SHORT COMMUNICATION

Pine root exploration of standing dead tree trunks: a short-cut biocycling process

Rangel CONSALTER[1], Antonio C. V. MOTTA[1], Julierme Z. BARBOSA[2], Fabiane M. VEZZANI[1], Rafael A. RUBILAR[3], Stephen A. PRIOR[4] and Marcos V. M. BASSACO[5*]

[1] Federal University of Paraná, Dept. of Soils and Agricultural Engineering. Rua dos Funcionários, Curitiba, PR, Brazil.
[2] Federal Institute of Southeast Minas Gerais. Barbacena, MG 36205-018, Brazil. [3] Universidad de Concepción, Facultad de Ciencias Forestales, Casilla 160-C, Concepción, Chile. [4] USDA-ARS, National Soil Dynamics Laboratory, 411 South Donahue Drive, Auburn, AL, 36832 USA. [5] State University of the Central-West (UNICENTRO), Dept. of Forest Engineering, Rua Professora Maria Roza Zanon de Almeida, Irati, PR, Brazil.

*Correspondence should be addressed to Marcos V. M. Bassaco: marcos.bassaco@hotmail.com

Abstract

Aim of study: To characterize the colonization of *Pinus herrerae* roots in trunks of dead standing trees and to evaluate the composition of roots and decomposing tissues of standing dead trees.

Area of study: Jaguariaíva, Paraná state, Southern Brazil.

Material and methods: This study evaluated root attributes in the soil, litter, and trunks of dead standing trees and the composition of wood and bark of trees. Root traits (length, mass mycorrhizal colonization, and mean nutrient concentrations), soil and organic layers, and mean nutrient concentrations of wood and bark for were analyzed by non-parametric test.

Main results: Approximately 2 to 3.5 years after tree death, roots of adjacent trees in F and H horizon litter migrate into the wood/bark interface. Eight and a half years after tree death, roots of adjacent trees reached up to 3.3 m above the litter surface. At the wood/bark interface, a root mantle formed (length greater than 1 km m^{-2}) with ~5% ectomycorrhizal colonization. Root presence in the wood/bark interface reduced P, K, and Fe concentration of dead wood and Zn concentration in bark.

Research highlights: Our results indicate that roots of *P. herrerae* are capable of colonizing dead tree trunks as a nutrient resource pool. This nutrient acquisition mechanism may function as a shortcut in the biogeochemical cycling of nutrients in forest systems.

Additional key words: gravitropism; nutrient acquisition strategies; root traits; ectomycorrhizal colonization; ecosystem processes; *Pinus herrerae*.

Abbreviations used: AT (alive trees); DT (dead trees); DTCR (dead trees colonized by roots of adjacent living trees)

Introduction

Large quantities of plant debris can accumulate on the soil surface in mature forest ecosystems to form a top organic horizon called litter, which is an important pool in the nutrient biogeochemical cycle. Litter accumulation occurs due to several factors but is primarily influenced by soil, vegetation, and climate types (Berg & McClaugherty, 2020; Harmon, 2021). Regarding soil variation, litter accumulating on low fertility soils is generally low in nutrients due to translocation processes prior to leaf litter fall, which results in low microbial activity and decomposition rates (Viera & Schumacher, 2010; Tangjang et al., 2015; Samuelson et al., 2017). Despite the low level of nutrients in this type of litter, some tree species have abundant root growth in the litter layer. In addition to the ability to explore soil with low levels of nutrients and high acidity, root growth in the litter can contribute to the maintenance of tree growth under these harsh soil conditions (Brunner & Sperisen, 2013; Lopes et al., 2013; Batista et al., 2015; Rodríguez-Robles et al., 2017; Consalter et al., 2021a; Prescott & Vesterdal, 2021).

Trees will often allocate photosynthates to belowground tissues to acquire resources that are limiting growth (Prior et al., 1997). Initially, trees obtain nutrients from the mineral soil, but following a few years of litterfall accumulation and decomposition, nutrient uptake can be increased by root exploration of the litter layer (Achat et al., 2008; Prescott & Vesterdal, 2021). It is also interesting to note that beneficial associations between mycorrhizal fungi and tree roots growing in soil and litter are common. In addition to roots, mycorrhizal fungi affect litter decomposition and consequent nutrient mineralization (Lang et al., 2021; Carteron et al., 2022). The importance of the litter layer as a nutrient source increases as the forest stand ages, and this process becomes key in the biogeochemical cycling of nutrients in forest stands (Krishna & Mohan, 2017; Consalter et al., 2021b).

Root growth in the H horizon (fully decomposed litter) is generally more extensive than in the F horizon (partially decomposed litter); these horizons are primarily composed of leaf debris (Lopes et al., 2013; Batista et al., 2015; Consalter et al., 2021a). Woody debris can also be found in the litter, but is difficult to study these components due to the range in size and temporally erratic input from both natural and human-caused events (Berg & McClaugherty, 2020). However, there are reports that tree roots can grow on woody materials on the litter surface (Motta et al., 2014; Prescott & Vesterdal, 2021). Not only do roots grow on woody debris (e.g., tree stumps), they thrive in it; observations showed that a stump occupying 1.2% of total soil volume contained 19% of total fine-root length in a temperate forest system (Sucre & Fox, 2009). In the literature, *Pinus* species have been commonly reported to have high root growth capacity in different litter layers (Brunner & Sperisen, 2013; Batista et al., 2015; Consalter et al., 2021a), including abundant root growth

between bark and wood in branches on the litter surface in a *Pinus taeda* (loblolly pine) forest stand (Motta et al., 2014). In addition, *Pinus herrerae* (Herrera's pine) root growth on dieback trees has also been observed at our study location in southern Brazil, where root systems of living trees were invading adjacent standing dead trees. Since trunks of dead trees were still standing (i.e., not yet been deposited on the ground), they technically were not part of the litter layer.

Root growth in adjacent standing dead trees can be a means of harnessing resources in nutrient-poor environments. Our hypothesis is that root growth in the trunk of dead trees occurs to attain nutrients from decaying tissues. The aims of this study were to characterize the colonization of *P. herrerae* roots in trunks of dead standing trees and to evaluate the composition of roots and decomposing tissues of standing dead trees.

Material and methods

Study site

The study site was a *P. herrerae* plantation located in Jaguariaíva, Paraná state, Brazil. On average, trees had a 24.5 ± 3 cm ground line diameter, a 20.5 ± 2 cm diameter at breast height, and a total height of 7.55 ± 0.2 m. The regional climate is Cfb (Humid subtropical oceanic climate with a temperate summer and no dry season) with an average annual rainfall of 1412 mm, and mean annual minimum and maximum temperatures of 13.6 and 20.6 ºC, respectively (Alvares et al., 2013). This area contains soils derived from two sandstone parent materials (Furnas and Itararé) (Mineropar, 2010). The soil at the study site was classified as a Typic Hapludox (Soil Survey Staff, 2014). Site soils were low in organic matter and available nutrients, were highly acidic, and had high Al^{3+} saturation (Table S1 [suppl]). Particle size analysis (densimeter method) classified the topsoil as a sandy clay loam texture with 75% sand, 2.5% silt, and 22.5% clay.

The *P. herrerae* plantation was established in 1994 using a 3 × 3 m seedling spacing. Prior to establishment of this plantation, aboveground residues from a previous *P. taeda* stand and any native vegetation was removed by burning. Neither the *P. herrerae* nor the previous *P. taeda* plantations received any fertilization.

Soil, plant, and litter sampling

In August 2014, four trees within each of the following three categories were sampled: 1) alive trees (AT), 2) dead trees (DT), and 3) dead trees colonized by roots of adjacent living trees (DTCR). DTCR trees were found after examining the plantation, while AT and DT trees were randomly

sampled. The maximum height that roots of a neighboring live tree attained in the DTCR wood/bark interface was measured and all roots in the wood/bark interface were extracted by hand. For each tree, a 5 g sub-sample of roots was collected from the lower, middle, and upper thirds of the maximum height of roots in the wood/bark interface. These sub-samples were then mixed to form a composite sample.

Litter sampling methodology followed that of Consalter et al. (2021a). For each DTCR, four litter samples were collected at the four cardinal points using a 0.1 × 0.1 m frame; these samples were taken one meter from the trunk. Two samples were collected along the planting line, and two were collected perpendicular to the planting line. After litter removal, samples from the four points for each tree were separated into several components, which were then composited. The components were: (1) recently deposited needles that did not break when formed into a loop, called new litter; (2) brittle needles, called old litter; (3) organic horizon where organic residues are fragmented, partially decomposed (F horizon); and (4) organic horizon where tissue origin was not recognizable (H horizon). However, roots were only found in the F and H horizons, therefore, only these two horizons were used. Individual litter layer samples were homogeneously mixed and a sub-sample (10% of total volume) was collected after manually removing roots using tweezers. To fully characterize the elemental composition of plantation litter, additional litter samples were collected near living trees following the same procedures described above (Table S2 [suppl]).

Surface soil was also collected for root samples from each of the four litter sampling points. A knife and straight shovel were used to collect soil monoliths (10 cm × 10 cm × 10 cm) containing roots, which were composited for each evaluated DTCR. Roots were separated from each composite sample using a 2 mm mesh sieve.

A trunk disc was cut from the base of each study tree (i.e., AT, DT, and DTCR) at the top height of the litter layer. Bark was removed manually, and wood sample plugs (0–5 mm depth) were collected using a hollow metal cylinder (2 cm internal diameter). A total of 10 wood and bark subsamples were collected from each trunk disc for all evaluated tree condition (AT, DT, and DTCR).

Identification of roots that colonized dead trees was performed. Bark and litter near the ground line of dead trees colonized by roots were manually removed. Litter and top surface mineral soil were excavated to visually trace these roots for several meters (~6 m) until they reached a neighboring living tree. The roots were classified into branch orders following the protocols described by Fitter (1987).

Plant tissue and litter analysis

The percentage of ectomycorrhizal roots colonizing all compartments (i.e., mineral soil, F horizon, H horizon, and wood/bark interface) was also determined. From each root sample, 100 segments (~2 cm) were acquired randomly, and a magnifying glass (30x magnification) was used to determine the presence of ectomycorrhizal fungi in the root segments. From the number of root segments in which the presence of mycorrhizae was observed, the average percentage of mycorrhizal colonization was determined (Danielsen et al., 2013).

Thinner roots (< 0.4 mm) from each compartment were analyzed by Safira software (Jorge & Silva, 2010) to determine total root length. Root traits were expressed per unit of area based on the surface area of each sample collected in the different environments (soil, litter, or wood/bark interface). For dead trees, only the surface area of wood with root presence was considered.

Samples from trunk discs, bark, roots, litter, and needles were dried in an air circulating oven at 65 ºC. After drying, samples were ground in a Wiley mill to pass a 1 mm mesh sieve. Duplicate samples of each dried tissue (1 g) were incinerated in a muffle furnace at 500 ºC for 4 hours, and the ash was digested to determine K, Ca, Mg, P, Mn, Fe, Zn, and Cu using an inductively coupled plasma optical emission spectrometer (ICP-OES) (Varian, 720-ES). This analysis was performed following the protocols described by Martins & Reissmann (2007).

Growth ring analysis

To determine time after death of DT and DTCR trees, tree age analysis was conducted by counting rings in the trunk discs. The counting of growth rings was performed manually using a magnifying glass (Stokes, 1996). Time after death of each tree was calculated as the difference in age between dead trees (DT and DTCR conditions) and the average age of living trees (AT treatment).

Data analysis

Root traits (length, mass mycorrhizal colonization, and mean nutrient concentrations) in DTCR, soil and organic layers, and mean nutrient concentrations of wood and bark for AT, DT, and DTCR were analyzed by Kruskal-Wallis test, and different means were compared by the Dunn test. Statistical analyses were performed using Statistica® software (StatSoft, Tulsa, OK, USA).

Results and discussion

Death of *P. herrerae* trees began with leaf-fall and needle chlorosis, followed by mortality in lower branches that progressed upward until the whole crown was lost. Dead trees remained standing for several years after death due to protection of neighboring tree from local winds. Based on estimated time after death of trees, the period between tree death and root colonization (Fig. 1) of tissue was 2 to 3.5 years.

Table 1. Root mass, total root length, contribution of fine roots (diameter<0.4 mm) to total root length, root mycorrhizal colonization, specific root length and nutrient concentrations (g or mg per kilogram of dry matter – DM) of colonizing roots of *Pinus herrerae* located in the mineral soil (n = 4), H (n = 4) and F organic (n = 4) soil horizons, and at the wood/bark (W/B) interface (n = 4) associated with dead trees colonized by roots of adjacent living trees

	W/B interface	F horizon	H horizon	Soil
Root mass, g m^{-2}	100 b	162 b	370 a	310 a
Total root length, km m^{-2}	0.9 c	2.2 b	4.3 a	0.4 c
Fine roots in total root length, %	50 a	62 a	39 b	11 c
Mycorrhizal colonization, %	5 c	55 b	73 a	42 b
Ca, g kg^{-1}	0.80 a	0.47 a	0.58 a	0.72 a
Mg, g kg^{-1}	0.29 b	0.22 b	0.21 b	0.70 a
K, g kg^{-1}	0.80 b	0.82 b	0.77 b	1.30 a
P, g kg^{-1}	0.30 b	0.55 a	0.52 a	0.55 a
Fe, g kg^{-1}	1.12 a	0.81 b	0.60 b	0.11 c
Mn, mg kg^{-1}	82 a	30 b	33 b	110 a
Zn, mg kg^{-1}	19 a	20 a	14 b	16 ab
Cu, mg kg^{-1}	6.5 a	8.0 a	7.5 a	5.5 a

Different lowercase letters within a row represent difference by the Dunn test (p<0.05).

An initial colonization stage was observed in only one tree where roots were present up to 0.7 m above the ground. Other trees were found in a more advanced stage of colonization where roots in the wood/bark interface reached heights of 2.0 to 3.3 meters. Trees in this advanced stage remained standing for at least 8.5 years after death. Roots that colonized dead trees originated from living trees within 3 to 6 m away and mainly consisted of first order roots originating from surface soil roots.

Roots growing at the wood/bark interface in DTCR had lower values of total length, mass, and mycorrhizal colonization compared to the other growth substrates (soil, horizon H, horizon F). On the other hand, at both the wood/bark interface and F horizon, there was a greater contribution of thin roots (<0.4 mm) to total root length (Table 1). Regarding root composition, the nutrients that mainly differentiated roots of the wood/bark interface of dead trees were P and Fe, which were respectively lower and higher compared to other evaluated environments (Table 1).

Phosphorous, Fe, and K concentrations in DTCR wood were lower than concentrations recorded for AT or DT (Fig. 2). On the other hand, Zn was the only element that had a lower concentration in DTCR bark compared to DT.

Root properties and colonization in dead trees

The results of our study demonstrate that *P. herrerae* roots showed great growth capacity in diverse environments and against gravity. Root growth of *Pinus* species in diverse environments has been previously documented (Batista et al., 2015; Rodríguez-Robles et al., 2017). How-ever, our study considerably expands knowledge regarding this ability of *P. herrerae*. Root growth is known to be influenced by gravity, water, oxygen, and other environmental factors (Singh et al., 2017). Gravity-oriented growth studies indicate that first and second order surface roots may grow in favor or against gravity (Coutts & Nicoll, 1991; Jourdan, 2000; Achat et al., 2008). This is considered an adaptive advantage since the surface layer often contains the greatest nutrient quantities due to deposition, decomposition, and mineralization of organic residues (Motta et al., 2014; Consalter et al., 2021a).

High ectomycorrhizal levels of root colonization have been associated with poor P availability (Smith & Read, 2008; Costa et al., 2022) as was seen in our nutrient analysis of soil and litter. This may explain the high mycorrhizal colonization of roots found in soil and litter. On the other hand, since DTCR did not have a canopy, they were exposed to higher incidence of solar radiation. In this regard, the amount of fungi inoculum in the wood/bark interface may have limited ectomycorrhizal colonization, and fungus longevity may have been lower due to abiotic factors (Fernandez et al., 2016), which had less impact on root growth. Additional factors that may have influenced results should be investigated in future studies.

Given that P concentrations in organic horizons (horizons F and H) were somewhat similar to concentrations in wood of dead trees, one reason for the low P concentration in colonizing roots could be low P accumulation in bark. Additionally, the nutrient biochemical forms in these organic structures may be different, which could affect root absorption capacity. Nevertheless, there was significant root growth at the wood/bark interface, especially for roots with a diameter <0.4 mm. This was likely related
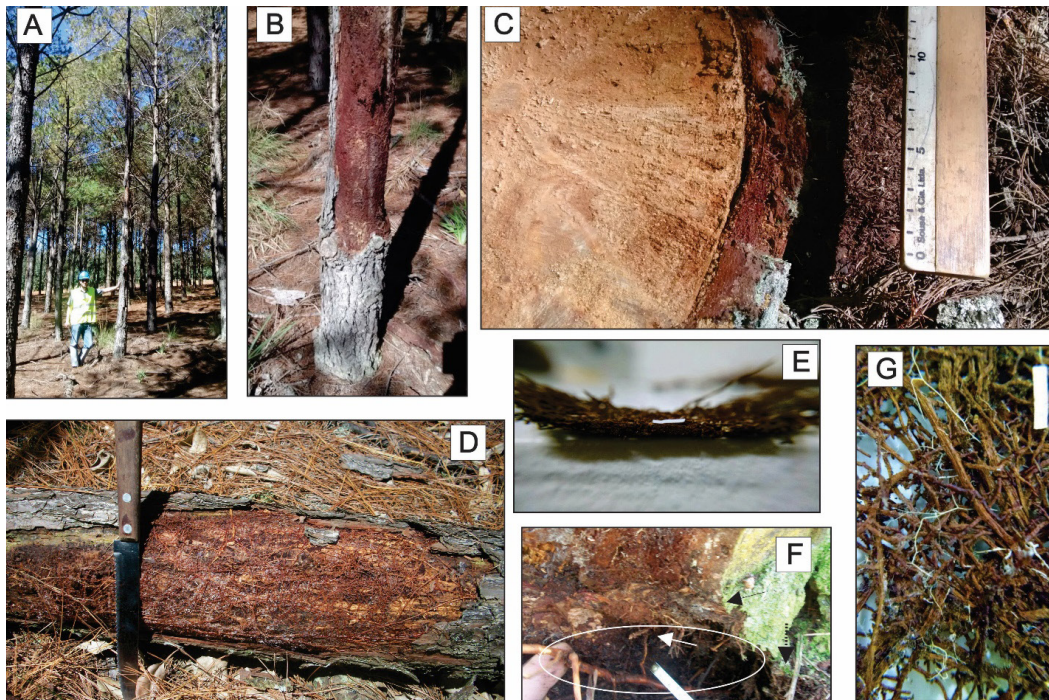
Figure 1. Dead standing *Pinus herrerae* tree (21 years old) at Jaguariaíva, Paraná state, Brazil (A); roots of adjacent living trees colonizing the interface region between wood and bark reaching up to 3.3 m above the litter layer (B); mantle of intermeshed roots under bark of a dead tree (C); close-up image of a dead tree trunk base colonized by living roots of an adjacent neighbor (D); close-up image of the mantle of roots collected from the dead tree trunk base (E); close-up image of secondary roots (white arrow) penetrating bark (black arrow) of a dead tree, and level of litter layer F (fragmented) and H (humified) organic soil horizons (dotted black arrow) after removal for observation of the root colonization process (F); close-up image of the root mantle and ectomycorrhizal fungi structures formed at the wood/bark interface of a dead tree (G). Figures (E, F, and G) were obtained at a scale of 5 x 1 mm

to the ability of *Pinus* root systems to grow in environments with low nutrient availability (Batista et al.*,* 2015; Rodríguez-Robles et al.*,* 2017).

Root colonization effects on nutrients in wood and bark of dead trees

Decreased P and K in the wood region of DTCR was possibly due to the absorption of these macronutrients. Growth of thin roots of *Pinus* species are favored by increased P and K availability (Sardans et al.*,* 2004; Lopes et al.*,* 2013; Zhang et al.*,* 2013; Pacé et al.*,* 2016; Sass et al.*,* 2020). Although requirements for Fe and Zn are relatively low since they are micronutrients, decreased concentrations in the wood and bark of DTCR suggest acquisition by root absorption. Other nutrients (Ca, Mg, Mn, and Cu) showed no significant decrease in DTCR wood and bark, probably due to contrasting root absorption capacity or plant requirements. However, the large differences in nutrient decrease (K, P, and Fe) found for DTCR wood indicate that, in addition to variation among nutrients, tree tissue type affects nutrient acquisition. Microbiological aspects related to

the presence and action of saprophytic fungi at the DTCR wood and bark interface were not considered, but these fungi have been shown to accelerate the decomposition of woody litter (Berg & McClaugherty, 2020). Corroborating results of our study, Sucre & Fox (2009) found decreased inorganic N in stumps as result of degree of decay due to absorption by roots.

Root growth in litter of forest ecosystems is recognized as having direct implications for plant nutrition and biogeochemical cycling of nutrients (Achat et al.*,* 2008; Krishna & Mohan, 2017). In this regard, compositional changes in DTCR wood and bark suggest that *P. herrerae* root growth at the wood/bark interface of dead trees can also have major effects on nutrient cycling. Additionally, the release of organic and inorganic substances by roots possibly contributed to the decomposition of DTCR dead tissue. This effect is probably not limited to *P. herrerae*, considering that species of the *Pinus* genus generally have a strong root growth capacity in diverse and harsh environments (Motta et al.*,* 2014; Batista et al.*,* 2015; Rodríguez-Robles et al.*,* 2017; Sass et al.*,* 2020). Thus, considering the novelty of this study, future multidisciplinary research is required to broaden knowledge of root growth in such unique aerial
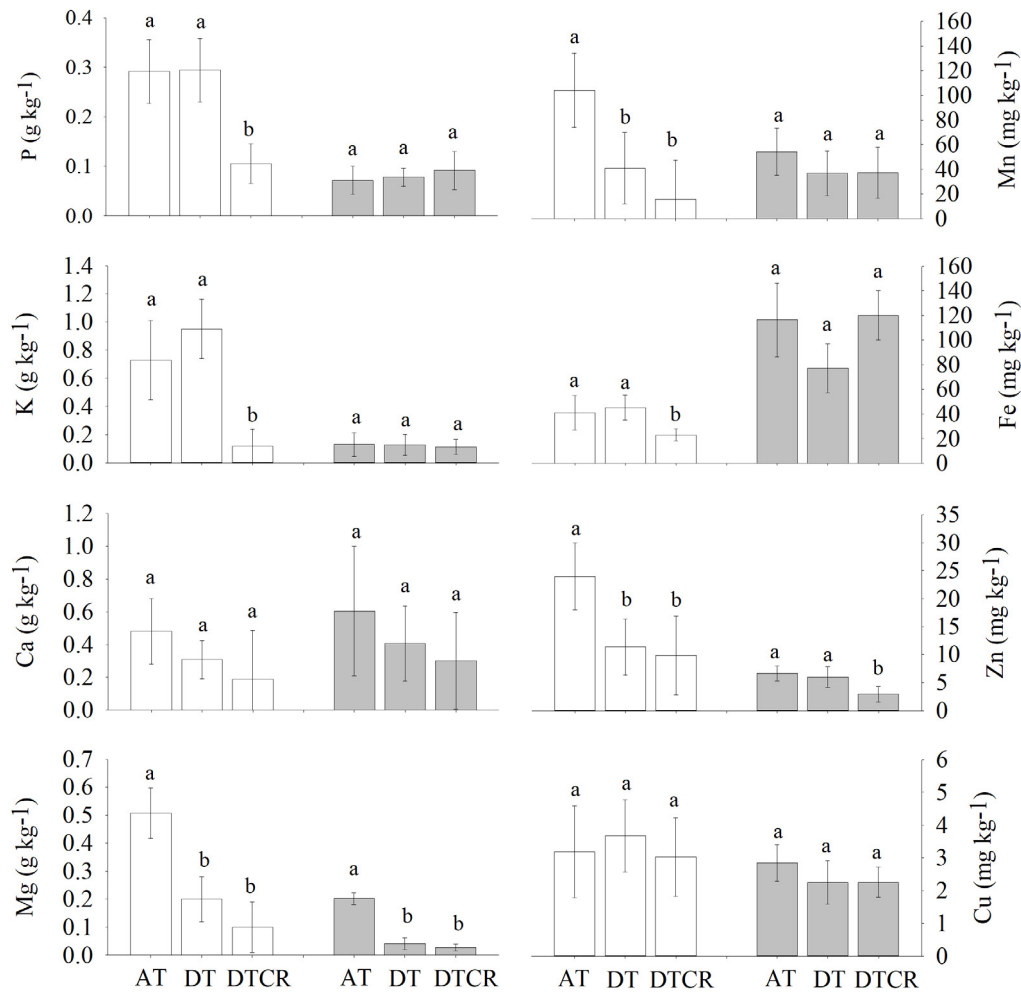
Figure 2. Comparative nutrient concentrations (g or mg kg⁻¹ of dry matter – DM) in the surface wood (white bars) and bark (grey bars) of *Pinus herrerae* trees. AT – alive trees; DT – dead trees and DTCR – dead tree wood/bark interface colonized by roots of adjacent living trees. Different lowercase letters above of bars represent difference by the Dunn test (p<0.05). Bars represent the standard errors.

environments and their impact on nutrient cycling in forest ecosystems.

Conclusion

This study demonstrated that *P. herrerae* roots of live trees can exit the forest litter layer to colonize the wood/bark interface of dead trees. Roots at the wood/bark interface of dead trees reached up to 3.3 m above the forest floor and displayed contrasting morphological characteristics, ectomycorrhizal colonization levels, and P concentration in comparison to roots found in the litter and mineral soil layers. This phenomenon could be considered a shortcut in biogeochemical cycling where colonizing roots decreased concentrations of P, K, and Fe in wood and Zn in bark of dead trees. Although preliminary, our study contributes to increasing the knowledge base on unique mechanisms affecting nutrient cycling in forest ecosystems. Due to the small sample size of this study, more in-depth investigations are required to further our understanding of this phenomenon and its extent in *Pinus* systems. Artificial termination of trees (dead trees) could possibly be utilized in an experimental set-up to evaluate this phenomenon under more controlled conditions.

Authors' contributions

Conceptualization: R. Consalter; J. Z. Barbosa
Data curation: Not applicable.
Formal analysis: A. C. V. Motta; F. M. Vezzani; R. A. Rubilar; S. A. Prior; M. V. M. Bassaco
Funding acquisition: A. C. V. Motta;
Investigation: R. Consalter; J. Z. Barbosa; C. V. Motta; F. M. Vezzani
Methodology: R. Consalter; J. Z. Barbosa
Project administration: R. Consalter; J. Z. Barbosa

Resources: R. Consalter; J. Z. Barbosa; A. C. V. Motta
Software: R. Consalter; J. Z. Barbosa
Supervision: Not applicable.
Validation: Not applicable.
Visualization: Not applicable.
Writing – original draft: R. Consalter; J. Z. Barbosa; A. C. V. Motta
Writing – review & editing: A. C. V. Motta; S. A. Prior; M. V. M. Bassaco

References

Achat DL, Bakker MR, Trichet P, 2008. Rooting patterns and fine root biomass of *Pinus pinaster* assessed by trench wall and core methods. J For Res 13: 165-175. https://doi.org/10.1007/s10310-008-0071-y

Alvares CA, Stape JL, Sentelhas PC, et al., 2013. Köppen's climate classification map for Brazil. Meteorol Zeitschrift 22: 711-728. https://doi.org/10.1127/0941-2948/2013/0507

Batista AH, Motta ACV, Reissmann CB, et al., 2015. Liming and fertilisation in *Pinus taeda* plantations with severe nutrient deficiency in savanna soils. Acta Sci Agron 37: 117-125. https://doi.org/10.4025/actasciagron.v37i1.18061

Berg B, McClaugherty C, 2020. Decomposition of cones and woody litter. In: Plant litter; Berg B, McClaugherty C (eds). Springer, Cham. pp. 209-226. https://doi.org/10.1007/978-3-030-59631-6_9

Brunner I, Sperisen C, 2013. Aluminum exclusion and aluminum tolerance in woody plants. Front Plant Sci 4: 1-12. https://doi.org/10.3389/fpls.2013.00172

Carteron A, Cichonski F, Laliberté E, 2022. Ectomycorrhizal stands accelerate decomposition to a greater extent than arbuscular mycorrhizal stands in a northern deciduous forest. Ecosystems 25: 1234-1248. https://doi.org/10.1007/s10021-021-00712-x

Consalter R, Motta ACV, Barbosa JZ, Vezzani FM, Rubilar RA, Prior SA, et al., 2021a. Fertilization of *Pinus taeda* L. on an acidic oxisol in southern Brazil: growth, litter accumulation, and root exploration. Eur J For Res 140: 1095-1112. https://doi.org/10.1007/s10342-021-01390-z

Consalter R, Barbosa JZ, Prior SA, Vezzani FM, Bassaco MVM, Pedreira GQ, et al., 2021b. Mid-rotation fertilization and liming effects on nutrient dynamics of *Pinus taeda* L. in subtropical Brazil. Eur J For Res 140: 19-35. https://doi.org/10.1007/s10342-020-01305-4

Costa LS, Grazziotti PH, Fonseca AJ, dos Santos Avelar DC, Rossi MJ, de Barros Silva E, et al., 2022. Eucalyptus field growth and colonization of clones pre-inoculated with ectomycorrhizal fungi. Agronomy 12: 1204. https://doi.org/10.3390/agronomy12051204

Coutts MP, Nicoll BC, 1991. Orientation of the lateral roots of trees: I. Upward growth of surface roots and deflection near the soil surface. New Phytol 119: 227-234. https://doi.org/10.1111/j.1469-8137.1991.tb01025.x

Danielsen L, Lohaus G, Sirrenberg A, Karlovsky P, Bastien C, Pilate G, et al., 2013. Ectomycorrhizal colonization and diversity in relation to tree biomass and nutrition in a plantation of transgenic poplars with modified lignin biosynthesis. Plos One 8(3): e59207. https://doi.org/10.1371/journal.pone.0059207

Fernandez CW, Langley JA, Chapman S, et al., 2016. The decomposition of ectomycorrhizal fungal necromass. Soil Biol Biochem 93: 38-49. https://doi.org/10.1016/j.soilbio.2015.10.017

Fitter AH, 1987. An architectural approach to the comparative ecology of plant root systems. New Phytol 106: 61-77. https://doi.org/10.1111/j.1469-8137.1987.tb04683.x

Gordon WS, Jackson RB, 2000. Nutrient concentrations in fine roots. Ecology 81: 275-280. https://doi.org/10.1890/0012-9658(2000)081[0275:NCIFR]2.0.CO;2

Harmon ME, 2021. The role of woody detritus in biogeochemical cycles: past, present, and future. Biogeochemistry 154: 349-369. https://doi.org/10.1007/s10533-020-00751-x

Jorge LAC, Silva DJCB, 2010. Safira: Manual de utilização. Embrapa Instrumentação Agropecuária, São Carlos.

Jourdan C, 2000. Root system architecture and gravitropism in the oil palm. Ann Bot 85: 861-868. https://doi.org/10.1006/anbo.2000.1148

Krishna MP, Mohan M, 2017. Litter decomposition in forest ecosystems: a review. Energ Ecol Environ 2: 236-249. https://doi.org/10.1007/s40974-017-0064-9

Lang AK, Jevon FV, Vietorisz CR, Ayres MP, Hatala Matthes J, 2021. Fine roots and mycorrhizal fungi accelerate leaf litter decomposition in a northern hardwood forest regardless of dominant tree mycorrhizal associations. New Phytol 230: 316-326. https://doi.org/10.1111/nph.17155

Lopes VG, Schumacher MV, Müller I, et al., 2013. Physical and chemical soil variables affecting *Pinus taeda* L. fine roots distribution in northeast of Rio Grande do Sul, Brazil. Ecol Nutr Florest 1: 14-23. http://dx.doi.org/10.13086/2316-980x.v01n01a02

Martins APL, Reissmann CB, 2007. Material vegetal e as rotinas laboratoriais nos procedimentos químico-analíticos. Sci Agr 8: 1-17. https://doi.org/10.5380/rsa.v8i1.8336

Mineropar, 2010. Mapa geológico do estado do Paraná: Unidades estratigráficas. https://www.iat.pr.gov.br/Pagina/Mapeamento-Geologico [26 Nov 2022].

Motta ACV, Barbosa JZ, Consalter R, Reissmann CB, 2014. Nutrição e adubação da cultura de pínus. In: Nutrição e adubação de espécies florestais e palmeiras, 1st ed; Prado R de M & Wadt PGS (eds) FUNEP, Jaboticabal, pp: 383-426.

Pacé M, Fenton NJ, Paré D, Bergeron Y, 2016. Ground-layer composition affects tree fine root biomass and soil nutrient availability in jack pine and black spruce forests under extreme drainage conditions. Can J For Res 47: 433-444. https://doi.org/10.1139/cjfr-2016-0352

Prescott CE, Vesterdal L, 2021. Decomposition and transformations along the continuum from litter to soil organic matter in forest soils. For Ecol Manag 498: 119522. https://doi.org/10.1016/j.foreco.2021.119522

Prior SA, Runion GB, Mitchell RJ, Rogers HH, Amthor JS, 1997. Effects of atmospheric CO_2 on longleaf pine: Productivity and allocation as influenced by nitrogen and water. Tree Physiol 17: 397-405. https://doi.org/10.1093/treephys/17.6.397

Rodríguez-Robles U, Arredondo T, Huber-Sannwald E, et al., 2017. Application of geophysical tools for tree root studies in forest ecosystems in complex soils. Biogeosci Discuss 1-22. https://doi.org/10.5194/bg-2017-91

Samuelson LJ, Stokes TA, Butnor JR, Johnsen KH, Gonzalez-Benecke CA, Martin TA, et al., 2017. Ecosystem carbon density and allocation across a chronosequence of longleaf pine forests. Ecol Appl 27(1): 244-259. https://doi.org/10.1002/eap.1439

Sardans J, Rodà F, Penuelas J, 2004. Phosphorus limitation and competitive capacities of *Pinus halepensis* and *Quercus ilex* subsp. *rotundifolia* on different soils. Plant Ecol 174: 305-317. https://doi.org/10.1023/B:VEGE.0000049110.88127.a0

Sass AL, Bassaco MVM, Motta ACV, Maeda S, Barbosa JZ, Bognola IA, et al., 2020. Cellulosic industrial waste to enhance *Pinus taeda* nutrition and growth: a study in subtropical Brazil. Sci Forest 48: e3165. https://doi.org/10.18671/scifor.v48n126.13

Singh M, Gupta A, Laxmi A, 2017. Striking the right chord: Signaling enigma during root gravitropism. Front Plant Sci 8: 1-17. https://doi.org/10.3389/fpls.2017.01304

Smith SE, Read D, 2008. Mycorrhizal symbiosis, 3rd edn. Academic Press and Elsevier, London.

Soil Survey Staff, 2014. Keys to soil taxonomy, 12th edn. USDA and NRCS, New York.

Stokes MA, 1996. An introduction to tree-ring dating. University of Arizona Press, Tucson.

Sucre EB, Fox TR, 2009. Decomposing stumps influence carbon and nitrogen pools and fine-root distribution in soils. For Ecol Manag 258(10): 2242-2248. https://doi.org/10.1016/j.foreco.2009.05.012

Tangjang S, Arunachalam A, Arunachalam K, Deb S, 2015. Litterfall , decomposition and nutrient dynamics in traditional agro-forestry systems of northeast India. Int J Ecol Environ Sci 41: 43-53.

Viera M, Schumacher MV, 2010. Teores e aporte de nutrientes na serapilheira de *Pinus* taeda L., e sua relação com a temperatura do ar e pluviosidade. Rev Árvore 34: 85-94. https://doi.org/10.1590/S0100-67622010000100010

Zhang Y, Zhou Z, Yang Q, 2013. Genetic variations in root morphology and phosphorus efficiency of *Pinus massoniana* under heterogeneous and homogeneous low phosphorus conditions. Plant Soil 364: 93-104. https://doi.org/10.1007/s11104-012-1352-y