. The stained root sections were mounted on glass slides, embedded in Canada balsam, and dried at 60°C for 24 h (Schweingruber, 1990; Gärtner et al., 2001; Gärtner and Schweingruber, 2013). Each thin section was photographed at 40x magnification using an Olympus BX43 microscope and SC30 Olympus camera.

## **2.5. Radial growth measurements and cross-dating**

High resolution digital images of root thin-sections were used for ring-width and wood anatomical measurements (Fig. 2). Ring-widths were measured using WinCELL software (Regent Instruments, Canada) with a precision of 0.001 mm. To assure the detection of all growth rings, each root cross section was divided into four quarters. One of the quarters always included the longest radius of a cross section, potentially representing the most complete radius. To trace all radial growth irregularities, the Zig-Zag Segment Tracing (ZZST) method was used (Wrońska et al., 2016). Four radii were measured per individual root cross section and up to eight radii were measured in roots that exhibited highly irregular growth patterns. Measurements of growth rings width did not include scars and

injured parts of the root. Annual ring dates of the same cross section were assigned by visual cross-dating, including the identification and comparison of well-developed, complete rings between the quarters of the same root cross section. For each root section, the total number of missing and wedging (i.e., discontinuous) rings was calculated on the cross-section level (Matulewski et al., 2021).

Cores were acquired from the studied tree stems using a standard procedure (Zielski and Krąpiec, 2004). Polished cores were scanned at 1200 DPI using an Epson Perfection V700 Photo. Annual growth rings were measured on a scanned image with an accuracy of 0.01 mm using CooRecorder ([www.cybis.se](http://www.cybis.se)). A mean tree-ring curve for each tree stem studied was obtained by applying an arithmetic mean over the two to four cores measured per stem.

A stepwise cross-dating procedure was performed to identify radial growth irregularities in each studied root. In the first step, all radial measurements performed for a single root cross section were compared to detect all wedging rings. Following this approach, average tree-ring series for each root cross section was determined as an arithmetic mean. The second step involved cross-dating between mean tree-ring curves obtained for all root cross sections, to detect missing rings. The third step consisted of cross-dating the mean tree-ring curve of the roots with the stem growth curve.

The correspondence between an individual root section and a stem radial growth, so called radial growth coherency (RGC, Matulewski et al. 2021), was determined using Pearson's correlation coefficients. For this purpose, raw chronologies (i.e., arithmetic means) for the B and the E root, together with raw stem and site chronologies (PRES) were used for RGC calculation for a common study period (1970-2015). In addition, RGC was calculated for each root section pair, i.e., for two root sections sampled from the B and the E root at the same distance from the stem.

## 2.6. Wood anatomical features and blue rings

The following wood anatomical parameters were measured on each root cross section: (i) percentage of latewood, (ii) year of scar formation, and (iii) year of occurrence of pronounced resin ducts (PRDs) (Matulewski et al., 2021). Additionally, the time of root exposure was assessed based on changes in the earlywood lumen area and the percentage of latewood, following the protocol established by Gärtner (2003). Moreover, number of growth rings with formation of compression wood (CW) and blue rings (BRs) were quantified, starting from the first annual growth ring for which CW and BR formation was documented (i.e., for the period 1971 - 2015). For each annual growth ring the mean width of the CW and/or the BR zone (Fig. 2) was measured manually along 30 randomly chosen radial files using ImageJ software. The CW and BR zones were expressed as a percentage of total annual ring-width.

The frequency distributions of mean percentage of CW and BR zones were plotted (Fig. 7) for the common period (1971-2015). For all histograms mean percentage of CW and BR zones assessed per calendar year was used and plots were composed using the 'hist' function from the 'graphics' package (Becker et al., 1988; Murrell, 2005) in R version 4.0.0 (R Core Team, 2020).

Climatic conditions for BR years were compared using mean monthly air temperature and precipitation data. Climate data were acquired via Climate Explorer (Trouet and van Oldenborgh, 2013) and calculated from the daily gridded observational dataset E-OBS 20.0e (Haylock et al., 2008) obtained for the 19-20° E and 53-54° N grid. The t-test was used to compare differences in mean monthly temperature and precipitation between BR and non-BR years.

### 3. Results

#### 3.1. Root characteristics

The total length of the B (i.e., buried unexposed) root was 5.7 m, whereas the E root (i.e., partly exposed root) was 1.8 m longer. The mean depth of the unexposed sections of both roots was  $13.44 \pm 2.91$  cm. 33% of the E root length was exposed within the hiking trail and the mean height of the exposed sections of the E root was  $1.65 \pm 0.11$  cm and all of them were in contact with the soil surface (Fig. 5). The mean diameters of the B and E roots were  $2.40 \pm 1.01$  cm and  $3.52 \pm 1.09$  cm, respectively. The mean root surface areas of the B and E roots were  $5.36 \pm 4.22$  cm<sup>2</sup> and  $10.78 \pm 6.46$  cm<sup>2</sup>, respectively. The unexposed cross sections of the B and E roots (i.e., R1-R9) located at a distance of <3.6 m from the tree stem, had almost equal root surface areas (Fig. 3a). In contrast, the root surface areas of the exposed cross sections of the E root were, on average, 14 times larger than those of the unexposed cross-sections of the B root, located in the trampling zone, i.e. at a distance of 4.6 to 5.3 m from the tree stem (Fig. 3b). The root surface area ratio for root section pairs increased with increasing distance from the tree stem ( $r^2 = 0.61$ ,  $p > 0.001$ ). The total volumes of the B and E roots were 2.28 cm<sup>3</sup> and 4.19 cm<sup>3</sup>, respectively. The mean circularity of the B root ( $0.93 \pm 0.02$ ) was higher than that of the E root ( $0.88 \pm 0.06$ ). The mean root eccentricity for the B root ( $34.8\% \pm 15.6$ ) was lower than for the E root ( $48.8\% \pm 30.5$ ). The root eccentricity increased with distance from the stem for both the B and E roots (Fig. 4a).

#### 3.2. Root age and mean ring-width

The mean age of the studied B root cross sections was  $52.3 \pm 8.6$  years, whereas for the E root it was  $54.3 \pm 4.7$  years. The unexposed sections of the B and E roots were of similar age and ranged from 50 to 62 years (Supplementary Material, Table S1). The exposed

root cross sections of the E root were, on average, eight years older than the ones of the unexposed root samples of the B root; both were located in the trampling zone at the same distance (i.e., >4.40 m) from the tree stem. The mean ring-width (MRW) of unexposed cross sections (i.e., R1-R12) of the B and E roots were  $0.31 \pm 0.16$  mm and  $0.33 \pm 0.17$  mm, respectively (Supplementary Material, Table S1). In the trampling zone (i.e., R13-R16 cross sections), the MRW was up to four times greater for the E root than for the B root.

### 3.3. Missing and wedging rings

The mean number of missing rings was 13% and 6% for the B and E root, respectively. All the unexposed cross sections of both roots (i.e., R1-R12) had missing rings, except for the R1 cross sections obtained from both roots, located 1.25 m from the studied tree stem (Fig. 4c). In the trampling zone (i.e., in R13-R16 cross sections) there were no missing rings encountered in the exposed samples of the E root, whereas cross sections from the B root had an average of 11.4% missing rings.

The mean number of wedging rings in the B and E roots was 33.4% and 52.0%, respectively. The number of wedging rings in both roots gradually increased with increasing distance from the tree stem (Fig. 4b). In the trampling zone the mean number of wedging rings in the E root equaled 88% and was, on average, 40% higher than in the B root. Considering the B root only, the number of wedging rings was positively correlated with the number of missing rings ( $r = 0.88$ ,  $p < 0.001$ ). No such correlation was observed for the E root ( $r = -0.35$ ,  $p = 0.184$ ).

### 3.4. Radial Growth Coherency

Ring-width chronologies were developed for the period 1954-2015 (Fig. 6a). The correlation between the raw stem chronology and the raw root chronologies was higher for the E root ( $r = 0.84$ ,  $p < 0.001$ ) than for the B root ( $r = 0.78$ ,  $p < 0.001$ ). The correlation

between the B and E root chronologies was  $r = 0.69$  ( $p < 0.001$ ). The strongest correlation between the B and the E root radial growth was noted for the R2 root sections located 1.58 m from the tree stem. Overall, the RGC of root section pairs decreased with increasing distance from the tree stem ( $r = -0.95$ ;  $p < 0.001$ ) and was not significant for all the cross sections located in the trampling zone (i.e.,  $>4.60$  m from tree stem) (Fig. 6b). The correlation between the B root and the REF root chronology was  $r = 0.63$  ( $p < 0.001$ ).

### 3.5. Wood anatomical changes

The unexposed cross sections of the B and E roots (i.e., R1-R12) had, on average, less than 30% latewood in the annual rings, whereas the exposed samples of the E root had, on average, more than 60% of latewood. In the trampling zone, the E root had on average three times more latewood than the B root (Fig. 5). All exposed cross sections (i.e., R13-R16) of the E root were exposed in 1971 (Fig. 6a). Root exposure was caused by secondary growth *sensu* Gärtner (2007) and numerous wood anatomical changes were formed in the E root only after the exposure event. These included 15 scars and 28 PRDs detected exclusively in the exposed part of the E root. Over 70% of the scars ( $n = 13$ ) and PRDs ( $n = 20$ ) were formed in the course of seven calendar years, i.e., 1972, 1973, 1976, 1986, 1990, 2002 and 2004. A total of 84% of the scars were formed in the middle of the vegetation period, i.e., at the transition between early- and latewood. No scars and no PRDs were formed in the unexposed cross-sections of both roots.

CW was identified only in the exposed parts of the E root (i.e., R13-R16 cross sections, Fig. 7a) and was always found in the lower part of the root. In total, 29 (i.e., 47%) annual rings with CW were documented. The highest occurrence of CW was detected in the periods 1971-1988 and 1995-2000. The mean width of the CW zone within the annual growth ring was 49% (Fig. 7a). The maximum width of the CW zone was 72% and was detected in 1998. In 14 calendar years the width of the CW zone was higher than 50%.



The mean width of the annual growth rings with CW was 25% greater than that in the other rings. The occurrence of CW between the E roots and broader exposed root pool (EX) was fairly coherent, i.e., in 61% ( $n = 25$ ) of all calendar years CW was documented in both root pools for the common period 1971-2015 (Fig. 7b). CW was not found in the broader reference root pool (REF root).

### 3.6. Blue rings

BRs were identified only in six root cross sections acquired from the E root. These included all exposed (i.e., R13-R16) and two adjacent unexposed sections (R11-R12) of the E root positioned less than 5 cm below the soil surface within the hiking trail. The BRs were formed over the course of 25 calendar years, i.e., in 40% of growth rings from the common period 1954-2015. Considering exposed roots only, the highest frequency of BRs was observed in the following calendar years and periods: 1973-1975, 1980-1981, 1984-1985, 1987-1988, 1993, 1995, 1998, 2001 and 2002. The calendar years of BR occurrences between the E root and broader exposed root pool (EX) were highly overlapping, i.e., in 82% ( $n = 23$ ) of all calendar years BRs were noted in both root pools for the common period (1971-2015) (Fig. 7d). BRs were not found in the broader reference root pool (REF root).

The maximum number of BRs was recorded in the exposed part of the E root (i.e., R14) and corresponded to 50% ( $n = 25$ ) of calendar years. In ten cases the width of the BR zone was greater than 10% of the total tree-ring width (Fig. 7c). The mean width of the BR zone was 7.8% and 10.1% of tree-ring width for the buried (i.e., R11-R12) and exposed (i.e., R13-R16) cross sections of the E root, respectively. For five calendar years, i.e., 1973-1975, 1978 and 1980, the mean width of the BR zone comprised over 15% of tree-ring width.

A comparison of mean monthly temperatures for years with ( $n = 25$ ) and without ( $n = 14$ ) BRs formation (for the common period 1971-2009) revealed significant difference in mean

November ( $p = 0.012$ ) and marginally significant difference in mean September ( $p = 0.051$ ) air temperatures (Fig. 8a). The mean November air temperature for BR years was  $2.7^{\circ}\text{C}$  ( $\text{sd} = 2.0$ ) and  $1.6^{\circ}\text{C}$  lower than that for years without BRs. The largest difference in mean November air temperature was found for the year 1978 in which the width of the BR zone equaled 19% of the annual ring-width. Difference in mean September air temperatures was lower and amounted to  $1^{\circ}\text{C}$ , with a mean September air temperature of  $12.8^{\circ}\text{C}$  ( $\text{sd} = 1.3$ ) and  $13.8^{\circ}\text{C}$  ( $\text{sd} = 1.7$ ) for BR versus non-BR years, respectively. Significant differences in mean monthly precipitation between BR versus non-BR years were calculated for July ( $p = 0.017$ ). Mean monthly precipitation was higher for July (mean =  $82.5\text{ mm}$ ,  $\text{sd} = 33.7$ ) in BR years (Fig. 8b) versus non-BR years (mean =  $55.9$ ,  $\text{sd} = 29$ ).

## 4. Discussion

### 4.1. Root characteristics

Unexposed root cross sections obtained from the B and E roots were characterized by similar morphologic features. In contrast, high discrepancies in the morphology between the two roots were noted in the trampling zone. The sections of the E root increased their size due to pronounced secondary growth after root exposure. The volume of the exposed part of the E root in the trampling zone was more than ten times larger than that of the unexposed B root, suggesting a key impact of trampling and root exposure on root biomass allocation. It is known that biomass and secondary growth are not evenly distributed within the tree-root system and can become altered in response to abiotic factors, such as soil conditions (Schroth, 1998; Puhe, 2003; Helmisaari et al., 2007; Stokes et al., 2009; Ji et al., 2012; Ghestem et al., 2011), geomorphologic processes (Fayle 1976), and trampling (Bodoque et al., 2005; Pelfini and Santili 2006; Rubiales et al., 2008). However, the effect of trampling on root biomass alteration was to our knowledge not previously quantified. Also, root biomass partitioning may depend on an optimal

distribution of available resources (Stokes and Mattheck, 1996). Nicoll et al. (2006) and Montagnoli et al. (2019a, b) noted that spatial variation in root biomass may be caused by continuous changes in environmental factors. The literature suggests that environmental factors such as light intensity and temperature affect the level of carbohydrates in roots (Tromp, 1983; Reid et al., 1983) which might induce higher biomass allocation in exposed root parts. In addition, observations by Nicoll et al. (1995) and Stokes et al. (1995) demonstrated that mechanical stress plays a fundamental role in the development of root architecture, causing significant changes to root biomass allocation that may impact overall tree stability.

#### **4.2. Radial growth discrepancies**

The unexposed root sections obtained from the B and E roots were of similar age and MRWs; however, large discrepancies between these roots were noted in the trampling zone. Despite the similar ages of both roots at close distances to the tree stem, the exposed parts of the E root were, on average, eight years older than the unexposed sections of the B root located at exactly the same distance from the tree stem. This might be related to the fact that the E root was 1.8 m longer than the B root, which suggests that increased light intensity stimulates primary growth and elongation of the E roots. These results are similar to those reported by Michniewicz and Stopińska (1980a, 1980b) for *Pinus sylvestris*.

Maximum ring-widths were observed, as expected, in the exposed cross sections subjected to increased light intensity and temperature (Gärtner, 2003, 2007) and mechanical stress (Bodoque et al., 2005) associated with trampling. The largest radial growth changes were previously observed in the exposed roots, but no missing rings were noted in the exposed second-order roots. Moreover, wedging rings were more frequently noted in the exposed root cross sections than in the unexposed ones. This was related to increased root biomass and the mechanical function of the root that began to dominate

over the conduction function once the root was exposed (Fayle, 1968; Pérez-Rodríguez et al., 2007). These growth irregularities are typical for roots that commonly manifest very irregular radial growth patterns, both in the longitudinal and cross-sectional profile (Fayle, 1968, 1975; Krause and Morin, 1995, 1999, Wrońska-Walach et al., 2016). *P. sylvestris* roots are not an exception in this respect, as shown in the previous study on exposed roots of this species from central Spain (Bodoque et al., 2005). Common radial growth irregularities in roots may be due to a delay or a deficiency in availability of growth hormones during earlywood formation (Panshin and de Zeeuw, 1970) or due to the progressive reduction in ring-widths as the age of the tree increases (Fritts, 1976). Moreover, common growth irregularities in roots may result from different cell division patterns along the root circumference caused by mechanical stress (Montagnoli, et al., 2019b). Mechanical impacts on root growth may be generated by trampling, as previously reported by Bodoque et al. (2005), Pelfini and Santili (2006) and Rubiales et al. (2008), and may cause the frequent formation of wedging rings. In our study root eccentricity was observed in both roots, but the greatest root eccentricity was found in the exposed cross sections of the E root subjected to mechanical stress. This agrees with previous observations of *Pinus ponderosa* (Montagnoli et al., 2019b) and *Picea abies* roots (Wrońska-Walach et al., 2016) exposed, however, by natural geomorphic processes rather than by trampling.

#### **4.3. Cross-dating and radial growth coherency**

The stepwise root cross-dating method employed in this study was similar to that used by Wrońska-Walach et al. (2016), and therefore it was possible to obtain high root-stem RGC. The highest root-stem RGC for a single root section was noted for the exposed part of the E root, which was characterized by the lowest number of missing rings. In contrast, previous studies have revealed relatively weak correlations between a root and a

corresponding stem tree-ring series (Bodoque et al., 2005; Pelfini and Santili, 2006). There are several key reasons that may explain low RGC between the roots and stem of the same tree. Most radial growth discrepancies may be due to divergent growth formation in roots and stems (Fayle 1968; Krause and Morin, 1995). This, in turn, may be related to differences between root and stem functions and differences in intrinsic regulation of cambial growth (Savidge, 2000). Numerous studies (e.g., LaMarche, 1968, Alestalo, 1971; Gärtner, 2003, Malik 2005, Bodoque et al., 2005, 2011; Corona et al., 2011; Ballesteros-Cánovas et al., 2013, 2015) have also broadly emphasized the role of geomorphologic processes, which may cause common growth discrepancies in roots subjected to exposure. Root exposure often results in increased ring-widths in exposed root parts and decreased radial growth in unexposed parts (Alestalo, 1971; Gärtner, 2003; Bodoque et al., 2011; Wrońska-Wałach et al., 2015). Moreover, the response of tree stems and roots to the same ecological and geomorphologic factors can often be temporally delayed (Krause and Morin, 1995) or even absent (Pelfini and Santili, 2006). In our study we observed growth constraints between the stem and roots, including differences between trampled and non-trampled roots. In addition, it should be noted that decreased radial growth in the tree stem often occurs after root exposure (Zielski et al., 1998; Gärtner, 2003; Ciapała et al., 2014; Matulewski et al., 2019). Despite reduced growth in tree stems and/or high discrepancies in radial growth in roots shown by this study we would like to emphasize that stepwise root cross-dating (Wrońska-Wałach et al., 2016) supplemented by serial-sectioning (Kolishchuk, 1990) enables reliable dendrochronological dating of tree roots and substantially minimizes dating errors.

#### **4.4. Compression wood**

Mechanical stress causes a change in cell division and cell dimensions which also leads to eccentric growth of tree-rings (Mattheck and Breloer, 1992; Bodoque et al., 2015). Such asymmetric ring-width distribution in the tree stem and branches is often related to the

presence of CW (Westing, 1965; Timell 1986; Mattheck and Breloer, 1996; Fischer et al., 2019). Our findings confirmed such results in *Pinus sylvestris* roots, especially in the root sections located within a hiking trail. In all exposed root cross sections from the E root, CW was always formed in the lower root part, i.e., in the opposite direction to the mechanical stress induced by trampling. By contrast, CW was not observed in the unexposed root cross sections of both roots. The formation of CW in exposed sections of the E root was strongly associated with the formation of wedging rings that substantially increased the total root volume. In fact, the volume of the exposed part of the E root was ten times greater than the volume of the unexposed part of the B root, both being located in the trampling zone and at the same distance from the stem. This key finding designates not only highly altered growth of exposed roots, but more importantly, documents that radial growth and biomass allocation of roots is substantially modified by trampling.

Gärtner (2007) found that the anatomical structure of roots changes due to transformation of its function triggered by exposure and modification of its position, i.e., below or above the soil surface. Our findings confirm that a tree adjusts its radial growth in the exposed portion of the root in response to modified environmental conditions (Carrara and Carroll, 1979), such as soil habitat or light availability. However, the identification of the dominant factor, i.e., mechanical forces or gravity, responsible for CW formation in the roots remains challenging (Lopez Saez et al., 2014). Despite this, our study clearly suggests that the occurrence of CW in the trampled sections on the E root acts as a proxy of the mechanical impact associated with trampling, since CW formation was commonly observed only in the exposed parts of the E root.

Analyses performed for CW using the broader root pool, suggests that CW formation is triggered by a wider range of ecological factors than climate itself. We still lack systematic knowledge of the potential influence of thermal and/or moisture conditions affecting CW formation in roots. CW formation is potentially influenced by either interrelated climatic

and/or ecological factors, including human impacts. CW formation is strongly affected by environmental conditions (Westing, 1965) and is commonly found in tree roots exposed by various geomorphic processes (Carrara and Carroll, 1979; Bodoque et al., 2005; Hitz et al., 2008; Malik and Wistuba, 2012), which can abruptly change soil cover stability and the root habitat. In the case of CW formation in exposed roots on a hiking trail, we hypothesized that natural geomorphic processes might act together with trampling activity, thus inducing greater instability of root growth conditions. For example, during summers hiking intensity not only increases soil compaction, but the mechanical impact of trampling triggers opening of little cracks in the trail surface and removes the soil from the roots located near the surface. As a consequence, the erosion intensity may increase within the hiking trail, especially during high precipitation events which have the potential to intensify surface erosion, deepen the trail and increase root exposure. This yields higher susceptibility of exposed roots to mechanical damage and CW formation. Findings reported by Lopez Saez et al. (2012) for a landslide area suggest that the onset of CW formation in tree stems coincides with intense summer precipitation. However, the lack of root-specific research hampers direct comparisons of CW observations performed in our study with other geographic regions or tree species.

#### **4.5. Blue rings**

BRs represented the most pronounced anatomical feature in the exposed cross sections of the E root (Fig. 2). BRs have been recently reported from tree stems (e.g. Piermattei et al., 2015; Tardif et al., 2020; Björklund et al., 2021; Edwards et al. 2021) and, to our knowledge, they have not yet been observed in tree roots of any conifer species. Numerous previous studies have indicated annual growth rings with unusually thin-walled latewood cells with incompletely or non-lignified tracheid cell walls called 'light' rings (e.g. Fillion et al., 1986; Yamaguchi et al., 1993; Hantemirov et al., 2000; Tardif et al., 2011).

Thanks to the use of the double-staining procedure for preparation of wood sections, that includes the application of Astra blue and Safranin (Gärtner and Schweingruber, 2013), such rings are sometimes (not always, see Piermattei et al., 2020) highlighted by the presence of blue-stained axial tracheid cell walls, thus called 'blue' rings (Piermattei et al., 2015). These not fully lignified annual growth rings are often attributed to climatic factors, such as low growing season temperatures and/or cool springs (Yamaguchi et al., 1993; Szeicz, 1996; Montwé et al., 2018; Gurskaya, 2019; Piermattei et al., 2020; Tardif et al., 2020). For example, Girardin et al. (2009) noted the importance of late onset of the growing season (i.e. cool April and May), generally cool conditions, and early radial growth cessation (cool August and September) for frequent formation of light rings in a mixed boreal forest in central Canada. Furthermore, many studies sometimes link incompletely lignified and frost rings, to global climatic events such as long-term cooling effects after major volcanic eruptions (e.g. LaMarche and Hirschboeck, 1984; Hantemirov et al., 2004; Janecka and Kaczka, 2015; Piermattei et al., 2020; Tardif et al., 2020). Regardless of the precise cause for their formation, the occurrence of light and blue rings is mainly reported for temperature-limited habitats such as boreal forests or upper treelines in mountain ranges. BRs studies in lowland temperate areas, such as our study, are not common (cf. Vitas, 2018; Matisons et al., 2020).

Examination of air temperature conditions prevailing in BR versus non-BR years in our study showed that BRs occurred in years characterized by lower September and November temperatures (Fig. 8a). These observations are coherent with previous studies that have shown high correlation between light rings formation and below average temperatures at the end of the growing season, i.e. lower September and October temperatures for *Picea abies* growth in the Austrian Alps (Gindl, 1999) and lower August-September temperatures for *Picea mariana* growth in northern Quebec (Filion, 1986). Given that BRs were found mainly in the exposed part of the E root, we hypothesize that



the exposed roots are subjected to more severe microclimatic conditions than the roots naturally buried in the soil. Indeed, only two cross sections of the E root (i.e. R11 and R12) located at the edge of the hiking trail and positioned less than 5 cm below the soil surface had BRs. In these two cases, only ca. 4% of annual growth rings had BRs, whereas BRs in the exposed cross sections of the E root were ten times more frequent. Exposed roots, and to a lesser extent shallow roots, are subjected to higher daily amplitudes and lower minimum temperatures than the adjacent buried roots, that grow under less variable soil temperature conditions. Buried roots are not exposed to high amplitudes of ambient temperatures, thus their habitat is more favorable for undisturbed cell wall deposition and lignification than the habitat of exposed roots within the hiking trail.

In contrast, some not-fully lignified growth rings examined in a semi-arid region located in northern China were not associated with cold temperatures but with severe droughts (Liang and Eckstein, 2006). Similarly, a recent study conducted along an altitudinal gradient in Bulgaria showed drought-induced light ring formation in stems of *Pinus sylvestris* (Panayotov, 2013). In our study, higher occurrence of BRs in exposed roots was significantly related to higher mean July precipitation. However, this relationship might be partially explained by the high collinearity between mean temperature and precipitation in July ( $r = -0.47$ ,  $p < 0.001$ ) and almost significantly ( $p = 0.087$ ) lower air temperatures in BR years compared to non-BR years (Fig. 8a). Nevertheless, it has been previously recognized that trampled roots are more prone to drought stress that may further hamper cambial activity in these roots (Montagnoli et al., 2019a). In comparison to tree stems, exposed roots often lack a thick layer of bark and are more likely exposed to colder ground temperatures and other external stressors such as insects and pathogens. Furthermore, we cannot exclude the detrimental effect of trampling as a triggering or co-triggering effect for the formation of BRs in roots growing in hiking areas. Considering the high frequency of BRs in exposed sections of the E root, future studies should aim to investigate possible

effects of both climate and ecological impacts on commonness of BR formation in tree roots.

## 5. Conclusions

Our study revealed altered growth between trampled and non-trampled roots of *Pinus sylvestris* in the lowland area in Poland. We identified a number of radial growth and wood anatomical changes in the longitudinal profile of two adjacent roots. Large discrepancies in root morphology, radial growth, and wood anatomy were noted in two parallel roots within the same root system. Detailed analyses performed in high spatial resolution found that the volume of the exposed portion of the E root was ten times greater than that of the unexposed B root, located at the same distance from the tree stem. Our results suggest that root exposure caused by trampling strongly amplifies biomass allocation in tree roots. Thus, exposed roots may play an important role in the carbon cycle of forest ecosystems used for recreational purposes.

Large discrepancies in RGC were observed between the B and the E roots, i.e. two adjacent roots of similar age. Root section pairs sampled closest to the tree stem showed the highest level of coherency in the radial growth pattern, which decreased with increasing distance from the stem. Nevertheless, the highest RGC between root and stem growth was noted for the exposed part of the E root, which was characterized by the lowest number of missing rings.

Our study has shown fairly ubiquitous formation of both CW and BRs in exposed *Pinus sylvestris* roots. We showed that the occurrence of CW in the exposed roots was probably caused by ecological factors like mechanical stress and human impact. Furthermore, we documented the occurrence of BRs in the roots, which were commonly formed in the exposed root sections of the E root. Both climatic and non-climatic factors require careful assessment in future studies on BR formation in tree roots. A very high share of BRs in

exposed root sections suggests their high potential for future dendroecological studies. Thus, our study opens new questions regarding the ecology of tree roots. Future studies should focus both on other tree species and higher sample replication in order to confirm or verify the outcomes this study.

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## References

- Alestalo, J., 1971. Dendrochronological interpretation of geomorphic processes. *Fennia. Soc. Geog. Fennia* 105, 1-140.
- Ballesteros-Cánovas, J.A., Bodoque, J.M., Lucia, A., Martín-Duque, J.F., Díez-Herrero, A., Ruiz-Villanueva, V., Rubiales, J.M., Genova, M., 2013. Dendrogeomorphology in badlands: methods, case studies and prospects. *Catena* 106, 113-122. <https://doi.org/10.1016/j.catena.2012.08.009>.
- Ballesteros-Cánovas, J.A., Corona, C., Stoffel, M., Lucia-Vela, A., Bodoque, J.M., 2015. Combining terrestrial laser scanning and root exposure to estimate erosion rates. *Plant Soil* 394 (1-2), 127-137. <https://doi.org/10.1007/s11104-015-2516-3>.
- Bank Danych o Lasach, 2020. Opis taksacyjny drzewostanu, <https://www.bdl.lasy.gov.pl/portal/mapy/> (accessed 7 December 2020).
- Becker, R.A., Chambers, J.M., Wilks, A.R., 1988. *The New S Language*. Wadsworth & Brooks/Cole.
- Björklund J., Fonti M.V., Fonti P., Van den Bulcke J., von Arx G., 2021. Cell wall dimensions reign supreme: cell wall composition is irrelevant for the temperature signal of late-wood density/blue intensity in Scots pine. *Dendrochronologia*, 65, 125785
- Bodoque, J.M., Díez-Herrero, A., Martín-Duque, J.F., Rubiales, J.M., Godfrey, A., Pedraza, J., Carrasco, R.M., Sanz, M.A., 2005. Sheet erosion rates determined by using dendrogeomorphological analysis of exposed tree roots: two examples from Central Spain. *Catena* 64, 81-102. <https://doi.org/10.1016/j.catena.2005.08.002>.

- Bodoque, J.M., Lucía, A., Ballesteros, J.A., Martín-Duque, J.F., Rubiales, J.M., Genova, M., 2011. Measuring medium-term sheet erosion in gullies from trees: a case study using dendrogeomorphological analysis of exposed pine roots in central. *Geomorphology* 134 (3-4), 417-425. <https://doi.org/10.1016/j.geomorph.2011.07.016>.
- Bodoque, J.M., Ballesteros-Cánovas, J.A., Lucia, A., Diez-Herrero, A., Martin-Duque, J.F., 2015. Source of error and uncertainty in sheet erosion rates estimated from dendrogeomorphology. *Earth Surface Processes and Landforms* 40(9), 1146-1157. <https://doi.org/10.1002/esp.3701>.
- Bohm, W., 1979. *Methods of Studying Root Systems*. Ecological Studies, Vol. 33. Berlin: Springer. <https://doi.org/10.1007/978-3-642-67282-8>.
- Cairns, M.A., Brown, S., Helmer, E.H., Baumgardner, G.A., 1997. Root biomass allocation in the world's upland forests. *Oecologia* 111, 1-11. <https://doi.org/10.1007/s004420050201>.
- Carrara, P.E., Carroll, T.R., 1979. The determination of erosion rates from exposed tree roots in the piceance basin, Colorado. *Earth Surface Process*. 4, 307-317. <https://doi.org/10.1002/esp.3290040402>.
- Chiatante, D., Scippa S. G., Iorio A. D., Sarnataro M., 2002. The influence of steep slopes on root system development. *J. Plant Growth Regul.*, 21, 247-260. <https://doi.org/10.1007/s00344-003-0012-0>.
- Ciapała, S., Adamski, P., Zielonka, T., 2014. Tree ring analysis as an indicator of environmental changes caused by tourist trampling - a potential method for the assessment of the impact of tourists. *Geochronometria* 41, 392-399. <https://doi.org/10.2478/s13386-013-0170-1>.
- Cook, E.R., Kairiukstis, L.A., 1990. (Eds.), *Methods of Dendrochronology - Applications in the Environmental Sciences*, Kluwer Academic Publishers, Dordrecht, Boston.
- Corona, C., Lopez Saez, J., Rovéra, G., Stoffel, M., Astrade, L., Berger, F., 2011. High resolution, quantitative reconstruction of erosion rates based on anatomical changes in exposed roots at Draix, Alpes de Haute-Provence - critical review of existing approaches and independent quality control of results. *Geomorphology* 125, 433-444. <https://doi.org/10.1016/j.geomorph.2010.10.030>.
- Coutts, M.P., 1983. Root architecture and tree stability. *Plant Soil* 71, 171-188. <https://doi.org/10.1007/bf02182653>.
- Coutts, M.P., 1987. Developmental processes in tree root systems. *Can. J. For. Res.* 17, 761-767. <https://doi.org/10.1139/x87-122>.
- Danjon, F., Fourcaud, T., Bert, D., 2005. Root architecture and wind-firmness of mature *Pinus pinaster*. *New Phytologist*. 168, 387-400. <https://doi.org/10.1111/j.1469-8137.2005.01497.x>.
- Danjon, F., Caplan, J.S., Fortin, M., Meredieu, C., 2013. Descendant root volume varies as a function of root type: estimation of root biomass lost during uprooting in *Pinus pinaster*. <https://doi.org/10.3389/fpls.2013.00402>.

de Zio, E., Montagnoli, A., Karady, M., Terzaghi, M., Sferra, G., Antoniadi, I., Scippa, G. S., Ljung, K., Chiatante, D., Trupiano, D., 2020. Reaction Wood Anatomical Traits and Hormonal Profiles in Poplar Bent Stem and Root. *Front. Plant Sci.* 11 :590985. <https://doi.org/10.3389/fpls.2020.590985>

Drexhage, M., Chauvière, M., Colin, F., Nielsen, C. N. 1999. Development of structural root architecture and allometry of *Quercus petraea*. *Canadian Journal of Forest Research*, 29(5), 600-608. <https://doi.org/10.1139/x99-027>.

Dunbabin, V.M., Diggle, A.J., Rengel, Z., van Hugten, R., 2002. Modelling the interactions between water and nutrient uptake and root growth. *Plant and Soil* 239, 19-38. <https://doi.org/10.1023/A:1014939512104>.

Edwards J., Anchukaitis K. J., Zambri B., Andreu - Hayles L., Oelkers R., D'Arrigo R., von Arx G., 2021. Intra - Annual Climate Anomalies in Northwestern North America Following the 1783-1784 CE Laki Eruption. *Journal of Geophysical Research: Atmospheres*, 126(3), <https://doi.org/10.1029/2020JD033544>

Fayle, D.C.F., 1968. Radial growth in tree roots, in: Technical Report No. 9. Faculty of Forestry, Univ., Toronto, pp. 183.

Fayle, D.C.F., 1976. Stem sway affects ring width and compression wood formation in exposed root bases. *Forest Science* 22, 193-194. <https://doi.org/10.1093/forestscience/22.2.193>.

Fischer, U., Kucukoglu, M., Heliarutta, Y., Bhalerao, R., 2019. The dynamics of cambial stem cell activity. *Annu. Rev. Plant Biol.* 70, 293-319. <https://doi.org/10.1146/annurev-arplant-050718-100402>.

Filion, L., Payette, S., Gauthier, L., Boutin, Y., 1986; Light rings in subarctic conifers as a dendrochronological tool. *Quaternary Research* 26, 272-279. [https://doi.org/10.1016/0033-5894\(86\)90111-0](https://doi.org/10.1016/0033-5894(86)90111-0).

Fritts, H.C., 1976. *Tree-Rings and Climate*. Academic Press London, pp. 567.

Gärtner, H., 2003. Holzanatomische Analyse diagnostischer Merkmale einer Freilegungsreaktion in Jahrringen von Koniferenwurzeln zur Rekonstruktion geomorphologischer Prozesse. *Diss. Bot.* pp. 378.

Gärtner, H., 2007. Tree roots-methodological review and new development in dating and quantifying erosive processes. *Geomorphology* 86 (3-4), 243-251. <https://doi.org/10.1016/j.geomorph.2006.09.001>.

Gärtner, H., Schweingruber, F.H., Dikau, R., 2001. Determination of erosion rates by analyzing structural changes in the growth pattern of exposed roots. *Dendrochronologia* 19, 81-91. <https://www.dora.lib4ri.ch/wsl/islandora/object/wsl:2853>.

Gärtner, H., Schweingruber, F.H., 2013. *Microscopic Preparation Techniques for Plant Stem Analysis*. Swiss Federal Research Institute WSL, Birmensdorf, pp. 78.

- Gärtner, H., Lucchinetti, S., Schweingruber, F.H., 2014. New perspectives for wood anatomical analysis in dendrosciences: the GSL1-microtome. *Dendrochronologia* 32, 47-51. <https://doi.org/10.1016/j.dendro.2013.07.002>.
- Ghestem, M., Sidle, R.C., Stokes, A., 2011. The influence of plant root systems on subsurface flow: implications for slope stability. *BioScience* 61, 869-879. <https://doi.org/10.1525/bio.2011.61.11.6>.
- Gindl, W., 1999. Climatic significance of light rings in Timberline spruce, *Picea abies*, Austrian Alps. *Arctic Antarctic and Alpine Research*, 31(3), 242-246. <https://doi.org/10.1080/15230430.1999.12003304>.
- Girardin, M.P., Tardif, J.C., Epp, B., Conciatori, F., 2009. Frequency of cool summers in Interior North America over the past three centuries. *Geophysical Research Letters* 36, L07705. <https://doi.org/doi:10.1029/2009GL037242>.
- Glock, W.S., Douglass, A.E., Person, G.A., 1937. Principles and methods of tree-ring analysis. Carnegie Institute, Publ., Washington, vol. 486, pp. 100.
- Grochowski, J., 1973. *Dendrometria*. PWRiL Warszawa, pp. 594.
- Gurskaya, M.A., 2019. Effect of summer monthly temperatures on light tree ring formation in three larch species (*Larix*) in the Northern Forest-Tundra of Siberia. *Russian Journal of Ecology*, 50(4), 343-351. <https://doi.org/10.1134%2FS1067413619040088>.
- Hantemirov, R.M., Gorlanova, L.A., Shiyatov, S.G., 2000. Pathological Tree-Ring Structures in Siberian Juniper (*Juniperus sibirica* Burgsd.) and Their Use for Reconstructing Extreme Climatic Events. *Russian Journal of Ecology* 31(3), 167-173. <https://doi.org/10.1007/BF02762816>.
- Hantemirov, R.M., Gorlanova, L.A., Shiyatov, S.G., 2004. Extreme temperature events in summer in northwest Siberia since AD 742 inferred from tree rings. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 209, 155-164. <https://doi.org/10.1016/j.palaeo.2003.12.023>.
- Haylock, M., Hofstra, N., Klein Tank, A., Klok, L., Jones, P., New, M., 2008. A European daily high-resolution gridded dataset of surface temperature and precipitation for 1950-2006. *J Geophys Res Atmos* 113:113. <https://doi.org/10.1029/2008JD010201>.
- Helmisaari, H., Derome, J., Nöjd, P., Kukkola, M., 2007. Fine root biomass in relations to site and stand characteristics in Norway spruce and Scots pine stands. *Tree physiology* 27, 1493-1504. <https://doi.org/10.1093/treephys/27.10.1493>.
- Hitz, O.M., Gärtner, H., Heinrich, I., Monbaron, M., 2008. Application of ash (*Fraxinus excelsior* L.) roots to determine erosion rates in mountain torrents. *Catena* 72 (2), 248-258. <https://doi.org/10.1016/j.catena.2007.05.008>.
- Jagodziński, A.M., Kałucka, I., 2010. Fine roots biomass and morphology in a chronosequence of young *Pinus sylvestris* stands growing on a reclaimed lignite mine spoil heap. *Dendrobiology* 64: 19-30.



Jagodziński, A.M., Kałucka I., 2011. Fine root biomass and morphology in an age-sequence of post-agricultural *Pinus sylvestris* L. stands. *Dendrobiology* 66: 71-84.

Jagodzinski, A.M., Ziółkowski, J., Warnkowska, A., Prais, H., 2016. Tree age effects on fine root biomass and morphology over chronosequences of *Fagus sylvatica*, *Quercus robur* and *Alnus glutinosa* stands. *PLoS One* 11 (2): e0148668.  
<https://doi.org/10.1371/journal.pone.0148668>.

Janecka, K, Kaczka, R.J., 2015. Tree rings of *Pinus cembra* L. in the Tatra Mts as a proxy of significant volcanic eruptions in the last 280 years. *TRACE-Tree rings in archaeology, climatology and ecology* 13:49-55 (GFZ Potsdam, Scientific Technical Report STR15/06, Potsdam).

Ji, J., Kokutse, N., Genet, M., Fourcaud, T., Zhang, Z., 2012. Effect of spatial variation of tree root characteristics on slope stability. A case study on black locust (*Robinia pseudo-acacia*) and arborvitae (*Platycladus orientalis*) stands on the Loess Plateau, China. *Catena* 92, 139–154. <https://doi.org/10.1016/j.catena.2011.12.008>.

Jose A. Guijarro 2019. climatol: Climate Tools (Series Homogenization and Derived Products). R package version 3.1.2. <https://CRAN.R-project.org/package=climatol>

Karliński, L., Jagodziński, A.M., Leski, T., Butkiewicz, P., Brosz, M., Rudawska, M., 2014. Fine root parameters and mycorrhizal colonization of horse chestnut trees (*Aesculus hippocastanum* L.) in urban and rural environments. *Landscape and Urban Planning* 127: 154-163. <https://doi.org/10.1016/j.landurbplan.2014.04.014>.

Kojima, T., Saito, K., Kakai, T., Obata, Y., Saigusa, T., 1971. Circularity ratio. A certain quantitative expression for the circularity of a round figure. *Okajimas Folia Anat. Jpn.* 48 (2), 153-161.

Kolishchuk, V., 1990. Dendroclimatological study of prostrate woody plant. in: Cook, E.R., Kairiukstis, L.A. (Eds), *Methods of Dendrochronology Applications in the Environmental Sciences*. Kluwer Academic Publ, Dordrecht, pp. 51-55.

Kondracki, J., 2000. *Geografia Regionalna Polski*. Wydawnictwo Naukowe PWN, Warszawa, pp. 444.

Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. World Map of Köppen-Geiger Climate Classification updated. *Meteorol. Z.*, 15, 259-263.

Krause, C., 1992. *Ganzbaumanalyse von Eiche, Buche, Kiefer und Fichte mit dendroökologischen Methoden*. Dissertation, Universität Hamburg, pp. 163.

Krause, C., Eckstein, D., 1993. Dendrochronology of roots. *Dendrochronologia* 11, 9-23.

Krause, C., Morin, H., 1995. Changes in radial increment in stems and roots of balsam spruce (*Abies Balsamea* L. Mill.) after defoliation by spruce budworm. *Forest. Chronicle* 71 (6), 747–754. <https://doi.org/10.5558/tfc71747-6>.

Krause, C., Morin, H., 1999. Root growth and absent rings in mature black spruce and balsam fir, Quebec, Canada. *Dendrochronologia* 16-17, 21-35.  
[http://refhub.elsevier.com/S1125-7865\(19\)30135-3/sbref0250](http://refhub.elsevier.com/S1125-7865(19)30135-3/sbref0250).

- Krause, C., Morin, H., 2005. Adventive-root development in mature black spruce and balsam fir in the boreal forests of Quebec, Canada. *Canad. J. Forest Res.* 35 (11), 2642-2654. <https://doi.org/10.1139/X05-171>.
- LaMarche Jr., V.C., 1968. Rates of slope degradation as determined from botanical evidence, White Mountains, California. US Geological Survey Professional Paper 352-I.
- LaMarche Jr., V.C., Hirschboeck, K.K., 1984. Frost rings in trees as records of major volcanic eruptions. *Nature* 307 (5946), 121-126. [https://doi.org/0028-0836/84/020121-06\\$01.00](https://doi.org/0028-0836/84/020121-06$01.00).
- Lee, P.W., Eom, Y.G., 1988. Anatomical comparison between compression wood and opposite wood in a branch of Korean pine (*Pinus koraiensis*). *IAWA Bull.* 9, 275-284. <https://doi.org/10.1163/22941932-90001077>.
- Liang, E., Eckstein, D., 2006. Light rings in Chinese pine (*Pinus tabulaeformis*) in semiarid areas of north China and their palaeo-climatological potential. *New Phytologist* 171, 783-791. <https://doi.org/10.1111/j.1469-8137.2006.01775.x>.
- Lopez Saez, J., Corona, C., Stoffel, M., Rovéra, G., Astrade, L., Bérger, F., 2011. Mapping of erosion rates in marly badlands based on coupling of anatomical changes in exposed roots with slope maps derived from LIDAR data. *Earth Surface Process. Landf.* 36 (9), 1162–1171. <https://doi.org/10.1002/esp.2141>.
- Lopez Saez, J., Corona, C., Stoffel, M., Berger, F., 2014. Assessment of forested shallow landslide movements coupling tree ring records from stems and exposed roots. *Géomorphologie: relief, processus, environnement* 2, 159-174. <https://doi.org/10.4000/geomorphologie.10616>.
- Malik, I., 2005. Przebieg erozji wąwozowej na podstawie datowania odsłonięcia korzeni drzew-na przykładzie badań z Wysoczyzny Proboszczowskiej (Wyżyna Śląska), *Przegląd Geograficzny* 77(3), 367-381.
- Malik I., 2008a. Dendrochronologiczny zapis współczesnych procesów rzeźbotwórczych kształtujących stoki i doliny rzeczne wybranych stref krajobrazowych Europy Środkowej, *Prace Naukowe Uniwersytetu Śląskiego* Nr 2566, Wyd. UŚ, Katowice, pp. 156.
- Malik, I., 2008b. Dating of small gully formation and establishing erosion rate in old gullies under forest by means of anatomical changes in expose tree roots (Southern Poland). *Geomorphology* 93 (3-4), 421-436. <https://doi.org/10.1016/j.geomorph.2007.03.007>.
- Malik, I., Pawlik, Ł., Ślęzak, A., Wistuba, M., 2019. A study of the wood anatomy of *Picea abies* roots and their role in biomechanical weathering of rock cracks. *Catena* 173, 264-275. [doi:10.1016/j.catena.2018.10.018](https://doi.org/10.1016/j.catena.2018.10.018).
- Malik, I., Wistuba, M., 2012. Dendrochronological methods for reconstructing mass movements - an example of landslide activity analysis using tree-ring eccentricity, *Geochronometria* 39(3), 180-196.
- Matisons, R., Gärtner, H., Elferts, D., Karklina, A., Adamovics, A., Jansons, A., 2020. Occurrence of 'blue' and 'frost' rings reveal frost sensitivity of eastern Baltic provenances of Scots pine. *For. Ecol. Manage.* 457, 1-8. <https://doi.org/10.1016/j.foreco.2019.117729>.



Mattheck, C., Breloer, H., 1992. Der Wurzelquerschnitt als Protokoll der Lastgeschichte. Allg Forst Jagdz 163: 142-145.

Mattheck, C., Breloer, H., 1996. The Body Language of Trees - A Handbook of Failure Analysis. HMSO, London.

Matulewski, P., 2018. Impact of Human-Induced Denudation on Radial Growth and Wood Anatomy of the Scots Pine (*Pinus sylvestris* L.) Roots. Case Study From the Brodnica Lakeland. PhD Thesis. Adam Mickiewicz University in Poznań, pp.216

Matulewski, P., Buchwal, A., Makohonienko, M., 2019. Higher climatic sensitivity of Scots pine (*Pinus sylvestris* L.) subjected to tourist pressure on a hiking trail in the Brodnica Lakeland, NE Poland. Dendrochronologia 54, 78-86.  
<https://doi.org/10.1016/j.dendro.2019.02.008>.

Matulewski, P., Buchwal, A., Zielonka, A., Wrońska-Walach, D., Čufar, K., Gärtner, H., 2021. Trampling as a major ecological factor affecting the radial growth and wood anatomy of Scots pine (*Pinus sylvestris* L.) roots on a hiking trail. Ecological Indicators, 107095.  
<https://doi.org/10.1016/j.ecolind.2020.107095>.

McMichael, B.L, Burke, J.J., 1998. Soil temperature and root growth. HortScience 33, 947-951.

Michniewicz, M., Stopińska, J., 1980a. The effect of potassium nutrition on growth and on plant hormones content in Scots pine (*Pinus sylvestris* L.) seedlings. Acta Soc. Bot. Pol. 49 (3), 235-244. <https://doi.org/10.5586/asbp.1980.021>.

Michniewicz, M., Stopińska, J., 1980b. The effect of nitrogen nutrition on growth and plant on hormones content in Scots pine (*Pinus sylvestris* L.) seedlings grown under light of different intensity. Acta Soc. Bot. Pol. 49 (2), 221-234.  
<https://doi.org/10.5586/asbp.1980.020>.

Montagnoli, A., Dumroese, R.K., Terzaghi, M., Onelli, E., Scippa, G.S., Chiatante, D., 2019a. Seasonality of fine root dynamics and activity of root and shoot vascular cambium in *Quercus ilex* L. forest (Italy). For. Ecol. Manag. 431, 26-34.  
<https://doi.org/10.1007/s10342-014-0814-6>.

Montagnoli, A., Terzaghi, M., Chiatante, D., Scippa, G.S., Lasserre, B., Dumroese, R.K., 2019b. Ongoing modifications to root system architecture of *Pinus ponderosa* growing on a sloped site revealed by tree-ring analysis. Dendrochronologia 58, 125650.  
<https://doi.org/10.1016/j.dendro.2019.125650>.

Montwé, D., Isaac-Renton, M., Hamann, A., Spiecker, H., 2018. Cold adaptation recorded in tree rings highlights risks associated with climate change and assisted migration. Nature Communications 9(1), 1574, <https://doi.org/10.1038/s41467-018-04039-5>.

Morawska, M., 2012. Zapis erozji wąwozowej w anatomii drewna w odsłoniętych korzeni drzew w Dolinie Błędzianki (Pojezierze Litewskie). Studia i Materiały CEPL w Rogowie 1 (30), 166-175.

Murrell, P., 2005. R Graphics. Chapman & Hall/CRC Press.

- Nicoll, B.C., Easton, E.P., Milner, A.D., Walker, C., Coutts, M.P., 1995. Wind stability factors in tree selection: distribution of biomass within root systems of Sitka spruce clones. in: Coutts, M.P., Grace, J. (Eds.), In Wind and Tress. Cambridge University Press, Cambridge, U.K., pp 276-292.
- Nicoll, B.C, Ray, D., 1996. Adaptive growth of tree root systems in response to wind action and site conditions. *Tree Physiology* 16, 891-898. <https://doi.org/10.1093/treephys/16.11-12.891>.
- Nicoll, B.C., Berthier, S., Achim, A., Gouskou, K., Danjon, F., van Beek, L.P.H., 2006. The architecture of *Picea sitchensis* structural root systems on horizontal and sloping terrain. *Trees* 20, 701-712. <https://doi.org/10.1007/s00468-006-0085-z>.
- Niewiarowski, W., Wysota, W., 1986. Moraine plateau levels of the Brodnica Moraine Plateau and their genesis. *AUNC Geogr.* 19(60), 39-46.
- Ostonen, I., Puttsepp, U., Biel, C., Alberton, O., Bakker, M.R., Lohmus, K., Majdi, H., Metcalfe, D., Olsthoorn, A.F.M., Pronk, A., Vanguelova, E., Weih, M., Brunner, I., 2007. Specific root length as an indicator of environmental change. *Plant Biosyst.* 141, 426-442.
- Pagès, L., 2002. Modelling root system architecture. in: Weisel, Y., Eshel, A., Kafkafi, U., (Eds), *Plant roots: the hidden half*. 3rd edn. Marcel Dekker, New York, pp. 175-186.
- Panayotov, M. P., Zafirov, N., Cherubini, P., 2013. Fingerprints of extreme climate events in *Pinus sylvestris* tree rings from Bulgaria. *Trees* 27, 211-227. <https://doi.org/10.1007/s00468-012-0789-1>.
- Panshin, A.J., de Zeeuw, C., 1970. *Textbook of Wood Technology, Volume 1: Structure, Identification, Uses and Properties of the Commercial Woods of the United States and Canada*. McGraw-Hill, New York.
- Pazdrowski, W., Szymański, M., Kaźmierczak K., Nawrot, M., Mańka, K., 2009. Axial and radial variation of sapwood and heartwood in stems of common oak (*Quercus robur* L.) and selected biometric traits of trees and site fertility. *Acta Sci. Pol. Silv. Colendar. Rat. Ind. Lignar.* 8(2), 31-45.
- Pelfini, M., Santilli, M., 2006. Dendrogeomorphological analyses on exposed roots along two mountain hiking trails in the Central Italian Alps. *Geografiska Annaler: Series A* 88A (3), 223–236. <https://doi.org/10.1111/j.1468-0459.2006.00297.x>.
- Perez-Rodriguez, R., Marques, M.J., Bienes, R., 2007. Use of dendrogeomorphological method in *Pinus halepensis* to estimate the soil erosion in the South East of Madrid (Spain). *Science of the Total Environment* 378, 156-160. <https://doi.org/10.1016/j.scitotenv.2007.01.042>
- Piermattei, A., Crivellaro, A., Carrer, M., Urbinati, C., 2015. The ‘blue ring’: anatomy and formation hypothesis of a new tree-ring anomaly in conifers. *Trees* 29, 613-620. <https://doi.org/10.1007/s00468-014-1107-x>.
- Piermattei A., Crivellaro A., Krusic P. J., Esper J., Vitek P., Oppenheimer C., Felhofer M., Gierlinger N., Reinig F., Urban O., Verstege A., Lobo H., Büntgen U., 2020. A millennium-long ‘Blue Ring’ chronology from the Spanish Pyrenees reveals severe ephemeral summer

cooling after volcanic eruptions. *Environmental Research Letters* 15, 124016, <https://doi.org/10.1088/1748-9326/abc120>

Pregitzer K.S., King J.S., Burton A.J., Brown S.E., 2000. Responses of tree fine roots to temperature. *New Phytologist* 147(1), 105-115. <https://doi.org/abs/10.1046/j.1469-8137.2000.00689.x>.

Puhe, J., 2003. Growth and development of the root system of Norway spruce (*Picea abies*) in forest stands - a review. *For Ecol Manage* 175, 253-273. [https://doi.org/10.1016/S0378-1127\(02\)00134-2](https://doi.org/10.1016/S0378-1127(02)00134-2).

R Core Team, 2020. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, <https://imagej.nih.gov/ij/>, 1997-2018.

Ran, Y., Bar-Yosef, B., Erez, Z., 1992. Root volume influence on dry matter production and partitioning as related to nitrogen and water uptake rates by peach trees. *Journal of Plant Nutrition* 15 (6-7), 713-726. <https://doi.org/10.1080/01904169209364357>.

Reid, C.P.P, Kidd, F.A, Ekwebelam, S.A., 1983. Nitrogen nutrition, photosynthesis and carbon allocation in ectomycorrhizal pine. *Plant and Soil* 71, 415-432. [https://doi.org/10.1007/978-94-009-6833-2\\_48](https://doi.org/10.1007/978-94-009-6833-2_48).

Rubiales, J.M., Bodoque, J.M., Ballesteros, J.A., Diez-Herrero, A., 2008. Response of *Pinus sylvestris* roots to sheet-erosion exposure: an anatomical approach. *Nat. Hazards Earth Syst. Sci.* 8, 223-231. <https://doi.org/10.5194/nhess-8-223-2008>.

Ruelle, J., 2014. Morphology, anatomy and ultrastructure of reaction wood. in: Gardiner, B., Barnett, J., Saranpää, P., Gril, J. (Eds), *The biology of reaction wood*. Springer, Berlin Heidelberg, pp 13-35.

Rybniček, M., Gryc, V., Vavřík, H., Horaček, P., 2007. Annual ring analysis of the root system of Scots pine. *Wood Res.* 52 (3), 1-14.

Savidge, R.A., 2000. Intrinsic regulation of cambial growth. *J. Plant Growth Reg.* 20, 52-77. <https://doi.org/10.1007/s003440010002>.

Schroth, G., 1998. A review of belowground interactions in agroforestry, focussing on mechanisms and management options. *Agroforestry Systems* 43, 5-34. <https://doi.org/10.1023/A:1026443018920>.

Schulman, E., 1945. Root growth-rings and chronology. *Tree-ring bull.* 12: 2-5. <https://repository.arizona.edu/handle/10150/255308>.

Schweingruber, F.H., 1996. *Tree Rings and Environment: Dendroecology*. Berne, Stuttgart, Vienna, Haupt., Birmensdorf. Swiss Federal Institute for Forest, Snow and Landscape Research, pp. 609.

- Scuderi, L.A., 2017. Quantification of long-term erosion rates from root exposure/tree age relationships in an alpine meadow catchment. *Geomorphology* 283, 114-121. <https://doi.org/10.1016/j.geomorph.2017.01.029>.
- Stokes, A., Fitter, A.H., Coutts, M.P., 1995. Responses of young trees to wind and shading- effects on root architecture. *J. Exp. Bot.* 46, 1139-1146. <https://doi.org/10.1093/jxb/46.9.1139>.
- Stokes, A., Mattheck, C., 1996. Variation of wood strength in tree roots. *J. Exp. Bot.* 47, 693-699. <https://doi.org/10.1093/jxb/47.5.693>.
- Stokes, A., Atger, C., Bengough, A.G., Fourcaud, T., Sidle, R.C., 2009. Desirable plant root traits for protecting natural and engineered slopes against landslides. *Plant Soil* 324, 1-30. <https://doi.org/10.1007/s11104-009-0159-y>.
- Szeicz, J.M., 1996; White spruce light rings in northwestern Canada. *Arctic and Alpine Research* 28, 184-189. <https://doi.org/10.1080/00040851.1996.12003164>.
- Tardif, J.C., Girardin, M.P, Conciatori, F., 2011. Light rings as bioindicators of climate change in Interior North America. *Global and Planetary Change* 79, 134-144. <https://doi.org/10.1016/j.gloplacha.2011.09.001>.
- Tardif, J.C., Salzer, M.W., Conciatori, F., Bunn, A.G., Hughes, M.K., 2020. Formation, structure and climatic significance of blue rings and frost rings in high elevation bristlecone pine (*Pinus longaeva* D.K. Bailey). *Quaternary Science Reviews* 244, 106516. <https://doi.org/10.1016/j.quascirev.2020.106516>.
- Terzaghi, M., Di Iorio, A., Montagnoli, A., Baesso, B., Scippa, G.S., Chiatante, D., 2016. Forest canopy reduction stimulates xylem production and lowers carbon concentration in fine roots of European beech. *For. Ecol. Manage.* 379, 81-90. <https://doi.org/10.1016/j.foreco.2016.08.010>.
- Timell, T.E., 1986. *Compression wood in gymnosperms*. Springer, Verlag, New York, pp. 1339-2150.
- Tromp, J., 1983. Nutrient reserves in roots of fruit trees, in particular carbohydrates and nitrogen. *Plant and Soil* 71, 401-413. <https://doi.org/10.1007/BF02182682>.
- Trouet, V., van Oldenborgh, G. J., 2013. KNMI climate explorer: a web-based research tool for high-resolution paleoclimatology. *Tree Ring Research*, 69, 3-13. <https://doi.org/10.3959/1536-1098-69.1.3>.
- Yamaguchi, D.K., Fillion, L., Savage, M., 1993. Relationship of temperature and light ring formation at subarctic treeline and implications for climate reconstruction. *Quaternary Research* 39, 256-262. <https://doi.org/10.1006/qres.1993.1030>.
- Vandekerckhove, L., Muys, B., Poesen, J., De Weerd, B., Coppé, N., 2001. A method for dendrochronological assessment of medium-term gully erosion rates. *Catena* 45, 123-161. [https://doi.org/10.1016/S0341-8162\(01\)00142-4](https://doi.org/10.1016/S0341-8162(01)00142-4).
- Vitas, A., 2018. Climatically induced light rings of European larch (*Larix decidua* Mill.) in Lithuania. *Trees* 32, 791-800. <https://doi.org/10.1007/s00468-018-1672-5>.

- Vogt, K.A., Vogt, D.J., Brown, S., Tilley, J.P., Edmonds, R.L., Silver W.L., Siccama T.G., 1995. Dynamics of forest floor and soil organic matter accumulation in boreal, temperate, and tropical forests. in: Lal, R., Kimble, J., Levine, E., Stewart, B.A. (Eds), Soil management and greenhouse effect. CRC, Lewis Publishers, Boca Raton, FL, 159-178.
- Wagenführ, R., 1999. Anatomie des Holzes. Leinfelden-Echterdingen, DRW-Verlag Weinbrenner GmbH & Co.
- Wagner, B., Gärtner, H., Ingensand, H., Santini, S., 2010. Incorporating 2D tree-ring data in 3D laser scans of coarse-root systems. *Plant and Soil*, 370, 175-187. doi: 10.1007/s11104-010-0370-x
- Wagner, B., Gärtner, H., Santini, S., Ingensand, H., 2011. Cross-sectional interpolation of annual rings within a 3D root model. *Dendrochronologia*, 29, 201-210. doi: 10.1016/j.dendro.2010.12.003
- Walter, H., Lieth, H., 1960. Klimadiagramma-Weltatlas. G. Fischer Verlag, Jena.
- Waring, R.H., Schlesinger, W.H., 1985. Forest ecosystems: concepts and management. Academic Press, Orlando, pp. 440.
- Westing, A.H., 1965. Formation and function of compression wood in gymnosperms. *Bot Rev* 31, 381-480. <https://doi.org/10.1007/BF02859131>.
- Wiersum, L.K., 1957. The relationship of the size and structural rigidity of pores to their penetration by roots. *Plant Soil* 9, 75-85.
- Wójcik, G., Marciniak, K., 1993. Precipitations in Lower Vistula Valley in the years 1951-1980. in: Churski, Z. (Eds.), Environmental and socio-economic development of the Lower Vistula Valley. IG UMK. Toruń, pp. 107-121.
- Wrońska-Walach, D., Zielonka, A., Sobucki, M., Oleszko, B., 2015. Longitudinal and cross-sectional wood anatomy variability of vertical fir roots (*Abies alba* Mill.) as a record of landslide processes? an example from the Carpathian foothills. *TRACE* 13, 102-109.
- Wrońska-Walach, D., Sobucki, M., Buchwał, A., Gorczyca, E., Korpak, J., Wałdykowski, P., Gärtner, H., 2016. Quantitative analysis of ring growth in spruce roots and its application towards a more precise dating. *Dendrochronologia* 26, 61-71. <https://doi.org/10.1016/j.dendro.2016.03.009>.
- Yamaguchi, K., Shimaji, K., Itoh, T., 1983. Simultaneous inhibition and induction of compression wood formation by morphactin in artificially inclined stems of Japanese larch (*Larix leptolepis* Gordon). *Wood Sci. Technol.* 17, 81-89. <https://doi.org/10.1007/BF00369125>.
- Yamaguchi, D.K., Filion, L., Savage, M., 1993. Relationship of temperature and light ring formation at subarctic treeline and implications for climate reconstruction. *Quaternary Research* 39, 256-262. <https://doi.org/10.1006/qres.1993.1030>.
- Zadworny, M., McCormack, M.L., Rawlik, K., Jagodziński, A.M. 2015. Seasonal variation in chemistry, but not morphology, in roots of *Quercus robur* growing in different soil types. *Tree Physiology* 35 (6), 644-652. <https://doi.org/10.1093/treephys/tpv018>.

Zielski, A., Błaszowski, A., Barankiewicz, A., 1998. Dynamika przyrostu radialnego sosny zwyczajnej (*Pinus sylvestris* L.) na obszarze leśnym eksploatowanym turystycznie nad jeziorem Wielkie Partęczyny (Nadleśnictwo Brodnica). Sylwan 3, 69-78.

Zielski, A., Krąpiec, M., 2004. Dendrochronologia. PWN, Warszawa, pp. 328.

**Declaration of interests**

☐ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☒ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Pawel Matulewski reports financial support was provided by Erasmus. Pawel Matulewski reports financial support was provided by Adam Mickiewicz University.



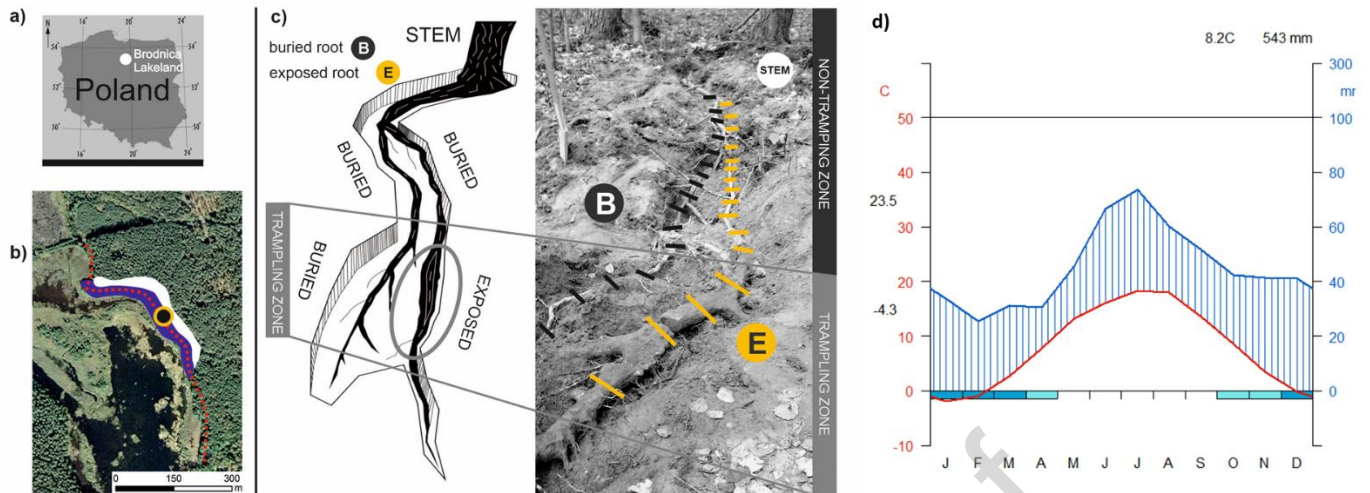


Fig. 1. *Pinus sylvestris* L. stem and root sampling locations in a) the Brodnica Lakeland, NE Poland. The sampling strategy consisted of b) two roots subjected to serial sectioning (black circle with orange margins), and 18 exposed roots subjected to trampling (blue area) and 18 reference roots (white area) sampled outside the hiking trail (dashed red line). c) The sketch of the studied tree (STEM) with the two roots (B - the BURIED root; E - the EXPOSED root) partially located within the hiking trail (trampling zone). The E root represents the root partially exposed within the hiking trail (grey ellipse), whereas the B root represents a non-exposed root. From each root there were 16 cross sections sampled at exactly the same distances from the stem. In each root, cross sections were labelled in the same way, i.e., from R1 (i.e., those located closest to the tree stem) to R16 (i.e., positioned in the outermost part from the tree stem). Cross sections from R13 to R16 were located in the trampling zone. These sections in the B root were non-exposed (and excavated only for the purpose of sampling) while the ones of the E root were exposed due to trampling on a hiking trail. d) Walter-Lieth climate diagram for the study area (1971-2015) with blue horizontal bars indicating the months with likely (dark blue) and probable frost (light blue)



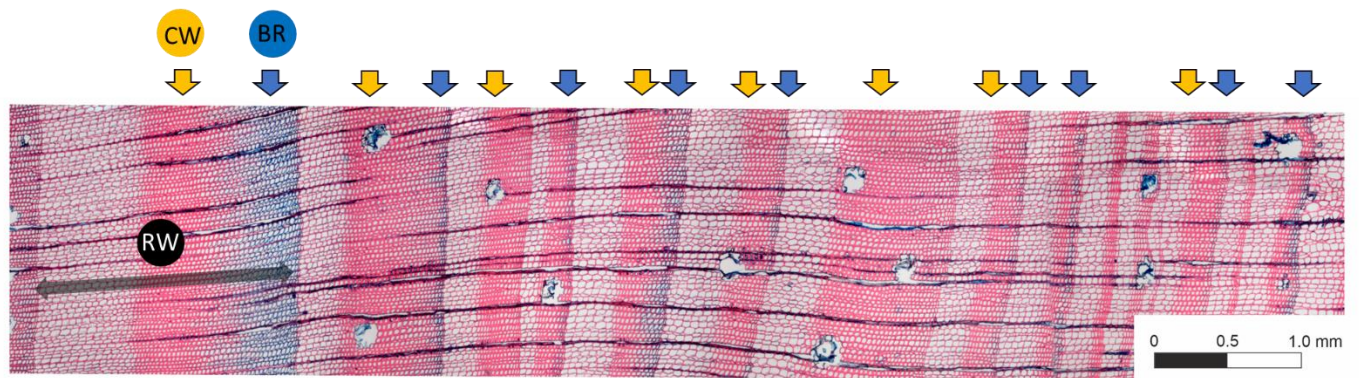


Fig. 2. Thin section of the exposed E root (R14 cross section) with compression wood (CW, yellow arrows) and blue rings (BRs, blue arrows). The percentage of the CW and the BR zones was assessed in relation to total width of the annual growth ring (RW, black arrow).

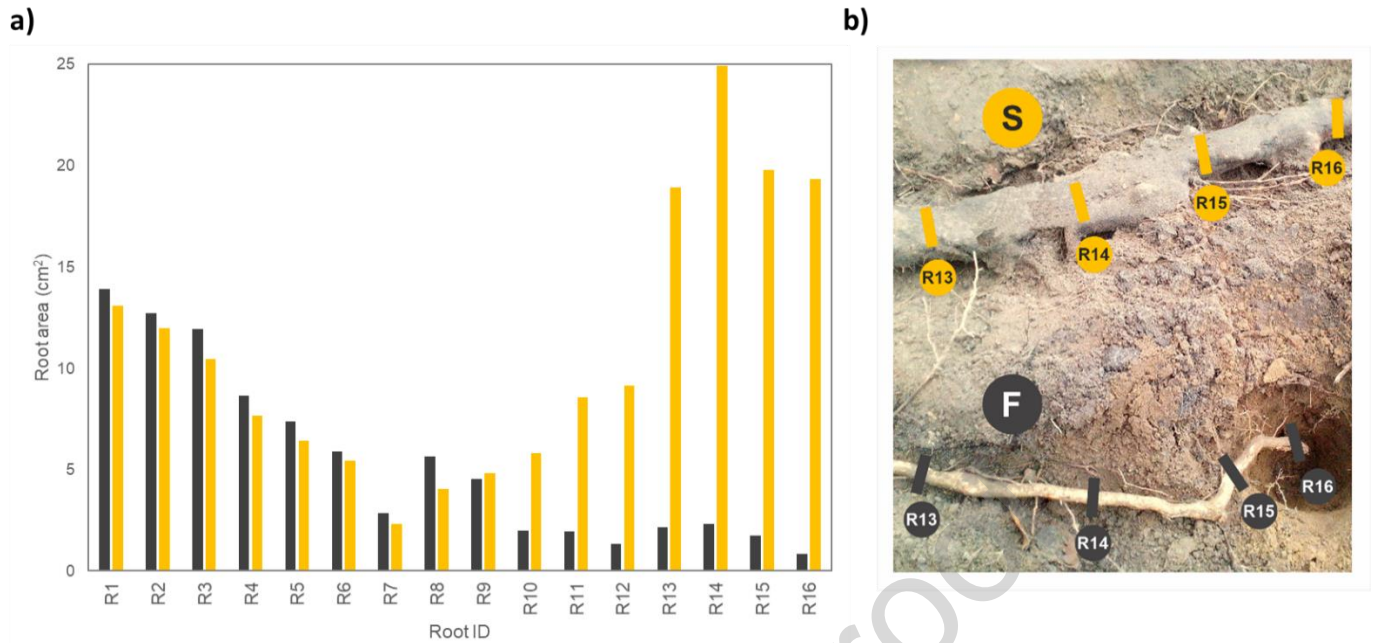


Fig. 3. Comparison of a) *Pinus sylvestris* root surface area between the B (buried root, black bars) and the E (exposed root, yellow bars) root performed on 16 cross-sections (R1-R16) acquired from each root at the same distance from the tree stem and at 25 cm long intervals. b) Root volume differences between the B and the E root observed in the trampling zone. The B root was non-exposed and was excavated only for sampling purpose, while the E root was exposed due to trampling on a hiking trail.

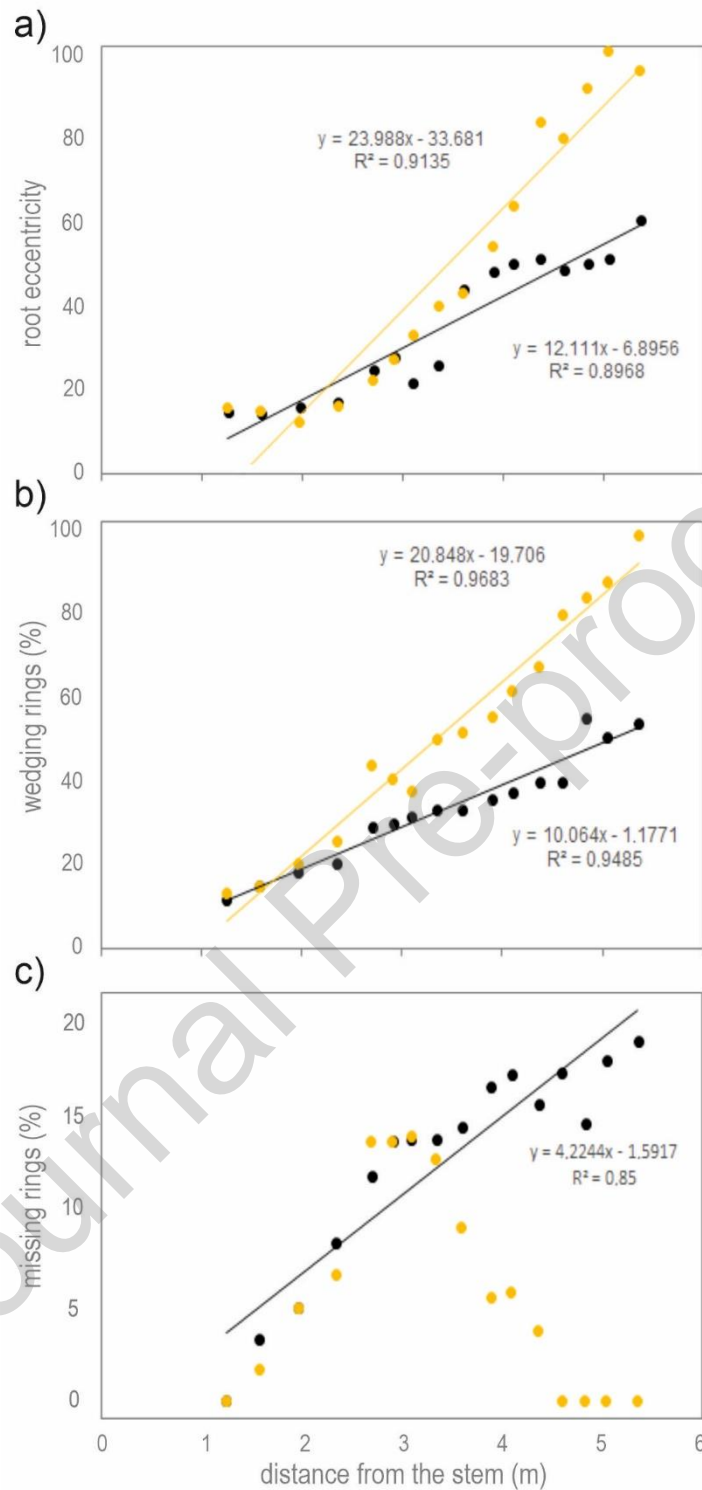


Fig. 4. Comparison of the root eccentricity (a), percentage of wedging rings (b) and missing rings (c) presented for the B and E roots. The results for the B root (buried root, black dots) and the E root (exposed root, yellow dots) are presented in relations to the distance from the tree stem.

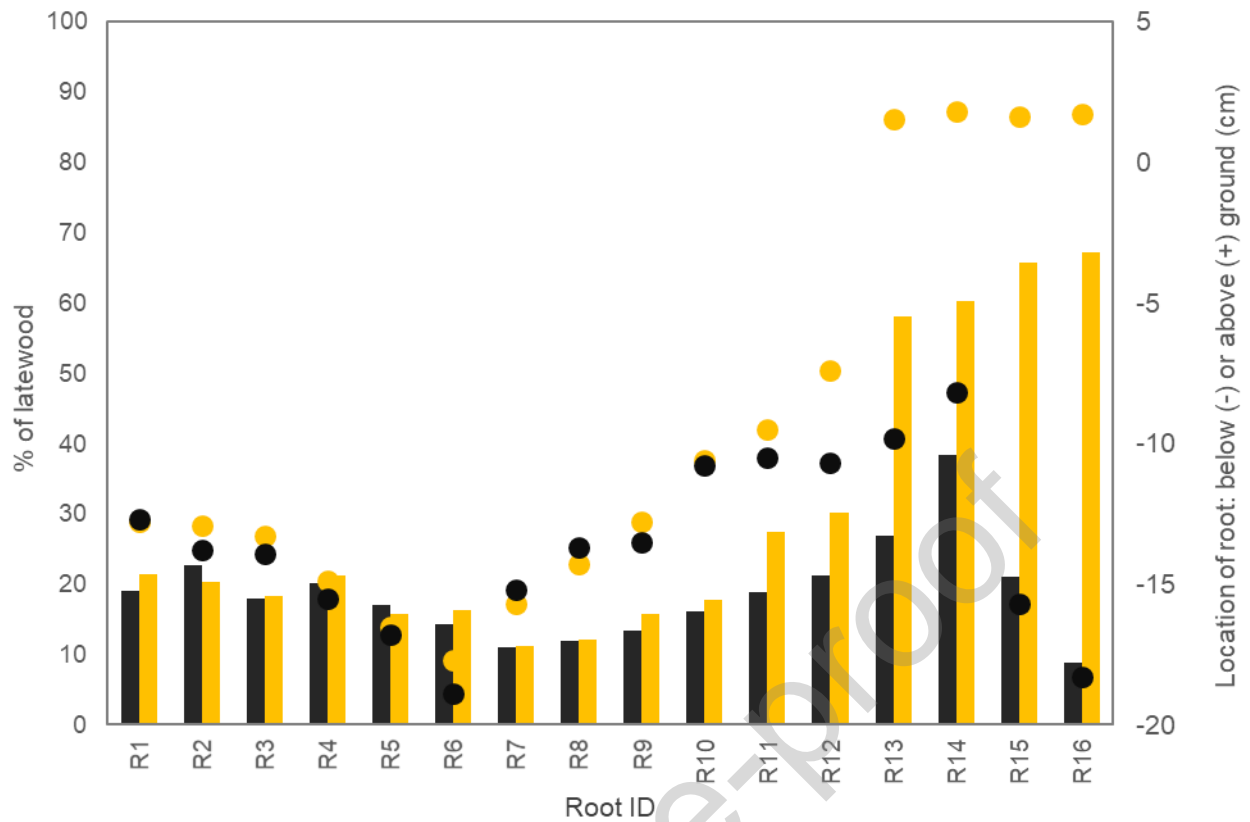
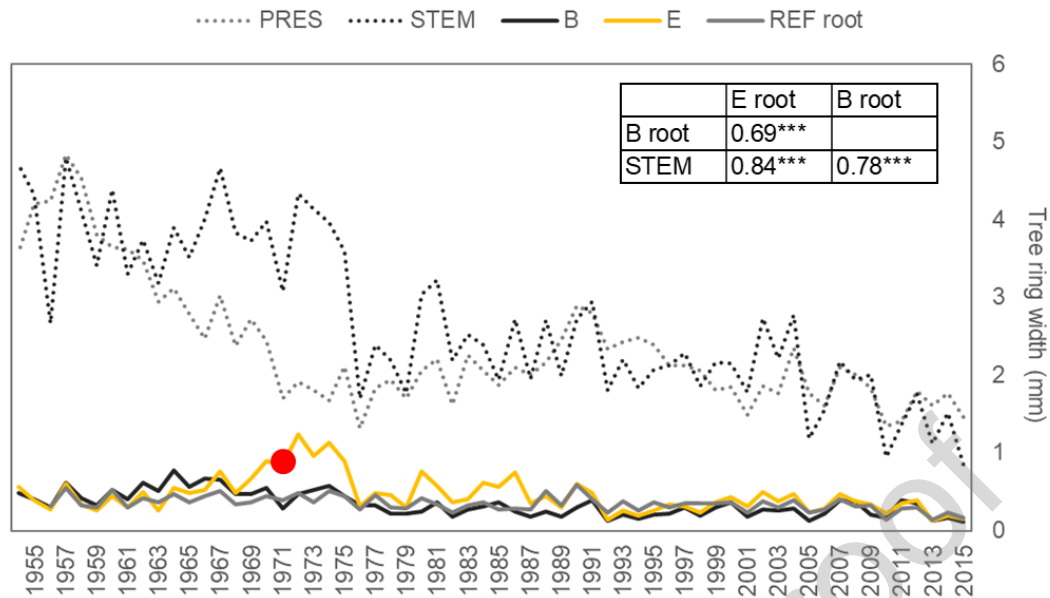


Fig. 5. Proportion of the mean percentage of latewood (left y-axis) between the B (buried root, black bars) and the E (exposed root, yellow bars) root cross-sections with the position of the B and the E root (black and yellow dots, respectively) assessed in relation to soil surface (right y-axis).

a)



b)

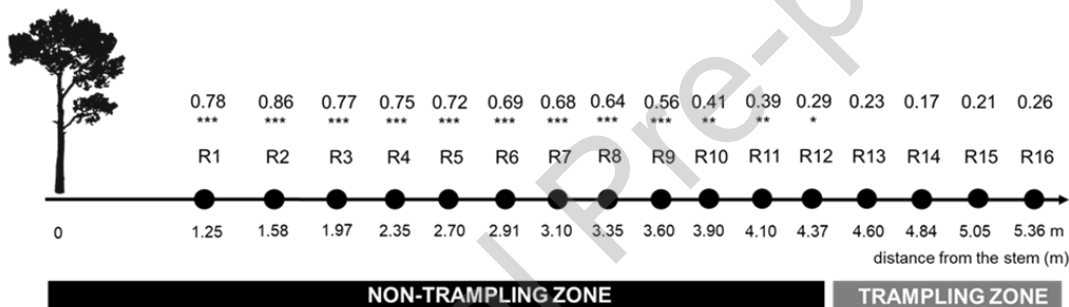


Fig. 6. Comparison between raw *Pinus sylvestris* stem and root tree-ring width (TRW) chronologies: a) chronology from the trees subjected to trampling pressure on a hiking trail (PRES; grey dotted line), stem chronology (STEM; black dotted line) with the B root chronology (black solid line), the E root chronology (yellow solid line) and the REF root chronology (grey solid line). Pearson's correlation coefficients computed for the common period (1970-2015) between stem and each root chronology are presented in the top right corner. Red dot marks the E root exposure year. b) Correlation coefficients between the B and the E root sections sampled at the same distances from the stem. Significance levels: \*\*\* -  $p < 0.001$ ; \*\* -  $p < 0.01$ ; \* -  $p < 0.05$ .

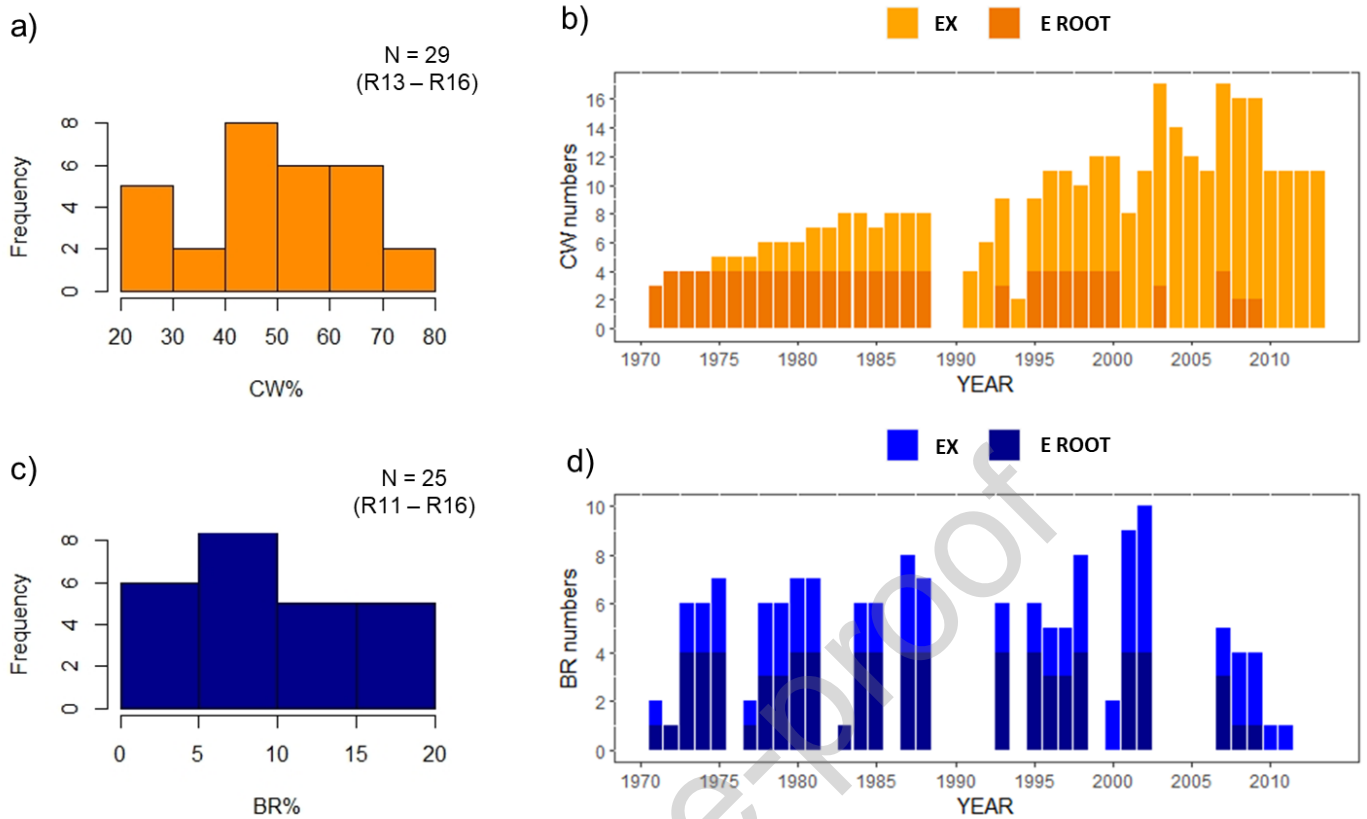


Fig. 7. Frequency distribution of a) percentage of compression wood (CW), and c) percentage of blue ring (BR) zones assessed in relationship to the total width of annual growth rings of the E root.  $N$  – total number of growth rings with ID of root section below. Comparison of b) CW and d) BR occurrences for calendar years between the E root (darker colours, all cross sections with BRs counted) and broader root pool (EX,  $n = 18$  roots) (lighter colours, individual roots counted).

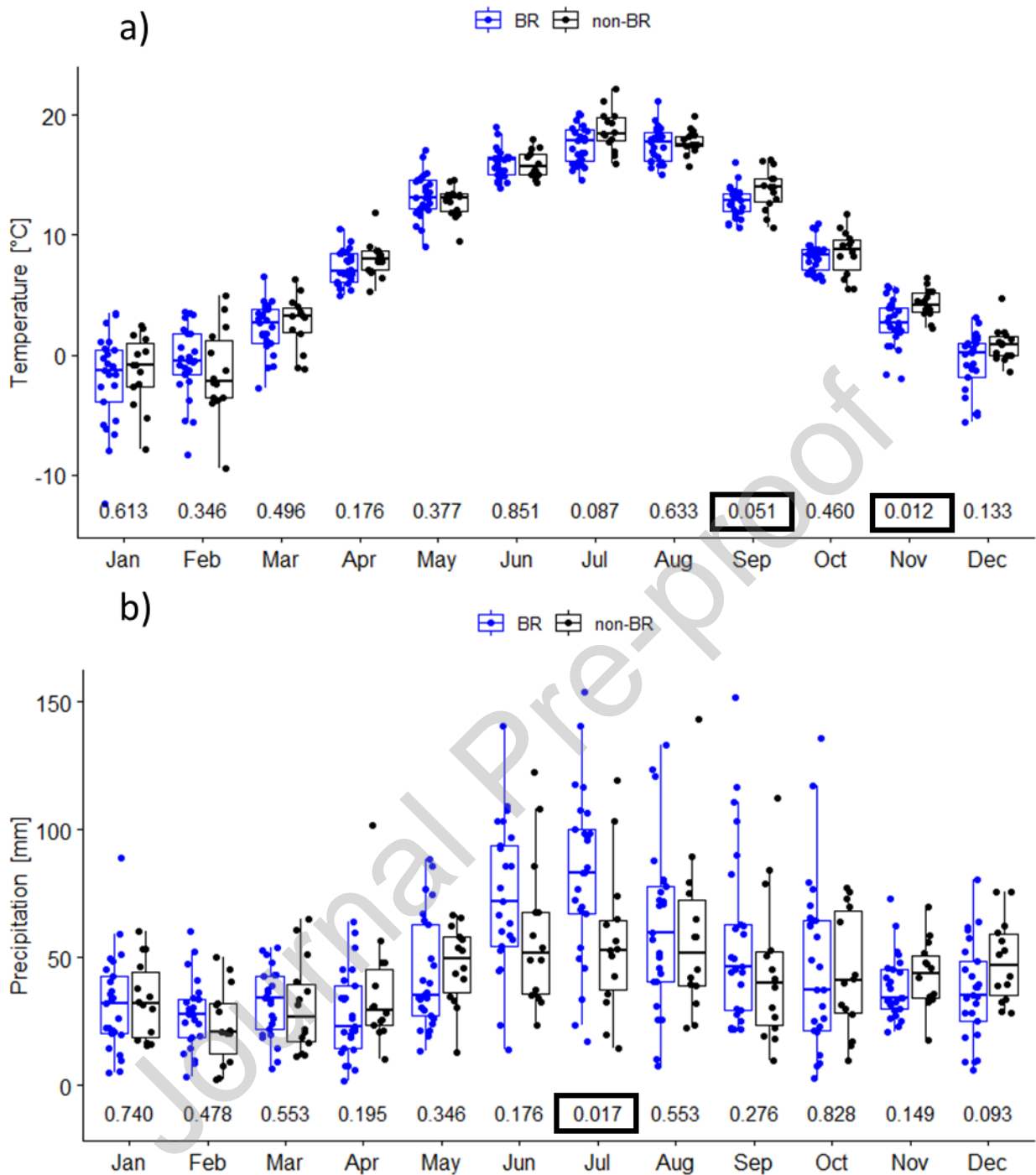
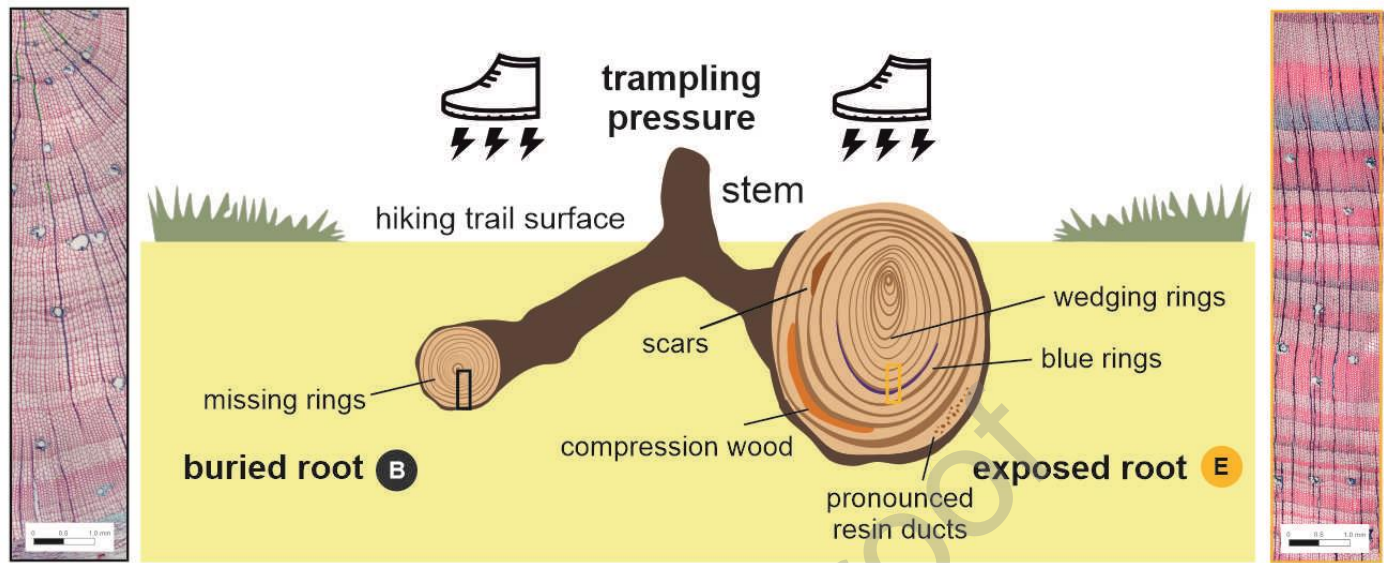


Fig. 8. Differences in mean monthly air temperature (a) and precipitation (b) for blue ring (BR) years. The years in which BRs (blue) were formed were compared with the non-BR years (black). Study period (1971-2015); total number of growth rings with BRs was 25. Significant differences in means are marked with black squares.



## Graphical abstract:



**Highlights**

- The volume of exposed root exceeded ten times that of the unexposed root.
- 29 calendar years with compression wood (CW) were found only in the exposed roots.
- For the first time, blue rings (BRs) were recognized in tree roots.
- 40% of growth rings in exposed root subjected to trampling had BRs.