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Trampling as a major ecological factor affecting the radial growth and wood anatomy of Scots pine (*Pinus sylvestris* L.) roots on a hiking trail

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ABSTRACT

The impact of hiking in forested areas is one of the main factors affecting the condition of tree growth along hiking trails. Trampling causes common exposure of roots and quantification of the human impact on root radial growth and wood anatomy requires careful assessment. To accurately identify the radial growth changes in *Pinus sylvestris* roots, we conducted a stepwise cross-dating using trampled roots from a hiking trail and reference roots. Such approach was previously not applied in a lowland area. In addition, we investigated the factors that influence the root-stem radial growth coherency, including soil properties, root and trail morphology. Changes in radial growth and wood anatomy were examined in three parts of the root system: buried, transition and trampling zone. The radial growth for each root zone was compared with corresponding stem and reference root and stem chronology. In total, we investigated 204 roots and 97 tree stems for the common period 1970–2015. Missing rings were found to be a common phenomenon in all root zones, except in the exposed lateral roots in the trampling zone. The highest number of wedging and missing rings was observed in the trampling and transition zones, respectively. The total number of wedging rings increased with an increasing distance from the stem. The events of root exposure in the trampling zone were highly coupled with the formation of scars ($r = 0.51$, $p < 0.001$) and pronounced resin ducts (PRDs) ($r = 0.52$, $p < 0.001$). The majority of the wood anatomical changes (i.e., 84% of scars and 85% of PRDs) were identified in the trampling zone. The highest degree of correlation between raw stem chronology and raw root chronology was found for the exposed trampled roots ($r = 0.69$, $p < 0.001$). In the trampling zone, the root-stem radial growth coherency was determined primarily by root type (77.3%) and root age (17.4%), whereas in the buried zone, by the soil organic matter content (55.4%) and soil compaction (39.7%). It has been proved that the record of radial growth and wood anatomy changes in Scots pine roots serve as a valuable ecological archive of trampling impact with high temporal resolution.

1. Introduction

Increased trampling activity associated with hiking has a substantial ecological impact (Leung and Marion, 2000; Cole, 2004; Marion and Olive, 2006). Trampling effects, both from humans and animals, can adversely impact natural habitats and forested trail surfaces (Tomczyk and Ewertowski, 2013), commonly leading to the degradation of plant communities (Kuss and Graefe, 1985; Sun and Walsh, 1998; Pescott and Stewart, 2014; but see also Kidron, 2016, who reports an increase in annual plant cover following goat trampling on dune-covered biocrusts). Moreover, trampling activity affects soil properties through changes in soil compaction and surface hydrology (Dadkhah and Gifford, 1980; Pietola et al., 2005). The negative impact of human trampling is the most visible at locations of highly concentrated tourist traffic, such as hiking trails. Trampling activity together with natural geomorphic processes induce common root exposure within the trail surface in

Abbreviations: stem-root RGC, stem-root radial growth coherency; PRES, tree stems subjected to trampling pressure; REF, tree stems in a reference site; REF root, root in a reference site; MRWs, mean ring width; EREs, events of root exposure; PRDs, pronounced resin ducts.

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forested areas (Buchwał, 2009; Zhou et al., 2013; Bodoque et al., 2017). It is known that trampling can substantially inhibit the radial growth of trees (Zielski et al., 1998; Ciapała et al., 2014; Matulewski et al., 2019). Both exposed tree roots and stems growing along the trail can be used for dendrochronological analysis, although combined studies using both are very rare.

Dendrochronology studies tree-rings in the xylem which represents the radial growth of trees. The tree-ring data of stems and roots can serve as valuable records of environmental changes that occurred in the past (Alestalo, 1971; Fritts, 1976; Shroder, 1980; Schweingruber, 1996). The tree-ring pattern of stems and roots provides reliable information on the spatial and temporal activity of ecological processes (Zielski and Krąpiec, 2004; Koprowski and Duncker, 2012; Koprowski et al., 2019; Amoroso et al., 2017). Specifically, exposed roots can be used to study the intensity and frequency of, for example, lakeshore erosion (Maleval and Astrade, 2003; Fantucci, 2007), seashore dynamics (Rovéra et al., 2013), gully erosion (Vandekerckhove et al., 2001; Hitz et al., 2008; Malik, 2008; Lopez Saez et al., 2011; Morawska, 2012), or sheet erosion (Bodoque et al., 2005, 2011; Corona et al., 2011; Ballesteros-Cánovas et al., 2013, 2015). In recent decades, dendrochronological studies have begun to use exposed roots to study trampling activity, mainly in order to assess trail erosion rates (Pelfini and Santilli, 2006; Rubiales et al., 2008; Bodoque et al., 2017).

Even though roots play a significant role in the stability and water uptake in trees (Coutts, 1983) their growth patterns are still not fully understood (Coutts, 1987; Polomski and Kuhn, 1998; Krause and Morin, 2005), including the relation between root growth and trampling (Pelfini and Santilli, 2006). Tree ring chronologies of roots have only been studied to a limited extent (LaMarche, 1963; Fayle, 1968; Krause and Eckstein, 1993; Wrońska-Wałach et al., 2016). Moreover, although previous studies have examined geomorphological processes by producing ring series of roots (Fayle, 1968; Fritts, 1976), only a few have analysed the radial growth pattern along the horizontal root profile (Krause and Morin, 1995, 1999a, 1999b, 2005; Wrońska-Wałach et al., 2012, 2016). The existing dendrogeomorphological literature agrees that common radial growth irregularities, such as missing and wedging rings, hamper precise root dating (Larson, 1956; Krause and Morin, 1995; Bodoque et al., 2011; Wrońska-Wałach et al., 2012, 2016; Zielonka et al., 2014). Incomplete root tree-ring series might lead to dating errors of ecological events, including human impact.

In the literature, dendrochronological analyses of root radial growth have mainly been focused on the occurrence of growth irregularities in single cross-sections (Lyford and Wilson, 1964; Fayle, 1968, 1975a, 1975b; Carrara and Carroll, 1979; Bodoque et al., 2005; Zhou et al., 2013). Only a few authors have attempted to compare the pattern of radial growth between the stem and corresponding root system in coniferous trees (Krause and Morin, 1995; Pelfini and Santilli, 2006; Wrońska-Wałach et al., 2012, 2016). Specifically, in *Abies balsamea*, Krause and Morin (1995) reported a temporal delay in the response of tree stems and roots to the same environmental factor such as defoliation caused by spruce budworm. Additionally, the annual growth of stem and roots was found to vary as a result of root exposure for *Pinus sylvestris and Pinus pinaster,* where wider ring formation was found in the exposed part of the root (Alestalo, 1971; Bodoque et al., 2011).

Dendrochronological dating of roots is inherently challenging due to the common anatomical changes encountered in roots (Krause and Eckstein, 1993). Radial growth irregularities in the roots are often caused by differences in cambial activity along the root length and within the entire tree (Fritts, 1976; Schweingruber, 1996). In fact, in a study conducted on *Picea mariana* (Thibeault-Martel, et al., 2008), the duration of xylogenesis was found to be 22 days longer in the roots in comparison with the stem. Cambial activity in roots may depend on root age (Fayle, 1968), competition (Bodoque et al., 2005) or the rockiness of the soil (Grissino-Mayer, 2002). Missing and wedging rings can occur due to deficiencies in availability of nutrients and growth hormones during growth ring formation (Larson, 1956; Fayle and Farrar, 1965; Panshin and de Zeeuw, 1970; Thibeault-Martel, et al., 2008; Wrońska-Wałach, et al., 2016). In addition, the orientation of the root, aeration, light availability, soil moisture and temperature are known to induce the formation of wedging and missing rings in the roots (Fayle, 1968; Krause and Eckstein, 1993). The radial growth irregularities of roots have not yet been quantified in relation to these factors, which might be further modified by human impact.

The radial growth of trees, and especially roots, is known to be affected by hiking (Pelfini and Santilli, 2006; Rubiales et al., 2008; Buchwał, 2009; Matulewski et al., 2019). Analyses of radial growth and wood anatomical changes in exposed roots offer a great opportunity to determine the exact time of the root exposure (Gärtner et al., 2001; Gärtner, 2003). Studies on exposed roots from hiking trails have mainly carried out quantitative analysis of erosion rate in mountain areas (Bodoque et al., 2005, 2017; Pelfini and Santilli, 2006; Rubiales et al., 2008; Buchwał, 2009; Zhou et al., 2013), and similar studies in the lowlands are missing. Moreover, detailed quantitative and qualitative information on the changes in radial growth and wood anatomy in tree roots and stems subjected to human impact is still unexplored.

The main goal of our study was thus to characterize the radial growth and wood anatomical changes in the roots of Scots pine (*Pinus sylvestris* L.) subjected to trampling on a hiking trail in the lowland area of the Brodnica Lakeland, NE Poland. For this reason, we first quantified growth irregularities and wood anatomical changes in three root zones: i) the exposed zone with roots subjected to trampling and a partially exposed root system within the hiking trail; ii) the buried zone, outside of the trampling impact, with roots growing naturally in the soil at a close distance to the tree stem; iii) the buried transition zone located between the trampling and the buried zone. We then aimed to identify the factors that influence the radial growth coherency (RGC) between roots and respective stems, taking into account selected soil properties, root and trail morphology. In order to perform a precise dendrochronological dating of roots, a stepwise cross-dating procedure was conducted, including the comparison of tree ring series from different root zones with i) the corresponding stem, ii) stem chronology constructed from trees subjected to trampling pressure on a hiking trail, iii) reference stem chronology, and iv) reference root chronology. We hypothesized that trampling causes pronounced changes in radial growth and wood anatomy in Scots pine roots along the hiking trail, which can serve as a quantitative indicator of human impact in forest recreation areas. In addition, we hypothesized that root-stem RGC in each root zone depends primarily on soil properties.

2. Materials and methods

2.1. Study area

The study was conducted in the Brodnica Landscape Park located in the Brodnica Lakeland, NE Poland (53°31′ N, 19°45′ E) (Fig. 1). The landscape of the Brodnica Lakeland was strongly affected by the Scandinavian ice-sheet, which resulted in diversified landforms. The mean annual temperature of the study area is 7 °C, as assessed by using climate data from Gaj-Grzmięca meteorological station (located ca. 4 km from the study site) for the period 2000–2015. The warmest month is July while the coldest is January, with a mean air temperature of 18 °C and −3.8 °C, respectively. The mean June-July-August temperature is 15 °C. The growing season usually lasts 170 days (Puwalski, 2007). The mean annual precipitation is 570–600 mm.

The study area represents a mixed forest stand of Scots pine (*Pinus sylvestris* L.), European white birch (*Betula pendula* Roth), English oak (*Quercus robur* L.), European alder (*Alnus glutinosa* Gaertn.) and sporadic Norway maple (*Acer platanoides* L.). *P. sylvestris*, which commonly grows on sandy and highly permeable soils, is the dominant species and covers ca. 84% of the study area. The studied trees are located in a protective stand, i.e., naturally regenerated forest. The mean age of trees in the study site is ca. 70 years, with some individuals being more than 130

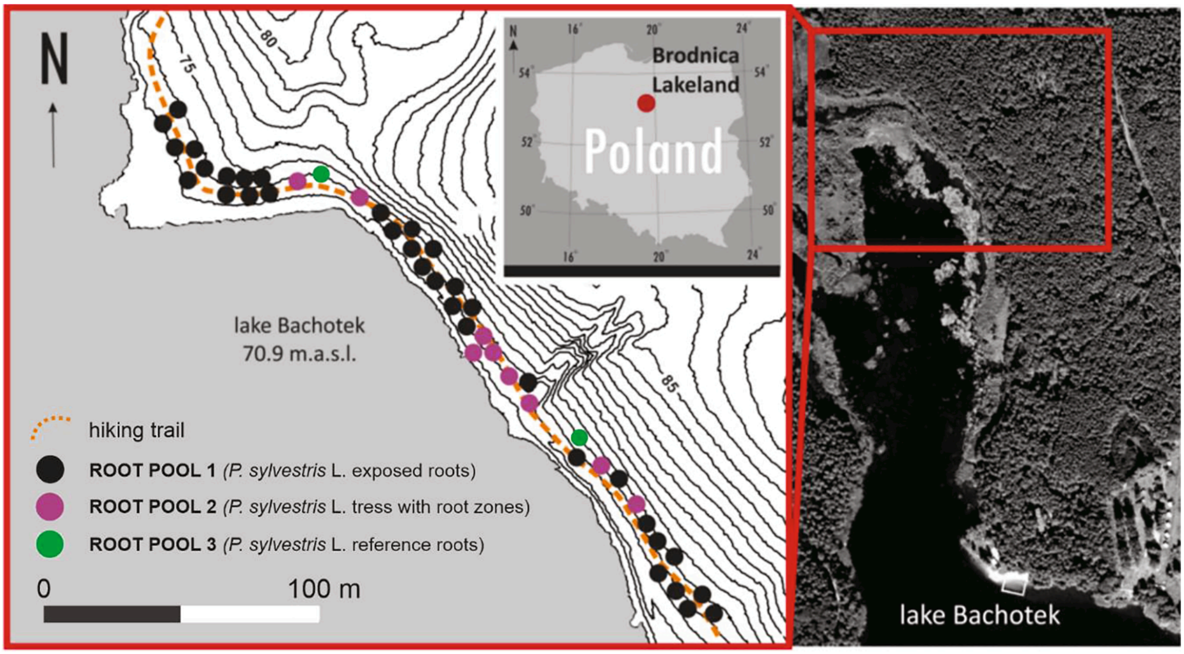

Fig. 1. *Pinus sylvestris* stem and root sampling locations in the Brodnica Lakeland, NE Poland. The sampling strategy consisted of i) ROOT POOL 1: random sampling of exposed roots (black circles) along the hiking trail (dashed orange line); ii) ROOT POOL 2: selected root systems sampling in buried, transition and trampling root zones (purple circles); iii) ROOT POOL 3: reference (i.e., non-trampled) roots sampling (green circles) (see Fig. 2).

years old (Danych and o Lasach, 2019). Rusty soils, classified as Brunic Arenosols (IUSS Working Group WRB, 2014), poor in nutrients cover the largest part of the area.

The research plot was selected in the Brodnica Lakeland and encompassed ca. 400 m of the hiking trail located in the north-eastern part of the Bachotek Lake (Fig. 1). The analysed part of the hiking trail stretches perpendicularly to the slopes at a relatively small altitudinal range (71.2–76.3 m a.s.l.). This hiking trail, excluded from vehicle traffic, 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 – from May to mid-September. The average tourist load during summer is up to 10,000 hikers per season, and is the highest in the period from June to August (Matulewski, 2018).

2.2. Root sampling

In total 204 root discs were sampled from 45*P. sylvestris* trees. The sampling strategy consisted of three designated root sampling pools i.e., i) ROOT POOL 1: random sampling of exposed roots performed along the hiking trail where only trampling root zone was considered (Fig. 1); ii) ROOT POOL 2: root system sampling with buried, transition and trampling root zones (Figs. 1 & 2) and iii) ROOT POOL 3: root sampling from the reference trees growing under natural conditions and not

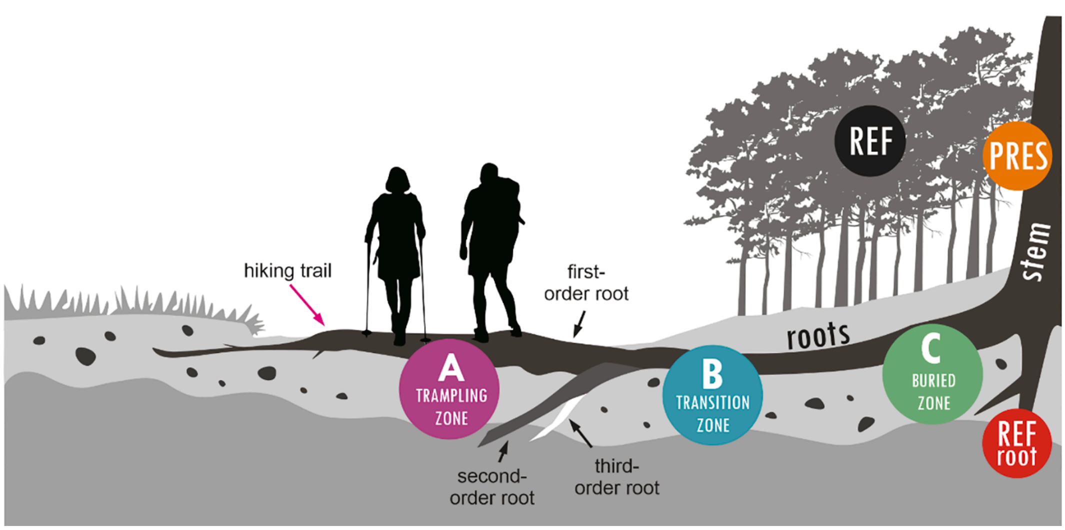

Fig. 2. *Pinus sylvestris* stem and root sampling design. Dendrochronological sampling consisted of i) tree stems taken from trees subjected to trampling pressure (PRES); ii) tree stems sampled in a reference site (REF), i.e., from non-trampled trees; iii) root systems with three root zones, i.e. buried zone (C zone; located outside of the hiking trail), transition zone (B zone; located at the edge of a hiking trail) and trampling zone (A zone; located within the hiking trail); iv) reference lateral roots (REF root) located outside of the trampling zone. Root types in the trampling zone were aggregated into lateral roots (i.e., first-order roots) and branches of lateral roots (i.e., second- and third-order roots).

subjected to trampling (Fig. 1). In ROOT POOL 1 we collected 88 exposed roots from 34 individual trees subjected to trampling pressure within the hiking trail (A zone). Among 88 exposed roots sampled, we identified 41 lateral roots (i.e., first-order roots) and 47 branches of lateral roots (i.e., 24 s-order and 23 third-order roots) (Fig. 2). All the exposed roots were in contact with the soil surface. In ROOT POOL 2 there were 97 root discs sampled from nine root systems, including exposed and not exposed root segments. Specifically, root samples were taken from three designated root zones: i) 31 roots from the buried zone located close to the tree stem with the roots growing outside of the trampling zone (C zone); ii) 26 roots from the transition zone with naturally buried roots located adjacent to the trampling zone (B zone); and iii) 40 exposed roots from the trampling zone (A zone) (Fig. 2). In addition, in ROOT POOL 3 there were 19 lateral root discs sampled from two trees growing under natural conditions. These roots were acquired in order to establish a reference root chronology (REF root) used in the cross-dating with other root chronologies.

- The following criteria were used for root sampling (ROOT POOL 1 and 2): presence of exposed roots along the hiking trail;
- presence of buried root systems, adjacent to the exposed roots, with various root types (i.e., first- to third-order roots, see distinction below);
- possibility for partially exposed root identification, with the respective tree stem;
- exclusion of trees with injuries and those in poor health conditions;
- elimination of roots with root centre damage.

All root samples were collected at a minimum distance of 0.8–1.0 m away from the base of the tree stem, avoiding the roots exhibiting radial growth disturbances caused by stem displacement (LaMarche, 1963; Gärtner et al., 2001; Scuderi, 2017). Complete root discs were collected using a hand saw. In ROOT POOL 2 from 8 to 14 cross-sections were taken from each root system, depending on the root length, with a mean of 11 ± 2.2 cross-sections sampled per root. The mean interval of root disc extraction was 26.7 ± 10.9 cm. In addition, the root type has been determined in the field where three main root types were recognized. The lateral roots emerging from the taproot were designated as i) first-order roots, and branches of those roots were assigned according to their order, i.e., ii) second-order, and iii) third-order roots (Fig. 2).

2.3. Root characteristics and trail morphology

We have determined selected root morphology characteristics, such as: mean root diameter, root area, root circularity and root eccentricity. Root area was vectorized using a scanned images of each root and calculated using ImageJ program (Rasband and ImageJ, 1997–2018). Root circularity was obtained following the equation by Kojima et al. (1971), while root eccentricity was measured using the equation proposed by Wrońska-Wałach et al. (2015). In addition to trail width measurements the aspect of each exposed root relative to the hiking trail axis was determined. A detailed description of the methods used to obtain the trail and root morphology characteristics is presented in Table S1.

The total length of the analysed roots was 45 m. In ROOT POOL 2, the longest and shortest roots were 536.8 and 311.4 cm long, respectively. The lengths of root exposures ranged from 17 to 187 cm, with a mean of 57.4 ± 41.4 cm. The mean length of the hiking trail (A zone) was 143.7 ± 23.6 cm.

2.4. Soil sampling

For each root zone we have determined the basic soil properties, such as: soil compaction, soil organic matter content and soil bulk density. Soil compaction was measured at two points adjacent to each root using a hand penetrometer. In total, there were 176, 52 and 62 penetrometer soundings performed in the A, B and C zones, respectively. Soil organic matter content was assessed at each root and there were 102, 34 and 51 samples acquired in zones A, B and C, respectively. The cylinder method was used to determine the soil bulk density. In total, there were 65, 18 and 22 cylinders taken in zones A, B and C, respectively. A detailed description of the methods used to assess the soil properties is presented in Table S1.

2.5. Laboratory work

In order to ensure precise detection of annual growth rings in the roots, microscopic analyses were conducted on thin-sections of the roots. The roots were sectioned according to the standard protocol (Gärtner and Schweingruber, 2013). In total, 530 cross-sections, with a thickness of 15–20 μm were prepared using a GSL1 sledge microtome (Gärtner et al., 2014). All thin sections were immersed in sodium hypochlorite (NaOCl) and stained with a mixture of Safranin and Astra blue, which enhanced the contrast between lignified (via Safranin) and non-lignified (via Astra blue) components of the roots' wood anatomy. After staining, the sections were dehydrated using a series of ethanol solutions of increasing concentration (50%, 75%, 96%) and immersed in xylene. The sections were then embedded in Canada balsam and dried at 60 °C for 24 h (Schweingruber, 1990; Gärtner et al., 2001; Gärtner and Schweingruber, 2013). The cross-sectional cut of each root was photographed at × 40 magnification using an Olympus BX43 microscope and SC30 Olympus camera. The individual root images were combined into panoramic compositions using the 'photomerge' function in Adobe Photoshop (Adobe Systems Incorporated, USA).

2.6. Radial growth measurements and cross-dating of roots

Radial growth and wood anatomical changes were analysed on thin sections using complete cross-sectional cuts obtained from various parts of the root system. Specifically, ring widths were measured on digital images using manual path analyses in WinCELL software (Regent Instruments, Canada). In the majority of roots there were 4 radii measured per individual root cross-section, and up to 8 radii were measured in the roots that expressed very irregular growth patterns. In the first step, cross-dating was performed between the radial growth measurements conducted in each individual root cross-section. In the second step, the arithmetic mean was calculated from all radial growth measurements performed on a single root cross-section. This allowed us to establish the average growth curve per root cross-section. In order to trace all radial growth irregularities within each cross-section, a Zig-Zag Segment Tracing method was used (Wrońska-Wałach et al., 2016). This step made it possible to identify all growth rings that often wedge in multiple directions within a single root cross-section, which further helped to minimize the dating errors. Radial growth measurements were performed omitting the scars and the injured parts of the roots. For each root sample, the total number of missing and wedging (i.e., discontinuous) rings was quantified at the cross-sectional (and not a single radial measurement) level. For e.g. if for the year 2010 we have encountered a wedging ring in 3 out of 4 radial measurements performed on that root cross-section, we have noted one wedging ring for that root statistics. If there was a particular annual growth ring missing in entire root cross-section (but present in adjacent root cross-section or stem growth curve), we have noted one missing ring for that root cross-section. Differences in mean percentage of missing and wedging rings and root age among the three root zones were assessed using one-way ANOVA. In order to assess statistically significant differences in the mean percentage of missing and wedging rings, as well differences in mean root age, Tukey's post-hoc test was performed. In addition, selected morphological traits (Supplementary Material, Table S1) were identified in each root cross-section (Fig. 3).

Root dating was improved by applying serial sectioning (Kolishchuk, 1990; Krause and Morin, 1995), which aimed to analyse multiple cross-

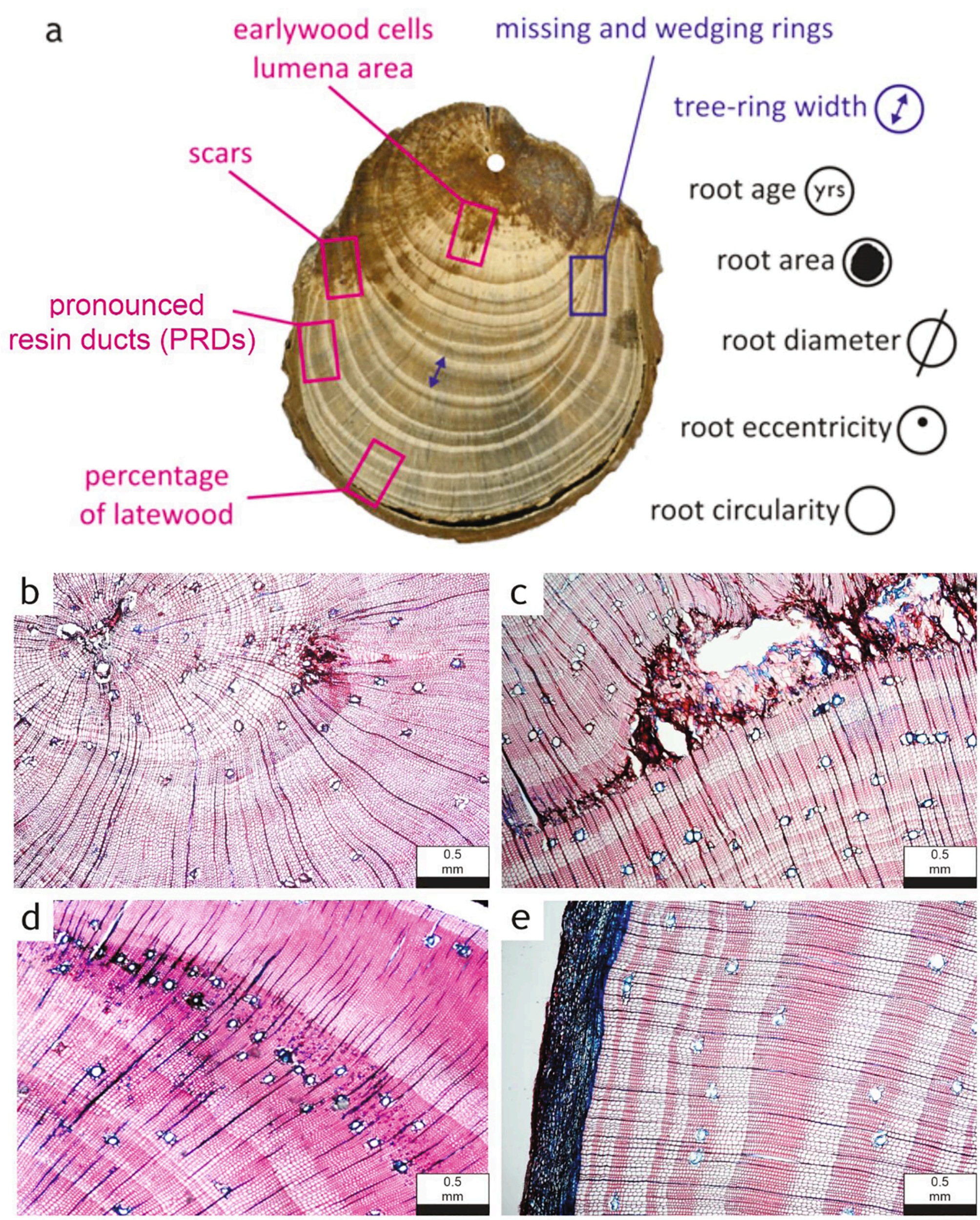

Fig. 3. Cross-section of an exposed *Pinus sylvestris* root (a) from the trampling zone located in the Brodnica Lakeland (NE Poland) illustrating the root morphology (black), radial growth (blue) and wood anatomical parameters (pink) measured in each root. Rectangles indicate an example position of the measured parameters. Detailed illustration of measured parameters: (b) abrupt change in earlywood cells lumen area and increased mean ring widths associated with sudden root exposure on a hiking trail; (c) scar with callus tissue formation; (d) pronounced resin ducts (PRDs) as a sign of mechanical pressure associated with trampling on a hiking trail; (e) interannual variation in latewood percentage.

sections along the root axis. To identify the changes in radial growth along the root length, that encompasses three root zones (i.e., zones A, B, and C), a stepwise cross-dating procedure was performed. This procedure included the comparison of growth curves from different parts of the root system with i) the corresponding stem growth curve, ii) the reference stem chronology and iii) the root reference chronology. Considering the high ratio of irregular growth rings in the roots, using two types of reference material (i.e., roots and stems of trees not subjected to trampling) allowed us to minimize potential dating errors (both over- and underestimations) and increased the reliability of root chronologies established for three root zones. Cross-dating between root time series from tree root zones was statistically verified using COFECHA software (Holmes, 1983; Grissino-Mayer, 2001). Due to the relatively short tree-ring series of some young roots (i.e., <20 yrs) and the high number of missing rings encountered in the roots, we could not use COFECHA and cross-dating between root and stem time-series was verified by visual comparison of tree-ring series.

Correlation in root radial growth between different parts of roots was not always statistically significant, as the root growth series often contained numerous wedging and missing rings. Therefore, visual agreement was crucial to confirm cross dating of roots' tree-ring series, especially as they were relatively short. Visual cross-dating of root series was also preferred over statistical tools in Vincent et al. (2009) and Wrońska-Wałach et al. (2016). The exclusive use of statistical tools in the cross-dating process also proved to be problematic when comparing: i) the radial growth patterns of different types of roots (i.e., lateral roots or their branches); ii) the radial growth patterns of roots that had been exposed at different time periods; iii) the radial growth patterns of roots exposed by various factors, including erosion and secondary growth (Gärtner, 2007); and iv) the radial growth patterns of roots between root systems of various trees.

2.7. Wood anatomical features in roots

Two anatomical parameters were characterized in each root sample, namely i) the year of scar(s) formation and ii) the year of occurrence of pronounced resin ducts (PRDs) (Fig. 3). According to Stoffel (2008) in the genus *Pinus* i) resin ducts are scattered and ii) traumatic resin ducts (TRDs) do not occur next to the injuries that resulted from mechanical wounding. In our study, resin ducts aligned in horizontal position were observed in multiple tree rings (Fig. 3d), and thus named as pronounced resin ducts (PRDs). Frequencies of PRDs were identified for each root. For the trampling zone (A zone), the calendar years of the formation of scars and PRDs were compared with the frequencies of missing rings. The time of root exposure in the trampling zone (A zone) was assessed based on changes in the lumen area of the earlywood cells and the percentage of latewood, following the protocol established by Gärtner (2003).

2.8. Root chronology

Each cross-dated tree-ring series obtained for an individual root disc was standardized using a spline function in the "dplR" package (Bunn, 2008) in R version 3.6.1 (R Core Team, 2016). The length of the spline

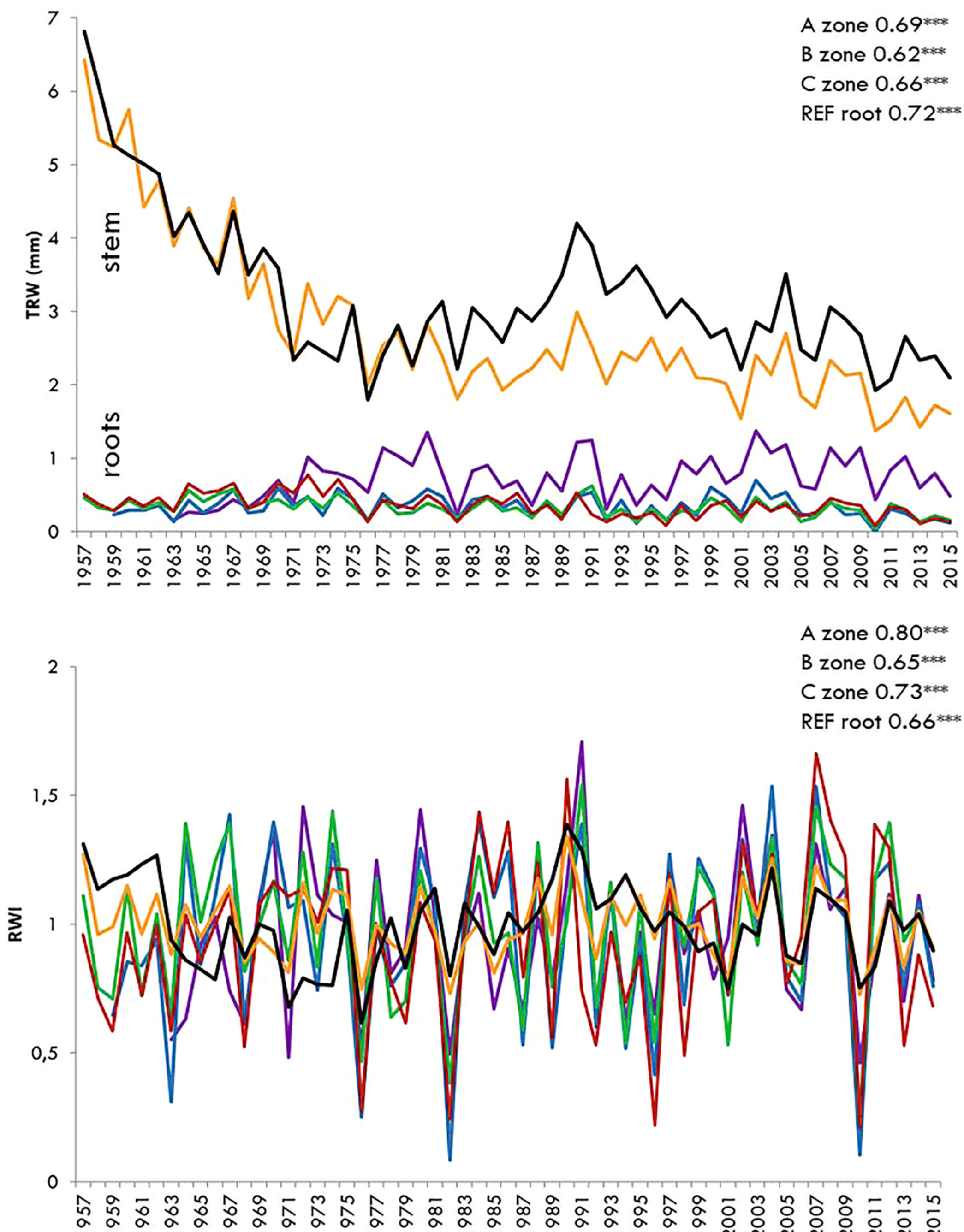

Fig. 4. Raw (a) and residual (b) *Pinus sylvestris* stem and root chronologies: stem chronology from trees growing under natural conditions (REF – black line); stem chronology from trees subjected to trampling pressure on a hiking trail (PRES – orange line); root chronology for the trampling zone (A zone – purple line); root chronology for the buried zone (C zone – green line); root chronology for the transition zone (B zone – blue line); reference root chronology (REF root – red line) from non-trampled trees. Pearson's correlation coefficients computed for the common period (1970–2015) between stem chronology from trampled trees (PRES) and each root chronology are presented in the top right corner. Significance levels are indicated with asterisks (* – p < 0.05; ** – p < 0.01; *** – p < 0.001).

was set independently at 2/3 of the wavelength of a growth series of each root. By using this standardization method, the random variation and juvenile period in the root radial growth were removed. For each root zone, a residual chronology (with first-order autocorrelation removed) was constructed and compared with the chronology of the respective stems (Fig. 4b). For this purpose, two previously constructed stem chronologies of *P. sylvestris* from the study area were used (Matulewski et al., 2019); these are i) the PRES chronology and ii) REF chronology. The REF chronology is based on 45 trees growing in natural habitat (without trampled soil) (Fig. 2). Whereas the PRES chronology encompassed 43 trees subjected to trampling, i.e., 9 stems from trees analysed with three root zones (ROOT POOL 2) and all trees (n = 34) analysed in ROOT POOL 1. A detailed description of PRES and REF chronologies construction is shown in Matulewski et al. (2019). The relationships between all chronologies, as well as between each root and respective stem tree ring series were investigated using Pearson's correlation. This relationship, called root-stem radial growth coherency (RGC), was computed primarily between each root chronology and an REF and PRES stem chronology. For this step we used both raw and residual chronologies from roots and stems and the common period (1970–2015). In addition, root-stem RGC was calculated for each individual root and stem and used as a response variable in the multiple regression models.

2.9. Statistical analysis

Stepwise multiple regression was used to identify the factors that influence root-stem RGC. Models were run separately for each root zone using the standardized growth series for all roots. Therefore, the response variables in each model were represented by correlation coefficients computed between individual standardized root vs. standardized stem growth curves, whereas predictor variables consisted of i) soil properties, ii) root and iii) trail morphology parameters (Table 1).

Direct relationships between the predictors, as well between each predictor and response variable, were explored using pairwise Pearson's correlation coefficients (Supplementary Material, Figs. S1–S3). Leven's test was used to verify data normality. All the data which did not correspond to the normal distribution was log-transformed, and all predictors were scaled using the *z*-score prior to the analyses.

To avoid the oversimplification of the models, we used the best subset regression model approach. This approach allowed us to identify the combined effects of the same factors for all three root zones analysed. To discern the relative importance of each predictor, the "lmg" method (Lindeman et al., 1980) was applied. Additionally, the proportion of variance explained by each model was determined. We used diagnostic plots to assess the normality of residuals, homogeneity of variance, and the assumption of linearity. All analyses were conducted with the R statistical language version 3.6.1 (R Core Team, 2016), using the following packages: "relaimpo" (Groemping, 2006), "corrplot" (Wei and Simko, 2017), "leaps" (Lumley, 2020), and "PerformanceAnalytics" (Peterson et al., 2019).

Table 1
List of predictors used in the stepwise multiple regression models for root-stem radial growth coherency (RGC) performed for three root zones (A – trampling, B – transition, C – buried). A detailed description of the predictors is presented in the Supplementary Material, Table S1. Diagnostic tests for predictors used in each model are illustrated in Figs. S1–S3.

	Environmental data	Root zone
Soil properties	Soil compaction	A,B,C
	Soil organic matter content	A,B,C
	Soil bulk density	A,B,C
Root morphology	Distance from the stem	A,B,C
	Location of the root: below (−) or above (+) the soil surface	A,B,C
	Root age	A,B,C
	Root circularity	A,B,C
	Root eccentricity	A,B,C
	Root type	A,B,C
	Type of root exposure	A,B,C
Trail morphology	Trail width	A
	Position of the root relative to the trail	A

3. Results

3.1. Root age and mean ring widths

The average root age was 39.9 ± 11.4 years, whereas the average stem age of trampled trees was 57.8 ± 4.1 years. Among the exposed roots (A zone), the average age of lateral roots was 35 ± 10.7 years, while that of the branching roots was 26 ± 9.3 years. The oldest root sample was 61 years (C zone), while the youngest was 12 years (A zone). The MRW for buried roots (i.e., from C, B and REF zone) does not exceed 0.4 mm. The MRW was up to three times greater in exposed roots (A zone) than in buried roots (C zone). Basic parameters for all stem chronologies and root zones are provided in Table 2.

3.2. Radial growth changes in roots

All root samples were characterized by a high number of missing and wedging rings (Fig. 5). The vast majority (i.e., 87%) of roots from the buried zone did not present a complete series of radial growth, i.e., had either missing or wedging rings. Moreover, except for four samples, all roots from the buried zone had missing rings. None of the root samples from the transition zone was characterized by a complete series of radial growth. Whereas in the trampling zone ca. 50% roots showed complete radial growth series. No missing rings were encountered in the exposed lateral roots, whereas all branches of lateral roots had missing rings with a mean number of 10% and there were no statistical differences in mean missing ring number between second- and third-order roots ($p = 0.755$) (Fig. 5b). The highest mean number of missing rings was observed in roots from the transition zone (15.3%) and the lowest in roots from the trampling zone (5.3%). The differences in mean number of missing rings among the three root zones were statistically significant ($F_{2,\,142} = 26.07$, $p < 0.001$). It was calculated that if serial sectioning was not applied, then the age of a single root sample could be underestimated by up to 27%. Especially numerous missing rings were recorded for the years 1982, 1994, 1996 and 2010. Almost 65% of missing rings were observed after 1990 (Fig. 6b). Considering all root zones, only 30% of roots had no missing rings and in 15% of roots the number of missing rings was above 20%.

The highest mean number of wedging rings was detected in the exposed root samples from the trampling zone (72%), whereas the lowest was observed in the buried roots (20.5%) (Fig. 5c). Differences in mean number of wedging rings among three root zones were statistically significant ($F_{2,\,142} = 59.19$, $p < 0.001$). In 13% of exposed roots from the trampling zone, the number of wedging rings equalled 100%. Only in 10% of exposed roots in this zone was the number of wedging rings observed to be < 50%. Considering all root zones, the lowest number of wedging rings observed in a single root was 9.3%. However, in the trampling zone there were no statistical differences in the mean number of wedging rings between second- and third-order roots ($p = 0.714$) (Fig. 5d).

3.3. Wood anatomical changes in roots

In total, 245 scars and 312 PRDs were detected in all root zones. Specifically, 84% (i.e., 208) of scars and 85% (i.e., 262) of PRDs were recognized in the trampling zone (Fig. 6 d). Over 50% of PRDs and scars recognized in this zone were found in the exposed first-order roots.

In the transition zone, 16% (i.e., 37) of scars and 15% (i.e., 50) of PRDs were identified in the roots (Fig. 6c, d). Interestingly, no scars or

Table 2
Descriptive statistics of residual *Pinus sylvestris* stem chronologies from the reference (REF), and the trampling site (PRES) together with root chronologies from buried (C zone), transition (B zone), trampling (A zone) and the reference (REF root) root zones in Brodnica Lakeland (NE Poland).

	Tree		Root			
CHRONOLOGY ID	REFERENCE SITE (REF)	PRESSURE SITE (PRES)	BURIED ZONE (C)	TRANSITION ZONE (B)	TRAMPLING ZONE (A)	REF ROOT
CHRONOLOGY LENGTH	1951–2015	1951–2015	1956–2015	1959–2015	1963–2015	1956–2015
MEAN AGE [YRS]	59.7	57.8	47.9	39.0	34.3	46.5
MEAN RING WIDTH [mm]	3.68	2.82	0.31	0.35	0.84	0.34
NUMBER OF SAMPLES	45	42	31	26	88	19
NUMBER OF RADII	104	138	164	124	512	86
INTER SERIES CORRELATION (Rbar)	0.501	0.565	0.481	0.388	0.392	0.666
EXPRESSED POPULATION SIGNAL (EPS)	0.967	0.977	0.944	0.931	0.952	0.925
STANDARD DEVIATION RWI (SD)	0.242	0.191	0.438	0.516	0.555	0.283
MEAN SENSITIVITY (MS)	0.212	0.208	0.534	0.629	0.687	0.391
SIGNAL TO NOISE RATIO (SNR)	5.345	6.332	16.908	13.275	19.834	10.804
FIRST-ORDER AUTOCORRELATION (AC1)	0.369	0.103	0.033	0.025	0.047	0.133

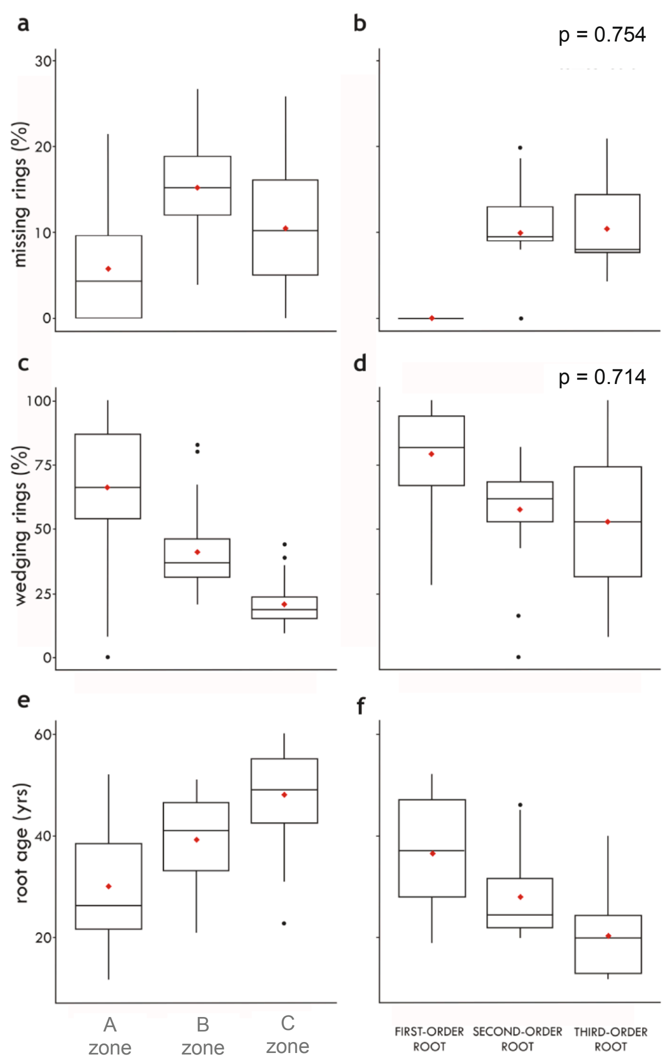

Fig. 5. Percentage of missing rings (a) and wedging rings (c) in trampling (A zone), transition (B zone) and buried root zones (C zone) supplemented with root age distribution (e). For the trampling zone only, the percentage of wedging rings (b), missing rings (d) and root age distribution (f) are presented in relation to the root order type. Mean values are represented by red diamonds. All differences in means, despite two indicated cases (i.e., b and d), were statistically significant (Tukey's post-hoc test).

PRDs were recognized in the roots from the buried zone (C zone). Over 50% of scars and PRDs were recorded for the period 2001–2010, i.e., during the time when 56% of roots were exposed (Fig. 6c, d).

In total, 17 events of root exposure (EREs) were recognized in the 88 exposed root samples from the trampling zone (Fig. 6a). Additionally, it was revealed that most of the analysed root exposures were attributed to the late-earlywood zone (i.e., 84% roots). The years of root exposure events were significantly correlated with the years of PRDs occurrences ($r = 0.52$, $p < 0.001$) and the years of scars formation ($r = 0.51$, $p < 0.001$). In addition, a significant correlation was found between the occurrences of PRDs and scars in exposed roots (from the trampling zone) ($r = 0.73$, $p < 0.001$). Moreover, a significant positive relationship was obtained between the occurrence of PRDs in the exposed lateral roots and the occurrences of missing rings in the exposed root branches from the trampling zone (i.e., in the second- and third-order roots) ($r = 0.39$, $p < 0.05$).

3.4. Radial growth comparison between roots and stems

The high number of root samples obtained via serial sectioning, and the thorough cross-dating process that was performed, allowed us to establish three root chronologies representing the radial growth patterns of the exposed, transition, and buried roots zones (Fig. 4a, b). They covered the period 1956–2015, 1959–2015, and 1963–2015, respectively, while both stem chronologies of *P. sylvestris* from the reference site (REF) and from the trampling site (PRES) covered the period 1951–2015 (Fig. 3). In addition, the reference root chronology was established and covered the period 1956–2015 (REF root, Fig. 4). Descriptive statistics for all stem and root chronologies are provided in Table 2.

The results revealed high variations in mean ring widths between root and stem chronologies, as well among root chronologies (Fig. 4). . The highest correlation between the raw stem and root chronologies was found for the reference root chronology ($r = 0.72$, $p < 0.001$) (Fig. 4). Among three root zones the highest correlation between the raw stem and root chronologies was found for the trampling zone ($r = 0.69$, $p < 0.001$). The lowest mean correlation between individual root and stem was observed in the transition zone ($r = 0.44$, $p = 0.001$), whereas the highest in the trampling zone ($r = 0.53$, $p < 0.001$). For the exposed lateral roots specifically, the mean root–stem RGC was $r = 0.59$ ($p < 0.001$). Only 9% of the exposed lateral roots were not significantly correlated with the stem. In contrast, the mean correlation coefficient between the stem and branches of lateral roots was $r = 0.39$ ($p < 0.05$). Around 50% of these roots (i.e., second- and third-order roots) were not significantly correlated with the stem.

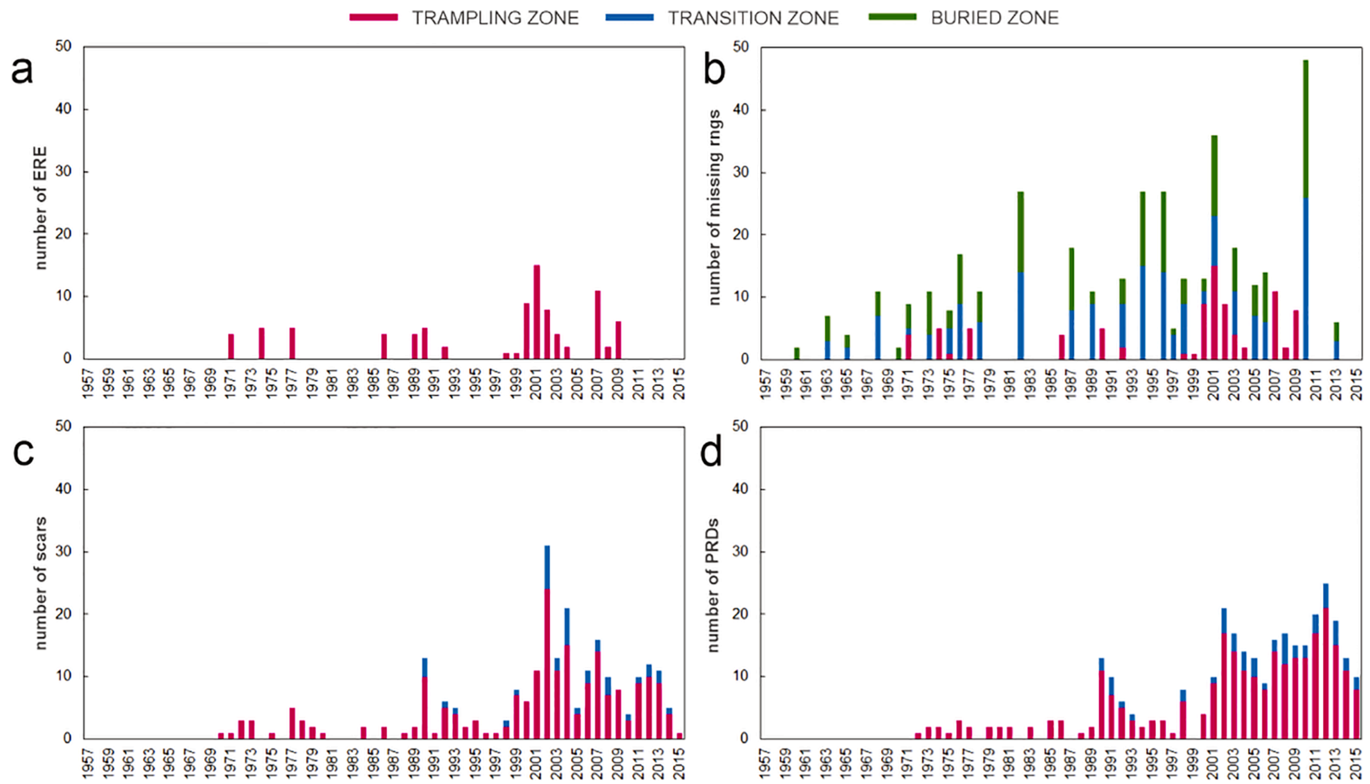

Fig. 6. Frequency of events of root exposure (ERE; a), missing rings (b), scars (c), and pronounced resin ducts (PRDs; d) in the trampling root zone (pink bars), the transition root zone (blue bars) and the buried root zone (green bars).

3.5. Impact of environmental factors on root-stem RGC

The multiple stepwise regression analysis revealed a set of exclusive environmental factors affecting the root-stem RGC in the three root zones. Among nine predictors included in the candidate model for the trampling zone (Table 3), four were used in the final model. For the trampling zone root-stem RGC was determined primarily by root type (77.3%) and root age (17.4%) (Table 3), whereas the highest proportion of variance in the model for the buried zone was explained by the soil organic matter content (55.4%) and soil compaction (39.7%). In contrast, the variables used in the final model for the transition zone were not found to be reliable predictors of root-stem RGC (Table 3). The final model for the trampling and buried zones explained 63.0% and 66.8% of the variance in stem-root RGC, respectively.

Table 3
Final model results for the buried, transition and trampling root zones. Parameter estimates (β) are presented with the associated 95% confidence intervals (derived from 1000 bootstrap iterations), *t*-test statistics and p-values. The response variable in each model is represented by the Pearson's correlation coefficients computed between standardized root vs. stem radial growth, i.e., root-stem RGC. A full list of the predictors with descriptions is presented in the Supplementary Material, Table S1; *n* roots represents the number of observations for each root zone. Significant values are marked in bold.

Root zone [*n* roots]	R^2	Adj R^2	Parameter	β	t	p
Trampling zone (A zone) [*n* = 88]	0.63	0.61	Intercept	−1.05 [−3.18:1.08]	−0.99	0.32
			AGE	**0.69 [0.11:1.26]**	**2.41**	**0.02**
			TRAIL	−0.38 [−0.92:0.15]	−1.43	0.16
			TYP	**−0.37 [−0.48:-0.27]**	**−7.10**	**0.00**
Buried zone (C zone) [*n* = 31]	0.67	0.61	Intercept	−1.37 [−1.66:-1.08]	−9.97	0.00
			DIST	0.00 [−0.00:0.00]	1.50	0.15
			COM	**0.07 [0.02:0.11]**	**2.71**	**0.01**
			ORG	**0.13 [0.05:0.20]**	**3.54**	**0.00**
Transition zone (B zone) [*n* = 26]	0.22	0.15	Intercept	−1.21 [−2.17:-2.75]	−2.67	0.01
			DIST	−0.00 [−0.00:1.09]	−2.03	0.06
			BULK	0.51 [−0.17:1.19]	1.56	0.13

Abbreviations: root age (AGE), hiking trail width (TRAIL), type of lateral root i.e., first-, second- or third-order root (TYPE), distance between collected root sample and stem base (DIST), soil compaction (COM), soil organic matter content (ORG), soil bulk density (BULK).

4. Discussion

4.1. Discrepancies in root radial growth and wood anatomy due to trampling

Stepwise cross-dating of the *P. sylvestris* roots subjected to trampling pressure revealed high discrepancies in the number and width of annual growth rings between the selected root zones. The wedging rings were found to be most frequent in the exposed lateral (i.e., first-order) roots from the trampling zone (Fig. 5d). In contrast to these findings, the study of Montagnoli et al. (2019) on *Pinus ponderosa* detected the highest occurrence of discontinuous rings in the second-order roots, but they did not consider the exposed roots subjected to trampling. Moreover, we identified that the total number of wedging rings, and thus the root eccentricity, increases along with the distance from the stem. Similar findings were previously reported by Krause and Morin (1995) in non-trampled roots of *Picea mariana*. Due to the lack of quantitative studies conducted on tree roots subjected to trampling, the direct comparison of our results with other trampled roots is remains limited.

The mechanism responsible for the common formation of discontinuous rings in the roots is not well known. We hypothesize that the highest number of wedging rings recognized in the trampling zone results from the discontinuation of cambial activity along the root circumference caused by mechanical pressure induced by trampling. Moreover, this pressure usually intensifies in the peak growing season and co-occurs with the peak impact of trampling. Unfortunately, a lack of long-term data on a hiking traffic inhibits direct comparison with root radial growth time-series. The negative effect of continuous mechanical pressure within the trampling zone might be highlighted by the fact that in 13% of the exposed roots the number of wedging rings equalled 100%. It was previously described (LaMarche, 1963; Gärtner, 2007) that continuous mechanical stress leads to changed distribution of photosynthates and growth hormones (auxin) (Forest et al., 2006), and intensifies the radial growth of roots in the downward part of the roots' cross-section, an area which is protected and often unexposed. Additionally, for 13% of the exposed roots in our study the root centre was eroded, which is considered as the most extreme effect of the mechanical impact of trampling.

Missing rings were encountered in all three root zones, except for the exposed lateral roots in the trampling zone. In contrast, all branches of lateral roots in the trampling zone (i.e., second- and third-order roots) showed a high number of missing rings (Fig. 5b). Interestingly, the occurrence of missing rings in the branches of lateral roots (i.e., second- and third-order roots) was positively correlated with the occurrence of PRDs in the lateral roots (i.e., first-order roots). This suggests that resources might be very limited in the years when formation of PRDs occurs in the first-order roots, and as a result radial growth in the branches of lateral roots ceases during the years when the mechanical pressure is high. The first occurrences of scars and PRDs were recognized in the exposed roots in the early 1970s, which synchronize with the reduction of radial growth observed in the stem. However, the highest amount of both (i.e., PRDs and scars) was found after 1990, i.e., in the period where almost 65% of missing rings were detected in all three root zones. This was the period when tourist traffic in the study area was the most intense (Matulewski, 2018). Indeed, trampling induces common root exposure and mechanical injuries that eventually lead to abrasion and scar formation (Pelfini and Santilli, 2006; Buchwał and Wrońska-Wałach, 2008; Buchwał, 2009). As Carrara and Carrol (1979) emphasized, dating of abrasion scars from the roots may indicate the time of the root exposure. A high correlation between the years of root exposure and the years of the formation of both scars and PRDs was observed for most of the roots in our study (Fig. 6). This indicates the high sensitivity of *P. sylvestris* roots to trampling pressure. Moreover, our study showed that stem growth might be affected by root exposure. Specifically, it was observed that radial growth reduction in the tree stems corresponded to an increase in events of root exposure (EREs), as well as to an increased frequency of the formation of scars and PRDs in the roots. Thus, in line with the results of Krause and Morin (1999a), we confirmed that roots' radial growth and wood anatomy can serve as ecologically sensitive indicators of environmental changes, including the impact of trampling.

Trampling activity, together with natural geomorphic processes, induces active soil loss within the root systems. This leads to common root exposure and changes in the intensity of the exposure processes over time (Bodoque et al., 2005). This fact was confirmed in our study as we observed 17 EREs in the trampling zone (Fig. 6a), where over 50% of root exposures occurred after the year 2000. After root exposure, increased ring widths were observed in each exposed root time-series, which is in accordance with previous studies (Alestalo, 1971; Carrara and Carroll, 1979; Gärtner, 2003, 2007; Rubiales et al., 2008; Wrońska-Wałach, 2009, 2014). Fayle (1968) emphasized that the radial growth changes along the root length depend on root age and soil conditions. On the other hand, Krause and Morin (1995) indicated that the maximum radial increments always occurred in the roots located close to the tree stem. However, none of these studies investigated roots subjected to trampling. This is in contrast to our study, where the largest tree rings were recognized primarily in the exposed root zones, located away from the stem along the hiking trail. Increased tree ring widths were related to an increased percentage of latewood that was observed in all exposed roots (A zone). In fact, in most of these roots compression wood was observed, although this was not quantified in this study.

The domination of latewood cells in exposed roots indicates the increased importance of the mechanical function of these roots. Additionally, as a result of more wood being allocated in the exposed roots, missing rings were not present in the first-order roots. Root exposure associated with trampling modifies the habitat conditions and stimulates the deeper development of roots (Pelfini and Santilli, 2006). Once a root gets exposed, its mechanical function dominates over the conduction of water and nutrients, and as a consequence, the frequency of radial growth irregularities increases (Fayle, 1968; Pérez-Rodríguez et al., 2007). In addition, root exposure associated with a decrease in the lumen area of earlywood cells modifies the hydraulic properties of the roots, and potentially decreases water conductance from the roots to the stem (Matulewski et al., 2019). This might lead to overall tree growth constraints, which were shown in our study in the reduction of stem growth right at the time of common root exposure.

4.2. Root-stem RGC

Although the roots in all three zones exhibited growth irregularities, a high correlation between the radial growth of stem and roots was detected. In previous dendroecological studies, the synchrony in radial growth between roots and stems was mainly observed in the root sections that were located close to the stem, i.e., at a distance of <0.4 m from the stem (Schulman, 1945; Fayle, 1968; Krause and Morin, 1995, 1999b; Rybníček et al., 2007). According to Rybníček et al. (2007), coherency in Scots pine radial growth was not found for the root samples that were located further away from the tree stem, in which many indistinct tree-ring boundaries and potentially false rings were recognized. In our study we did not encounter such constraints, including trampled and non-trampled roots.

Multiple regression models revealed that a diverse set of variables explained the root-stem RGC. Moreover, there was no single variable that significantly affected the root-stem RGC in all root zones. Instead, two sets of predictors from two different groups (Table 3) explained the root-stem RGC in the trampling and the buried zones, while no significant predictors were found for the transition zone. Root type and root age were determined as the most reliable predictors of the root-stem RGC in the trampling zone (Table 3). This highlights that, despite more advanced age, exposed lateral roots exhibit higher correlation with the stem growth than the branches of lateral roots. Previous studies revealed, under experimental work, that increased light intensity stimulates the formation and elongation of *P. sylvestris* lateral roots (Michniewicz and Stopińska, 1980a, 1980b). An exposed root is therefore, like the tree stem, probably more affected by external factors such as air temperature or rainfall (Fayle, 1968). The main lateral roots are characterized by an active cambium, while the branches of lateral roots are characterized by limited secondary growth (Hejnowicz, 1973). This could be a reason why in our study the branches of lateral roots showed the highest irregularity of radial growth, as manifested by numerous missing rings. Additionally, the fact that mechanical strength is required for the exposed roots and both wider rings and increased latewood zones are formed in these roots, leads us to hypothesize that a lack of resources might induce common growth constraints in the branches of exposed lateral roots.

In contrast, the final model for the buried zone revealed the importance of the soil organic matter content and soil compaction in root-stem RGC. The overall proportion of variance explained by the model for the buried zone was similar to that of the model established for the trampling zone, but none of the predictors had comparable importance in both models. The model results for the buried zone emphasized the importance of soil properties, whereas for the trampling zone they highlighted the predictors related to the root characteristics (Table 1). Such contrasting results indicate the important changes in root habitat conditions between the buried and trampling zones, and imply a pronounced impact of trampling on root radial growth. The nonsignificant effects of predictors related to soil properties in the trampling zone indicate that the growth of trampled roots is more sensitive to climatic conditions and human impact rather than to soil habitat conditions.

In the buried zone, increased soil organic matter content promoted the radial growth of roots, as expected in a natural root habitat (Sands et al., 1979). The average soil organic matter content in the buried zone was 13% higher than in the trampling zone. In contrast, mean soil compaction in the buried zone was three times lower than in the trampling zone (Matulewski et al., 2019). Nevertheless, the positive effect of soil compaction revealed for the buried zone suggests that buried roots might not be limited by moisture availability. In fact, the roots from the buried zone were located at a relatively close distance to the stem (ca. 1.7 m), and thus active water uptake might be of less importance in these roots compared to the roots located at a further distance from the stem. Furthermore, higher soil compaction in the buried zone was positively correlated with decreased soil moisture (Fig. 7), which might imply more stable thermal conditions in less porous soils and thus more favourable conditions for root radial growth. Generally, water content was found to have a greater impact on pine root growth than soil compaction (Blouin et al., 2008). In another pine study (Sands et al., 1979) soil compaction was found to reduce soil porosity but had little effect on the water storage capacity. In addition, previous studies conducted on ponderosa pine seedlings (Gomez et al., 2002) revealed that the effect of higher soil compaction on stem radial growth is not always detrimental, and depends strongly on soil texture. Therefore, further investigations will be needed to better explain the radial growth of pine roots in relation to variable soil characteristics and the duration of spring rehydration (cf. Turcotte et al., 2011) along the root length and across various root zones.

5. Conclusions

The study revealed several lines of evidence for the impact of trampling on Scots pine root growth and wood anatomy. High discrepancies in the wood anatomy between trampled and non-trampled roots were found. The largest variation in ring widths was determined for lateral exposed roots subjected to trampling along the hiking trail. In the roots exposed on a hiking trail we have observed a sequential transition in the roots' radial growth supplemented by changes in the wood anatomy. First, the widest rings were formed, right at the time when the root became exposed. Root exposure events were often associated with scars and PRDs formation, and their occurrence became more common in the following years. Years of PRDs formation in the first-order roots were associated with missing ring formation in the second- and third-order roots. This sequence in radial growth and wood anatomy changes observed in trampled roots mirrors the gradual transition in the root function associated with constant mechanical stress induced by trampling. In such roots water conduction and the transport of nutrients seem to be of less importance, and the role of these roots is more related to stabilization and maintenance of the remaining part of the root system.

High discrepancies between the different parts of the root i.e., trampled and non-trampled zones, were visible in root-stem RGC. Interestingly, the models for the trampling zone revealed the highest importance of root type and root age on root-stem RGC. In contrast, the highest importance of soil properties, i.e., soil organic matter content and soil compaction on root-stem RGC, was found for the buried zone. Such opposing results indicate key changes in root habitat conditions induced by trampling. Hence, the study demonstrated the important role of tree roots as ecological indicators, documenting changes in the ecosystem such as the impact of trampling recorded at annual resolution of root growth rings.

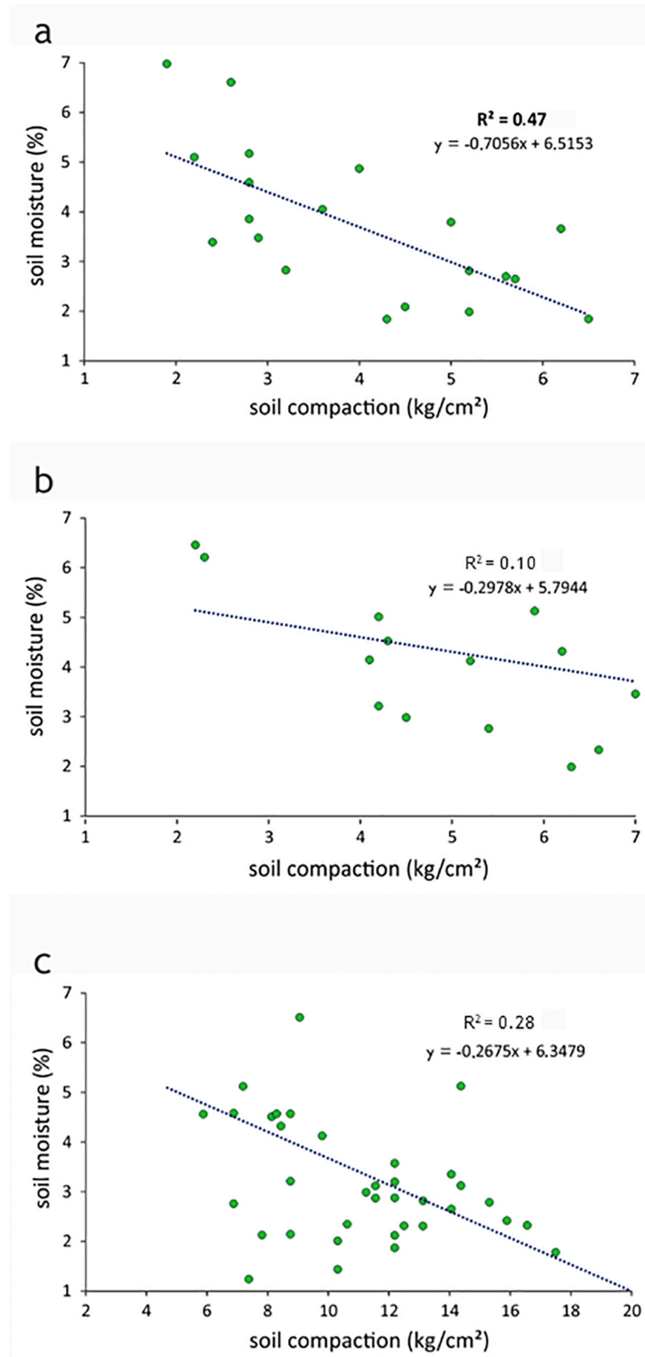

Fig. 7. Linear relationships between soil compaction and soil moisture for roots located in: (a) the buried (n = 20), (b) transition (n = 16) and (c) trampling root zones (n = 39). Significant relationships are marked in bold.

Overall, it has been proved that the record of radial growth and wood anatomy changes in Scots pine roots serve as a valuable ecological archive of trampling impact with high temporal resolution. Therefore, our results can be helpful to park and forest managers, who are responsible for the preservation of natural conditions for tree growth and meeting the recreational demand for hiking trails in forested lowland areas.

CRediT authorship contribution statement

P. Matulewski: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Visualization, Writing - original draft, Writing - review & editing, Funding acquisition. **A. Buchwal:** Conceptualization, Supervision, Methodology, Formal analysis, Visualization, Writing - review & editing. **A. Zielonka:** Methodology, Visualization, Writing - review & editing. **D. Wrońska-Wałach:** Methodology. **K. Čufar:** Writing - review & editing. **H. Gärtner:** Conceptualization, Methodology, Writing - review & editing, Supervision.

Declaration of Competing Interest

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.107095.

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