Ongoing modifications to root system architecture of Pinus ponderosa growing on a sloped site revealed by tree-ring analysis

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ABSTRACT

Our knowledge of the root system architecture of trees is still incomplete, especially concerning how biomass partitioning is regulated to achieve an optimal, but often unequal, distribution of resources. In addition, our comprehension of root system architecture development as a result of the adaptation process is limited because most studies lack a temporal approach. To add to our understanding, we excavated 32-year-old Pinus ponderosa trees from a steep, forested site in northern Idaho USA. The root systems were discretized by a low magnetic field digitizer and along with AMAPmod software we examined their root traits (i.e. order category, topology, growth direction length, and volume) in four quadrants: downslope, upslope, windward, and leeward. On one tree, we analyzed tree rings to compare the ages of lateral roots relative to their parental root, and to assess the occurrence of compression wood. We found that, from their onset, first-order lateral roots have similar patterns of ring eccentricity suggesting an innate ability to respond to different mechanical forces; more root system was allocated downslope and to the windward quadrant. In addition, we noted that shallow roots, which all presented compression wood, appear to be the most important component of anchorage. Finally, we observed that lateral roots can change growth direction in response to mechanical forces, as well as produce new lateral roots at any development stage and wherever along their axis. These findings suggest that trees adjust their root spatial deployment in response to environmental conditions, these roots form compression wood to dissipate mechanical forces, and new lateral roots can arise anywhere and at any time on the existing system in apparent response to mechanical forces.

1. Introduction

A comprehensive knowledge of the complex root phenotype (i.e. its structure and function; Atkinson et al., 2019) of a plant helps develop a better understanding of important aspects of the root’s behavior regarding water and nutrient absorption, anchorage, carbohydrate storage, and deposition and excretion of biochemical compounds (Danjon et al., 2013; Pagès, 2002; Terzaghi et al., 2016). A complete understanding of root properties becomes essential for woody species (shrubs and trees) as they live longer and achieve larger dimensions than their non-woody cohorts. The weight of woody, above-ground organs is considerable and the resulting, powerful mechanical forces need to be dissipated into the soil to avoid uprooting (Stokes and Mattheck, 1996).

Our understanding of root system architecture (RSA) in trees and shrubs relies heavily on studies using the shovelomic approach (that being a time-consuming, labor-intensive, destructive approach where a complete root system is excavated by hand), accomplished by using one of several principal methods (Chiatante et al., 2019; Colombi et al., 2015; Dumroese et al., 2019; Montagnoli et al., 2019). After excavation, coarse roots are manually mapped to measure traits such as the number, length, volume, surface area, and topological location of all lateral roots (classified according to their branching order) and wood density (Iyer-Pascuzzi et al., 2010), often assessed with regard to soil depth and volume and stand density (Böhm, 1979).

A long term aim of RSA studies is to underpin development of in silico predictive models able to foresee the plant response in its root system when environmental changes occur (Yang et al., 2016). These models could assist in development of next-generation planting
material that is more resilient to predicted climate change or simply be the modeling basis to provide a more realistic measurement of the amount of carbon stored as perennial roots (coarse structural roots) in forest ecosystems (King et al., 1996). Currently, however, knowledge of how RSA develops is still incomplete, and one aspect that needs to be understood is how biomass partitioning is regulated because the anchorage strength of a tree depends upon an optimal distribution of resources (Stokes and Mattheck, 1996). Indeed, if wood is laid down with a greater density at areas of mechanical stress, then the possibility to tolerate such stress increases (van Gelder et al., 2006; Chave et al., 2009; Anten and Schieving, 2010). This fact explains why root biomass allocation is not normally evenly distributed. On one hand, the literature suggests that the RSA may undergo variations throughout different developmental stages that characterize the growth cycle of a plant or in response to abiotic factors, such as wind, slope, and soil conditions that threaten its anchorage (Schroth, 1998; Pühe, 2003; Stokes et al., 2009; Ji et al., 2012; Ghestem et al., 2011). On the other hand, the literature also suggests that some tree species, such as Pinus pinaster, are unable to regenerate an appropriate spatial arrangement of main structural roots from a defective juvenile RSA that lacks some major anchorage component (Danjon et al., 2005).

The lack of a temporal approach in RSA studies that could reveal the chronology of lateral root formation limits our ability to describe the steps leading to a particular RSA development as the result of the adaptation process. Therefore, understanding the chronological sequence of lateral root emission in different zones surrounding the taproot could help unveil why RSA has changed during the lifespan of the tree as it grows to achieve a higher functional performance. Moreover, the analysis of a temporal factor could improve the reliability of two- and three-dimensional (2D and 3D) provisional models (reviewed in Dupuy et al., 2010) and leverage mechanistic studies where factors responsible for deployment of a certain type of RSA are investigated.

In addition to root deployment, the type of wood residing in the roots is undoubtedly important. Unlike the stem, occurrence of wood modification in roots has been poorly explored despite the occurrence of asymmetric annual rings and specialty roots (e.g. I- and T-beam) reported in both gymnosperms (Coutts et al., 1999; Dumroese et al., 2009) and angiosperms (De Zio et al., 2016; Di Iorio et al., 2005). Mechanical stress induced by stem sway has been suggested as the cause of annual rings at the rootstem base that are wider than those elsewhere on the root system (Fayle, 1975, 1976). This asymmetric growth could play an important role in increasing root stiffness with the consequent effect of reinforcing mechanical anchorage of a tree.

In cross section, the portion of wood showing an eccentricity of the annual rings and often a different coloring is defined as reaction wood. Ring eccentricity is the consequence of a different number of cell layers distributed around the circumference of the annual rings (Kim et al., 2016), whereas different coloring is due to a variation in the chemical and physical organization of the cell walls (Ruelle, 2014). Gravity is a major factor responsible for inducing reaction wood formation (Du and Yamamoto, 2007). In gymnosperms, reaction wood is termed compression wood and forms in the opposite direction of the mechanical stress (Westing, 1965; Alméras and Clair, 2016). Compression wood typically appears as wide, crescent-shaped bands of darker brown wood that sometimes resembles lateward, the darker colored, outer part of growth rings, although the cells are different (Donaldson and Singh, 2016). In an inclined stem of a gymnosperm tree growing on a level site, compression wood forms normally on the lower side in response to gravity (i.e. inertial force), but in Tsuga mertensiana (references in Westing, 1965), compression wood was observed in response to the presence of a slope, or on the lee side when a tree was bent by constant directional wind. In angiosperms, reaction wood is termed tension wood, and the annual ring eccentricity is visible in the opposite direction as that found in gymnosperms (Westing, 1965). At the cytological level, compression wood is formed by a single tissue with a type of cells (tracheid) playing both a nutritional and mechanical role, whereas in tension wood these two functions are entrusted upon different cell types, such as vascular, mechanical, and parenchyma. The formation of reaction wood in roots is, however, little explored (Hathaway and Penny, 1975) except in response to soil erosion (Gärtner, 2007; Hitz et al., 2008; Wistuba et al., 2013) or bending (De Zio et al., 2016).

Toward improving our understanding of root spatial deployment, we investigated root traits of a shrub (Spartium junceum, Lombardi et al., 2017), angiosperm trees (Quercus serris, Di Iorio et al., 2007; Quercus pubescens, Di Iorio et al., 2005), and a gymnosperm tree (Pinus ponderosa, Dumroese et al., 2019). In these studies we found that plants growing on slopes adapt their RSA to achieve stronger anchorage to the soil. Such reinforcement is achieved through the deployment of an asymmetric distribution of lateral roots surrounding the stump. Here we continue this series of shovelomic studies by describing a number of aspects of the RSA in P. ponderosa trees growing 32 years on a steep slope. Our hypotheses are that 1) environmental conditions (e.g. wind, slope conditions, soil hydrology) require adjustments of root spatial deployment, and 2) that continuous variability in conditions (e.g. changes in self-loading weight of shoots occurring during plant growth) require that, to satisfy mutable needs, the root biomass distribution changes in time and space by either the emission of new laterals and production of compression wood. Therefore, we used two analytical approaches to examine root length and volume in different root ordering in four quadrants surrounding the stump (downslope, upslope, windward, and leeward); furthermore, employing a tree-ring analysis, we investigated the chronological sequence of root development and explored the formation of compression wood in different root orders and along the roots axis.

2. Materials and methods

2.1. Site description, tree establishment, excavation, and 3-dimensional measurement

Typical forested sites occurring on the northern Rocky Mountains in northern Idaho, USA are comprised of mixed conifer species that reflect a wildfire-based disturbance regime; one dominant conifer species is Pinus ponderosa. Our sampled trees were growing on a typical forest site at about 1000 m elevation on the University of Idaho Experimental Forest in northern Idaho (lat. 46.842240, long. −116.871035) on a northeast aspect (Fig. 1), and were collected as part of another study because of the known history of the trees. The site has slopes of 30 to 50% and the deep (∼1.5 m) soil was derived from volcanic ash above weathered granite (Vassar series, Typic Udiferrands, Andisol; Soil Survey Staff, 2013). This soil type is characterized by a low cohesive friction (Johnson et al., 2007). Ecologically, the site is classified as a Thuja plicata/Clintonia uniflora/Clintonia uniflora phase habitat type (Cooper et al., 1987). In 1985, the forest was clearcut and the slash was broadcast burned during autumn 1985 to facilitate outplanting and reduce wildfire risk. In March 1986, one-year-old nursery seedlings of P. ponderosa grown in 60-mL containers following the growing regime of Wenny and Dumroese (1987) were hand-plant on a 2-m (between rows) × 1-m (within rows) spacing as part of an experiment (see Wenny et al., 1988). During autumn 1986, every other seedling was sampled leaving residual trees on a 2 × 2-m spacing. Weather data from the nearest stations (7 to 16 km) to the study site are shown in Table 1. The prevailing wind is west southwest during the growing season (Western Regional Climate Center, 2019). Similar sites have ~100 frost-free days per year (Soil Survey Staff, 2013). No irrigation, fertilization, weeding, or thinning was done after outplanting.

In early July 2017, we relocated the P. ponderosa trees. We randomly selected 15 trees to assess diameter breast height (DBH) measured cross slope, height, and canopy projected area (Table 2), and mapped their locations in relation to other nearby trees (Fig. 1). Of these, 10 trees were randomly selected for excavation and of these, 8
were digitized. See Dumroese et al. (2019) for complete details on root excavation and digitization. Briefly, to excavate the roots, we felled trees, marked stumps, and removed the soil with an air-spade. Root systems were brought to the laboratory, repositioned to their original orientation, and digitized using a low magnetic digitizer, transmitter, and receiver. Data were encoded in a standard format (MTG) commonly used for representing branching topological (i.e. branching hierarchic structure) relationships (Godin and Caraglio, 1998). The topology was coded according to the “acropetal-development approach” (Danjon et al., 2013; Sorgonà et al., 2018) with the seed-origin radicle, the

Fig. 1. Location of the study site in northern Idaho, USA, and locations of the sampled trees and nearby trees.

| Month | Air temperaturea | Precipitationa | Snowfalla | Windb |
|-------|------------------|----------------|-----------|-------|
|       | Maximum (°C)     | Minimum (°C)   | (mm)      | (cm)  | Direction | Speed (km/h) |
| Jan   | 2.2              | −6.1           | 72        | 38.4  | E         | 14.6         |
| Feb   | 5.3              | −4.0           | 61        | 19.8  | E         | 13.7         |
| Mar   | 8.9              | −2.1           | 61        | 11.4  | E         | 14.2         |
| Apr   | 13.9             | 0.4            | 51        | 3.0   | E         | 15.3         |
| May   | 18.9             | 3.3            | 54        | 0.3   | WSW       | 15.6         |
| Jun   | 22.6             | 6.2            | 48        | 0.0   | WSW       | 14.5         |
| Jul   | 28.2             | 7.7            | 20        | 0.0   | WSW       | 7.5          |
| Aug   | 28.3             | 6.8            | 20        | 0.0   | WSW       | 8.2          |
| Sep   | 23.0             | 3.8            | 33        | 0.0   | WSW       | 8.8          |
| Oct   | 15.8             | 0.6            | 48        | 0.8   | E         | 10.6         |
| Nov   | 7.3              | −1.9           | 75        | 12.4  | E         | 13.8         |
| Dec   | 2.9              | −4.9           | 79        | 29.0  | E         | 15.0         |
| Average | 14.8             | 0.8            | –         | 622   | 115.1     |             |
| Average total | – | – | – | – | – | – |

a Data from 1915 to 2016 (Potlatch 3 NNE [107301]).
b Data from 1996 to 2006 (Pullman‒Moscow Regional Airport).
primary roots (-axis) or taproot designated order zero (pink color in Fig. 3). Lateral roots emerging from the taproot were designated first-order roots (green color in Fig. 3), with second-order roots then originating from these first-order laterals (blue color in Fig. 3), and so on (Zobel and Waisel, 2010). We measured all roots having a proximal order (i.e. 1st-, 2nd-, and 3rd-order) emanating from it were also assigned to the downslope quadrant, regardless of whether or not the roots subsequently grew into other quadrants. For each emission quadrant, length and volume of roots were determined by dividing roots into segments of 10 to 30 cm length from their point of attachment to the parental root. On each end of the segment, we measured the largest diameter (D1; Fig. 2). From the midpoint of D1 we measured the diameter perpendicular to it (D2) and calculated an average diameter and an average radius. The average radius for each segment end (R1 and R2) was calculated as the average of D1 and D2 for each corresponding segment end.

We used AMAPmod software (Godin et al., 1997) to analyze the data, and computed root traits (i.e. length, diameter, and volume) from the 3-dimensional (3D) digitizing data of entire root systems. We analyzed data by four quadrants, considering root traits as a function of upslope down-slope direction and of west- (windward) versus east- (leeward) direction, with the downslope direction coinciding with north and the west-east axis coinciding with the direction of the prevailing wind. Moreover, the analysis was repeated at two depths: 0–30 cm (where zero coincides with the soil surface) and 30–60 cm with a maximum depth of ~1.5 m. See Dumroese et al. (2019) for more details.

2.2. Root system architecture

We followed the modified terminology suggested by Danjon et al. (2013) for P. pinaster. Our observations focused on the shallow roots branching from the upper portion of the taproot and that are characterized by an axis where the first portion shows a very rapid taper (i.e. “zone of rapid taper”). We use the term “sinker” to indicate lateral roots that grow straight downward independent of their branching order. Based on Danjon et al. (2005), the term “cage” was used to define a cylindrical zone surrounding the taproot and having a diameter of 2.2 × DBH (stem diameter at breast height, ~ 1.3 m), which is comprised of most of the sinker roots along with the taproot and part of the shallow coarse roots.

Using AMAPmod software, a lateral root that is emitted from one quadrant (i.e. downslope, upslope, windward, and leeward) but changes direction and grows into another quadrant has the relative portions of its traits assigned to both quadrants. In addition to this AMAPmod quadrant (AQ) approach, we also manually traced first- and second-order lateral roots back to their junction points with the taproot; we termed this point of initiation the emission quadrant (EQ). For example, if a first-order lateral root had its junction in the downslope quadrant of the taproot, all subsequent roots (second- and third-order) emanating from it were also assigned to the downslope quadrant, regardless of whether or not the roots subsequently grew into other quadrants. For each emission quadrant, length and volume of roots were determined by dividing roots into segments of 10 to 30 cm length from their point of attachment to the parental root. On each end of the segment, we measured the largest diameter (D1; Fig. 2). From the midpoint of D1 we measured the diameter perpendicular to it (D2) and calculated an average diameter and an average radius. The average radius for each segment end (R1 and R2) and the length of the segment (h) was used to calculate the segment volume as a truncated cone:

\[
V = \frac{1}{3}\pi (R_1^2 + R_1R_2 + R_2^2)h
\]

and total volume and total length of each lateral root was the sum of the all segment values. We also determined the cross sectional area (CSA) of the first-order lateral root where it met the taproot using the following formula:

\[
CSA = D_1 \times D_2 \times \pi
\]

where D1 and D2 are as described above.

2.3. Tree-ring analysis

One root system was randomly selected for detailed analysis. We divided the taproot axis into three sectors (0–30 cm; 30–60 cm; > 60 cm) because our previous work (Dumroese et al., 2019) showed that all the shallow lateral roots originated in the first 30 cm of the taproot axis and almost all the remaining lateral roots originated between 30–60 cm. We cut each lateral root at its respective branching point with a higher order root. At the branching point, we cut a 3-cm-thick cross section, polished it with a belt sander using progressively finer grits of sandpaper (60, 80, 120, 150, 220, 300, up to 600 grit), and then counted the number of annual rings with the aid of an Olympus microscope (BX41). We cross-dated each sample using the list year technique in which tree rings were counted backwards from the known year of felling (2017). Ring-dating of root sections presenting a number of discontinuous annual rings was accomplished using a modification of the Zig-Zag Segment Tracing Method (Wrońska-Wałach et al., 2016).

We observed that the discontinuous annual rings were always oriented in a single direction and therefore it was possible to divide the root section into four sectors with perpendicular radii placed to ensure one radius had maximum length. The radius with the greatest number of growth rings was selected (Krause and Morin, 1995). Although growth rings were usually measured along the radius, we deviated when

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**Table 2**

Characteristics of sampled trees.

| Tree | Canopy projected area (m²) | DBH (cm) | Height (m) |
|------|---------------------------|----------|------------|
| P1   | 8.0                       | 24.1     | 16.8       |
| P2   | 4.4                       | 24.8     | 17.0       |
| P3   | 12.5                      | 29.1     | 17.9       |
| P4   | 11.1                      | 24.1     | 15.2       |
| P5   | 9.7                       | 25.6     | 16.0       |
| P6   | 9.9                       | 23.3     | 17.1       |
| P7   | 7.2                       | 27.7     | 17.3       |
| P8   | 31.9                      | 34.2     | 16.2       |
| P9   | 15.8                      | 27.8     | 19.0       |
| P10  | 10.7                      | 19.6     | 16.5       |
| P11  | 13.6                      | 27.1     | 18.2       |
| P12  | 5.5                       | 21.4     | 14.9       |
| P13  | 11.1                      | 28.6     | 19.8       |
| P14  | 4.6                       | 19.3     | 17.5       |
| P15  | 13.9                      | 23.1     | 20.1       |

Mean ± standard deviation

11.3 ± 6.6
25.3 ± 3.9
17.4 ± 1.5

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*a* Canopy projected area was estimated by measuring from the stem outward to the edge of the canopy at 8 points around the tree: N, NW, W, SW, S, SE, E, and NE.

*b* Diameter breast height measured cross slope.
Fig. 3. Root hierarchy was reconstructed for each quadrant using the AMAPmod software. The taproot appears pink, first-order lateral roots emerging from the taproot are green, second-order roots are dark blue, and third-order roots are light blue. Panels A, C, E, and G have the root system oriented so that the downslope, upslope, windward, and leeward quadrants, respectively, are shown. Panels B, D, F, and H, oriented the same way as the root reconstructions, show the cross sectional areas for each first-order lateral root where it attached to the taproot.
necessary to account for ring eccentricity.

In this study we did not investigate the organization of cell walls and therefore cannot demonstrated that the reaction wood we observed is comparable to compression wood or normal wood. However, we stained the wood with a 1% phloroglucinol ethanol solution with one drop of 35% HCl to highlight the presence of a greater content of lignin in the cell walls with a darker/reddish zone (Kutscha and Gray, 1972; Kallavus et al., 2015). Presently we prefer to adopt these traditional terms to indicate wood presenting a considerable eccentricity of the annual rings. Therefore, in our samples, we normally have opposite wood (defined by having the minimum width between annual rings and typical normal wood characteristics; Pursatama et al., 2018) and occurring opposite was compression wood, a zone with the greatest widths between annual rings.

3. Results

3.1. Root system architecture

We observed that 83% of the first-order lateral root length present in the downslope quadrant occurred in the 0–30 cm layer (Table 3), whereas in the upslope quadrant 95% of the first-order root length occurred at depths exceeding 30 cm. For the windward and leeward quadrants, the greatest values for first-order root length were also at a depth of more than 30 cm. Values for second- or third-order lateral roots followed this same pattern. Summed across all four quadrants, 60% of the second- and third-order lateral root length occurred in the upper 30 cm of soil.

First-order lateral root volume in the downslope and upslope quadrants followed the root length pattern: 93% of the total downslope volume occurred in the upper 30 cm of the soil profile whereas 70% of the upslope volume was found below 30 cm. In the windward quadrant at the lower depth, only 40% of the root volume was present, whereas in the leeward quadrant this rooting depth had 97% of the volume. For the second- and third-order lateral roots, the most root volume was found in the upper 30 cm of soil in the downslope quadrant, whereas for the other quadrants the highest percentage was found below 30 cm.

Our data showed that, overall, values for root length and volume were fairly similar regardless of analysis technique (i.e. AQ or EQ) whereas considerable differences sometimes emerged when comparing the two types of measurements within a quadrant (Table 4). For example, in the upslope quadrant, EQ values for first-order length and volume were about 2X those for AQ. About 90% of the total cross sectional area of the downslope quadrant occurs in the upper 30 cm of the taproot (data not shown). Moreover, 43% of the total cross sectional area for the tree occurs in the downslope quadrant (Table 4) being about 25%, 2.5X, and 8X greater than the upslope, windward, and leeward quadrants, respectively.

Most first-, second- and third-order lateral roots emanate from the taproot in the downslope quadrant (Fig. 3A and B). In addition, the shallow lateral root presenting the largest cross sectional area (Table 4) was in the downslope quadrant; after a few centimeters its growth angle changes to a sinker root and it deviates from its originating quadrant elongating into the windward quadrant (Fig. 3B). Several second- and third-order lateral roots branched from this root to become sinker roots or to invade a different quadrant (blue and light-blue roots in Fig. 3A).

Fig. 3C shows the growth direction of lateral roots in the upslope quadrant. Unlike the downslope quadrant, the cross sectional area formed by the first-order roots is more diffuse, despite the fact that most of the cross sectional areas are located in the upper 30 cm of the taproot (Fig. 3D). Fig. 3E and G shows lateral roots emanating in the windward and leeward quadrants, respectively. A visual comparison clearly shows the number of roots emanating from the taproot is lower than that in the downslope and upslope quadrants. Only a low amount of cross sectional area occurred in the leeward quadrant (Fig. 3H).
preciable taper, eccentricity was absent. We also observed that eccentricity was absent when the root was no longer undergoing a downward (i.e., away from the soil surface) (Fig. 7A). Finally, at a certain depth, the direction of the taper changed. In respect to the entire length of the root axis, we found that outside the zone of the leeward quadrant (Fig. 6). As our tree-ring analysis extended along the root axis, we showed a T-beam shape while the I-beam shape was observed only in the upslope quadrant of the root. Rectangles are for first-order lateral roots for which age coincides exactly with the age of the taproot at three depths (0–30, 30–60, and > 60 cm) for each quadrant (downslope, upslope, windward, and leeward). Rectangles and circles contain the number of growth rings (i.e., age) observed at their junction with the taproot, and are accurate for topology along the taproot axis. Rectangles are for first-order lateral roots for which age coincides exactly with the age of the taproot at their relative junction points, whereas circles represent the ages of first-order lateral roots when ages did not coincide.

Fig. 4. Tree-ring sequencing of first-order lateral roots emanating from the taproot at three depths (0–30, 30–60, and > 60 cm) for each quadrant (downslope, upslope, windward, and leeward). Rectangles and circles contain the number of growth rings (i.e., age) observed at their junction with the taproot, and are accurate for topology along the taproot axis. Rectangles are for first-order lateral roots for which age coincides exactly with the age of the taproot found at their relative junction points, whereas circles represent the ages of first-order lateral roots when ages did not coincide.

Using AMAPmode, our data revealed an uneven distribution of roots in the four quadrants, with the greatest length and volume values in the downslope quadrant, suggesting that, among all the loading forces, the active force downslope requires the strongest mechanical reaction to avoid uprooting. It is reasonable to suggest that the mechanical slope-loading forces could have affected the downslope roots with compressive forces whereas those upslope faced tension forces (Di Iorio et al., 2005). The mechanical role of lateral roots deployed in the downslope quadrant is probably played by their considerable bending stiffness (i.e., product of the elastic modulus of the beam material and the area moment of inertia of the beam cross-section). Indeed, according to Coutts (1983), stiffness of a circular beam is related to the fourth power of its diameter, which means that a root with a large cross-sectional area will be much stiffer than two roots with the same cumulative cross-sectional area.

Volume of lateral roots in the windward quadrant exceeded that of the upslope quadrant, suggesting that wind loading forces are more active than those required to counteract tension forces associated with slope. Moreover, the presence of loading forces due to wind likely explains the higher length and volume values in our windward quadrant compared to the leeward quadrant. These findings, similar to those for Picea stichensis (Nicoll et al., 2006), suggest a root response to dissipate wind-mechanical forces into the soil. Length values in the upslope and windward quadrants were similar, contrasting with Stokes et al. (1995) who reported thinner and more branched roots per unit area of soil on the windward sides of trees. The mechanical efficiency of a root does not, however, depend exclusively on its diameter; Genet et al. (2005) suggest that root tensile strength increases with decreasing diameter.

We observed different values for length and volume depending on the method used to attribute roots to the quadrants. AMAPmode (AQ in Table 2; output based on the physical location of the root segments regardless of its emission point), yielded higher values for first-order lateral roots in all quadrants except upslope, whereas attributing the entire root to the quadrant where the emission is located (EQ in Table 2) yielded the opposite. For volume, upslope values based on AQ are much lower than those determined by EQ. These results highlight that after its emission from the taproot, each first-order lateral root may continue its growth in a different quadrant due to external factors. Our understanding of this phenomenon could be improved if future research work also included a tree-ring-analysis approach to determine if lateral roots found at the adult stage were the same ones present at the seedling stage.

Several authors report the occurrence of discontinuous annual rings indicative of discontinuous wood production (references in Wrońska-Walach et al., 2016). We noted discontinuous rings more frequently in second- and third-order roots than in first-order roots. While the mechanism responsible for discontinuous rings remains unknown, it may be the result of different cell division activity along the vascular cambium circumference caused by mechanical stress, similar to how this...
stress is responsible for asymmetric annual ring distribution observed in large-diameter roots (see below). We observed that the smaller-diameter roots outside the zone of rapid taper sometimes showed several discontinuous annual rings, suggesting they could be subjected to mild mechanical forces.

Asymmetric wood production in our roots reflects the presence of reaction wood (Fischer et al., 2019), analogous with the mechanism responsible for reorienting the stem axis (Sinnott, 1952). Indeed, Groover (2016) suggests that reaction wood is central to concepts of mechanical design and adaptive growth that describe how tree stem and branches respond to environmental stresses. Our data show that despite the likely qualitative and quantitative differences in mechanical forces (compression and tension) active in the various quadrants of our root system, the observed response was always formation of annual ring eccentricity oriented upward (i.e. toward soil surface), at least in the zone of rapid taper. Similarly, Du and Yamamoto (2007) demonstrated that reaction wood in branches always forms on the side where it will serve to reestablish the equilibrium position; in their research, the vascular cambium seems to respond by producing more wood in the direction where tissue perceives the gravity stimulus. Fayle (1968) observed root annual rings with downward eccentricity when soil erosion exposed them to the air, perhaps because exposure to air induces anatomical modifications in wood increments between the upper and lower part of the central root axis. In Larix decidua, Gärtner et al., 2006 reported that roots growing 20 cm below the soil surface lacked differences between and early- and late-wood whereas closer to the surface these differences were more evident. In our roots, the presence of soil might reduce the gravity stimulus whereas tension and compression forces could have the main influence, similar to results for Populus (Stokes and Mattheck, 1996) where increases in compression strength on the underside of lateral roots induced a radial growth reduction as consequence of the weight of the tree pressing the lateral root on to the soil. Given that compression wood in our roots was always formed in the upward direction, we suggest that the mechanical stimulation and/or inhibition of vascular cambium initials cells can take place in the upper and lower side of the root, respectively. This is independent of the type of mechanical force (i.e. compressive or tension).

Distinguishing the effects of different factors (i.e. mechanical forces
or gravity) responsible for inducing wood response in stems, branches, or roots remains a challenging objective (Lopez et al., 2014). Our finding that the compression wood orientation along the axis of first-order lateral roots within the zone of rapid taper changed when the root grew outside this zone may be explained as a root response to different dominant factors along its length.

Indeed, Coutts et al. (1999) suggest that the change in reaction wood direction coinciding with the exit from the root cage could be the response to the diminished need of root stiffness. Our finding also concurs with Nicoll and Dunn (2000) who concluded modifications in response to the diminished need of root stiffness. Our finding also wood direction coining with the exit from the root cage could be the dominant factors along its length.

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