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A META-ANALYSIS OF PHYSICOCHEMICAL CHANGES IN THE RHIZOSPHERE AND BULK SOIL UNDER WOODLANDS



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Abstract

Monoculture for timber production has been replacing natural environments as the demand for renewable energy sources increases. The lack of nutrient compensation may increase the risk of soil depletion, thus changing soil properties. To summarize the impact of forestry activities in edaphic environments, we present a meta-analysis on the rhizosphere effects of coniferous and broadleaved trees established as monoculture and natural regeneration on soil physicochemical properties. Records of soil attributes published in peer-reviewed journals from eight countries were collected. Clay content changed only in monoculture sites, decreasing 55.51% in the rhizosphere, while silt and sand presented significant variations in both monoculture and naturally regenerated areas. Conifers affected the soil more than broadleaved trees, evidenced by higher pH reduction (-2.96% vs. -1.98%) and higher increase of Al³⁺ (197.43% vs. 50.68%), K⁺ (80.40% vs. 69.90%), CEC (24.61% vs. 17.35%), and total organic carbon (82.21%) vs. 69.89%). Also, the rhizosphere affected regeneration soils more than monoculture, indicated by higher Al³⁺ (50.68% vs. *ns*) and available P (32.31% vs. *ns*), K⁺ (203.44% vs. *ns*), CEC (34.90% vs. 20.93), and total organic carbon (91.55% vs. 63.23%). These results indicate higher nutrient availability in naturally regenerated than monoculture sites, as higher species diversity and better plant litter quality are expected. This meta-analysis shows that coniferous and naturally regenerated trees had a higher influence on the rhizosphere and soil properties than broadleaved and monocultures. Management practices must be revisited to ensure the long-term sustainability of forestry activity, and studies in tropical zones must be intensified.

Keywords: Broadleaf. Coniferous. Monoculture. Regeneration. Rhizosphere.

1. Introduction

Sustainable forest policies require increased renewable energy production, implying more intensive land use worldwide (Lauri et al. 2014) and raising the risk of depleting the soil base cations that support forest growth (Akselsson et al. 2019; Rosenstock et al. 2019). Thus, the demand for planted forest expansion is evident, highlighting the need to assess the impacts on soil quality (Doran and Parkin 1994; Islam and Weil 2000; Usharani et al. 2019).

Soil characteristics may vary due to plant species, establishment forms, and management (Malysz and Overbeck 2018), even in species grown in equivalent locations and conditions (Wang et al. 2001). Temporal and spatial scales are relevant for soil processes, and studies on tree rhizospheres are promising to predict the long-term nutrient supply for sustainable forest growth, considering that forestry activity requires longer timescales. The number of studies on the rhizosphere's physical, chemical, and biological properties is appreciable. At the same time, these properties significantly differ from those of the surrounding bulk soil (Hinsinger 1998; Calvaruso et al. 2011; Collignon et al. 2011; Bortoluzzi et al. 2019; Hummes et al. 2019; Liu et al. 2019). Although the rhizosphere usually occupies between 1% and 5% of the soil, changes occur up to twice as fast as in the bulk portion (Kuzyakov and Blagodatskaya 2015).

Coniferous and broadleaved trees modify the soil differently, comparing mixed forests to monoculture stands, and these changes are evident in the rhizosphere compared to bulk soil (Calvaruso et al. 2011; Guan et al. 2016; Bu et al. 2020). Peng et al. (2020) found higher forest floor carbon stock in coniferous than in broadleaved forests, but Hou et al. (2020) verified a higher soil organic carbon rate in broadleaved than in coniferous trees. The nutrient availability in the rhizosphere and bulk soil of mixed coniferous (*Cunninghamia lanceolata*) and broadleaved (*Michelia macclurei* or *Schima superba*) species is higher than in pure coniferous trees (Bu et al. 2020). Malysz and Overbeck (2018) found differences in soil conditions caused by monocultures and regenerated tree patterns. However, a systematic review has never synthesized the potential of trees from the two high plant botanical groups and their establishment forms to influence physicochemical properties in the rhizosphere.

A meta-analysis is an efficient statistical approach for conducting systematic literature reviews. It combines results from two or more individual quantitative studies (Koutsos et al. 2019), estimates treatment effects more precisely, adjusting for experimental homogeneity (Lovatto et al. 2007), and provides objective, transparent, and replicable summaries of topics addressed in scientific research (Del Re 2015). General rhizosphere reviews have been recently published (Dotaniya and Meena 2014; Sokolova 2015; Dessaux et al. 2016; Broeckling et al. 2018), as well as systematic reviews considering carbon dynamics in forests (Hou et al. 2020; Peng et al. 2020). However, the literature lacks syntheses of individual studies across various conditions and sites statistically testing the rhizosphere effect from tree botanical groups and stand establishment forms on soil physicochemical properties.

This meta-analysis examined soil attributes under different tree botanical groups and establishment forms reported in published peer-reviewed studies over the last 20 years to address the rhizosphere effect of trees. Two research questions have guided the present study: (*i*) Do different botanical groups (coniferous and broadleaved trees) tend to influence the rhizosphere effect? (*ii*) Do rhizosphere effects change due to stand establishment forms (monoculture and regeneration sites)?

2. Material and Methods

Literature review

Published peer-reviewed journals were searched from July 11 to 12, 2020, in the *Web of Science Core Collection*. We considered soil attributes of the rhizosphere and bulk soil of trees grown in field conditions reported in studies published after 2000. The keywords were "rhizosphere AND bulk AND forest." The selection criteria were (*i*) rhizosphere *vs*. bulk soil, (*ii*) botanical group (coniferous and broadleaved), (*iii*) studies in field conditions, (*iv*) trees grown spontaneously from self-seedling (regeneration) or planted seedlings raised in forest nurseries (monoculture), (*v*) soils without chemical contamination and that did not receive chemical fertilizers, and (*vi*) observations that presented dispersion measures or, if absent, imputable to Furukawa et al. (2006).

Our search retrieved 240 publications, of which 90 were downloaded for detailed examination, and only 32 fulfilled all established criteria (Table 1). A total of 170 studies from eight countries were considered, including 66 on coniferous trees, 104 on broadleaved species, 95 on planted trees (monoculture), and 75 on naturally regenerated species (regeneration) (Table 2). We gathered sample size, mean, and standard deviation/standard error from ten soil attributes for the control (bulk soil) and the treatment (rhizosphere): (*i*) pH, (*ii*) available phosphorus (P_{av}), (*iii*) potassium (K^+), (*iv*) calcium (Ca^{2+}), (*v*)

aluminum (AI^{3^+}), (*vi*) total organic carbon (TOC), (*vii*) effective cation exchange capacity (*e*CEC), and particle-size distribution – (*viii*) sand, (*ix*) silt, and (*x*) clay. These data were extracted from tables or digitized from figures using Web Plot Digitizer software (Rohatgi 2019). When dispersion measures were not reported, as in Calvaruso et al. (2011) for pH and *e*CEC and Cloutier-Hurteau et al. (2010) for AI^{3^+} , the standard deviation (SD) was imputed to Furukawa et al. (2006). If the dataset presented dispersion measures equal to zero, we changed them to 0.0001 to prevent statistical errors. The units were standardized before the statistical analysis. Furthermore, we considered two moderator variables: (*i*) botanical group – coniferous or broadleaved trees, and (*ii*) establishment form – monoculture or regeneration sites.

Table 1. Origina	publications used in the meta-analy	/sis.
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Reference	Journal	Number of studies
(Agnelli et al. 2016)	Plant and Soil. 2016, 400, 297–314	7
(Álvarez et al. 2010)	Journal of Soils and Sediments. 2010, 10, 1236–1245	1
(Álvarez et al. 2011)	Journal of Soils and Sediments. 2011, 11, 221–230	1
(Angst et al. 2016)	Geoderma. 2016, 264, 179–187	1
(Bu et al. 2020)	Forests. 2020, 11, 461-477	4
(Calvaruso et al. 2011)	Plant and Soil. 2011, 342, 469–480	9
(Chen 2003)	Forest Ecology and Management. 2003, 178, 301–310	1
(Chen et al. 2016)	J. Plant Nutr. Soil Sci. 2016, 179, 67–77	4
(Chen et al. 2018)	Soil Biology and Biochemistry. 2018, 126, 237–246	12
(Chiellini et al. 2019)	Applied Soil Ecology. 2019, 138, 69–79	8
(Cloutier-Hurteau et al. 2007)	Environ. Sci. Technol. 2007, 41, 8104–8110	6
(Cloutier-Hurteau et al. 2010)	J. Environ. Monit. 2010, 12, 1274–1286	2
(Collignon et al. 2012)	Plant and Soil. 2012, 357, 259–274	12
(Collignon et al. 2011)	Plant and Soil. 2011, 349, 355–366	24
(Courchesne et al. 2006)	Environmental Toxicology and Chemistry. 2006, 25, 635–642	9
(Dai et al. 2018)	Canadian Journal of Forest Research. 2018, 48, 1398–1405	3
(De Feudis et al. 2017)	Geoderma. 2017, 302, 6–13	2
(Fang et al. 2017)	PLoS ONE. 2017, 12, e0186905	4
(Guan et al. 2016)	Journal of Tropical Forest Science. 2016, 28, 159–166	3
(He et al. 2020)	Geoderma. 2020, 374, 114424	20
(Hu et al. 2019)	Environ Monit Assess. 2019, 191, 99-114	1
(Korchagin et al. 2019)	Catena. 2019, 175, 132–143	1
(Liu et al. 2018)	Applied Soil Ecology. 2018, 132, 91–98	2
(Liu et al. 2019)	Plant and Soil. 2019, 436, 365–380	2
(Phillips and Yanai 2004)	Water, Air, & Soil Pollution. 2004, 159, 339–356	2
(Séguin et al. 2004)	Plant and Soil. 2004, 260, 1–17	9
(Turpault et al. 2007)	Geoderma. 2007, 137, 490–496	6
(Wang et al. 2016)	Journal of Soils and Sediments. 2016, 16, 1858–1870	2
(Yin et al. 2014)	Soil Biology & Biochemistry. 2014, 78, 213-221	4
(Zhang et al. 2019)	Journal of Soils and Sediments. 2019, 19, 2913–2926	4
(Zhao et al. 2015)	J Arid Land. 2015, 7, 475–480	2
(Zheng et al. 2016)	Biogeochemistry. 2016, 131, 65–76	2

Statistical analysis

A random-effects model provided the effect size, the outcome measure for meta-analyses. This model assumes that sets of studies are not identical in their methods and characteristics, potentially introducing heterogeneity/variability among the actual effects. An option to model heterogeneity is considering it completely random (Viechtbauer 2010).

The effect size is a quantitative index that reflects the magnitude of association among variables of interest in each study (Konstantopoulos 2006). To estimate the rhizosphere effect on soil properties, the *metafor* package (Viechtbauer 2010) in R software (R Core Team 2019) calculated the effect size for each data point as the natural log of the response ratio (*In RR*): $ln(R| = ln(X_t/X_c)$; where X_t is the rhizosphere mean (treatment), and X_c is the bulk soil mean (control). Log transformation balanced positive and negative effects and maintained symmetry in the analysis, especially when the data showed

discrepancies. The variance (v) of RR associated with each effect size was calculated by the equation: $v \frac{SD_t^2}{n_c X_c^2} + \frac{SD_c^2}{n_c X_c^2}$; where SD_t and SD_c are the standard deviations for treatment and the control, respectively, and n_t and n_c are the sample sizes for treatment and the control, respectively. In (RR) = 0 indicates no rhizosphere effect, In (RR) > 0 represents a positive rhizosphere effect, and In (RR) < 0 characterizes a negative rhizosphere effect.

The estimates for each soil attribute, represented by effect sizes, were transformed into percentages for better understanding. Negative rates indicated a numerical value decrease in soil attributes from the treatment compared to the control, whereas positive values indicated an increase. When a 95% confidence interval did not overlap with zero, a significant rhizosphere effect was considered.

A correlation analysis measured the correlation strength between the two crucial climatic factors that affect soil processes – mean annual precipitation (MAP) and mean annual temperature (MAT) - and pH, TOC, and *e*CEC in the rhizosphere and bulk soil. MAP was divided into three categories: low (<900 mm), moderate (900-1,500 mm), and high (> 1,500 mm). The same occurred for MAT: low (< 5°C), moderate (5-20°C), and high (>20°C). The three soil attributes were selected due to substantial records in the included manuscripts (116 for pH, 93 for TOC, and 41 for *e*CEC), relatively well distributed among the studies.

Number of studies						
Country		Botanical group		Establishment form		
		Coniferous Broadleaved		Monoculture	Regeneration	
Brazil	1	-	1	1	-	
Canada	26	4	22	3	23	
China/Tibet	66	35	31	32	34	
France	51	27	24	48	3	
Germany	1	-	1	1	-	
Italy	17	-	17	10	7	
Spain	2	-	2	-	2	
USA	6	-	6	-	6	
TOTAL	170	66	104	95	75	

Table 2. The number of studies by country, botanical group, and establishment form.

Heterogeneity and moderator variables

In an overall random effect size meta-analysis, the effect size means of all studies are estimated to verify potential homogeneity. Heterogeneity was quantified with l^2 , an index that describes the percentage of total variability over studies and compares meta-analyses of various study types and sizes with different outcome data and effect measures (Higgins et al. 2003). Approximate 25, 50, and 75% values indicate low, moderate, and high heterogeneity, respectively (Higgins et al. 2003). Significant l^2 values required a sensitivity analysis.

The meta-analysis considered study-level variables, or moderators, promoting a mixed-effects model that may account for at least part of heterogeneity in the actual effects (Viechtbauer 2010). Moderator variables of interest were the tree botanical group (coniferous and broadleaved trees) and stand establishment forms (monoculture and natural regeneration sites). However, conclusions were drawn from the subgroups with only one study to prevent misleading statements.

Publication bias and sensitivity analysis

A potential publication bias was assessed statistically with the *funnel* function in the *metafor* package and graphically represented with funnel plots of effect sizes vs. their standard errors) to verify

whether the literature review was subject to a publication bias, in which significant treatment differences are more likely to be published than non-significant ones. Without a publication bias, studies with high precision are assumed to be plotted near the average, and those with low precision to be spread evenly on both sides, creating a funnel-shaped distribution. Deviation from this shape may indicate a publication bias. The trim and fill analysis was also performed to estimate the number of potentially missing articles from the meta-analysis from suppressing the most extreme studies on one side of the funnel plot. This analysis demonstrates how the overall summary effect size would shift when removing an apparent bias.

Sensitivity was analyzed by assessing the variance and contribution of each study for the overall summary effect size. Studies with high variance and low contribution compared to others in the dataset were removed one at a time, and the meta-analysis was performed again. That shows the extent of changes in heterogeneity and summary effect size without the removed study.

All statistical analyses were conducted in R software (R Core Team 2019), and *SigmaPlot* Version 13.0 (Systat Software Inc., San Jose, CA) created the forest plots.

3. Results

pH and total organic carbon

The rhizosphere pH decreased by 1.98% relative to bulk soil (Figure 1a). The pH studies (n=116) presented high heterogeneity (l^2 =99.93%; 95% CI: 99.91 to 99.96%; df=115; $p \le 0.01$), which could not be explained by botanical group and establishment form moderators because l^2 remained higher than 97%. However, when comparing the rhizosphere with bulk pH within groups, the pH of conifers decreased more (2.96%) than broadleaved trees (1.98%), and the pH reduction in monoculture and regeneration rhizosphere was the same (1.98%). Considering the numerous records on this soil attribute, accounting for the overall effect size, each contribution is well distributed across the dataset.

Total organic carbon (TOC) was the second feature most recorded in our literature review (n=96). After examining the overall meta-analysis for sensitivity, studies by Dai et al. (2018) were removed from the TOC dataset due to their high variability and low contribution to the overall summary effect size (< 0.0005%). TOC significantly increased in the rhizosphere by an average of 75.07% (n=93) compared to bulk soil (Figure 1b). The contribution of each study to the overall effect size was not computed because of the uniform distribution across the dataset.

The botanical group effect analysis showed that TOC increased 82.21% in the coniferous rhizosphere compared to bulk soil, which is higher than in the broadleaved rhizosphere (69.89%) compared to the respective bulk soil. Furthermore, the rhizosphere effect on regeneration sites was higher (91.55%) than on monocultures (63.23%). Heterogeneity across studies was high and statistically significant for TOC (I^2 =98.19%), and the moderator variables could not explain it because I^2 remained high, i.e., the risk ratio estimate across studies was inconsistent.

Publication bias occurred for pH and TOC (Supplemental Material, Figure 4a-b), and the trim and fill analysis did not suggest plotting extra studies to balance the meta-analysis.



Figure 1. A - Rhizosphere summary effect size on pH and B - total organic carbon (TOC). Bars represent the response ratio (%) \pm 95% confidence interval. The numbers in parentheses indicate the number of studies (*n*). Significance occurred at * $p \le 0.1$; ** $p \le 0.05$; *** $p \le 0.01$; *ns:* not significant.

Particle size distribution and Al³⁺

Sand and silt did not show a rhizosphere overall effect size, while clay was 55.51% lower in the rhizosphere than in bulk soil (Figure 2a). Clay decreased more in monocultures than in regeneration areas, and clay response to the botanical group could not be evaluated due to missing studies on coniferous trees.

The overall meta-analysis showed inconsistencies in risk ratio estimates among the studies for all particle sizes (l^2 =98.95% for sand, 99.71% for silt, and 99.76% for clay). The establishment form moderator could not explain these high heterogeneities, whereas the l^2 index remained elevated (>98%) and highly significant ($p \le 0.01$).

The contribution of studies to the summary effect size was assessed. Three out of 19 articles explained the 62.98% effect size for sand, and four of 19 studies accounted for 86.44% of the summary effect size on silt. However, four of 19 articles justified a 54.06% effect size for clay. The few studies explaining most of the effect size justify their high heterogeneity.

Twenty-two studies were considered for AI^{3+} , but the sensitivity analysis eliminated one (Álvarez et al. 2010). In the overall meta-analysis (n=21), AI^{3+} increased by 68.20% in the rhizosphere compared to bulk soil (Figure 2b), and AI^{3+} was 197.43% higher in the coniferous rhizosphere than in the coniferous bulk soil. As for broadleaved trees, AI^{3+} was 50.68% higher in the rhizosphere. Considering there were only two studies on monocultures, any conclusion about the effect of establishment forms could lead to error. The high heterogeneity of the overall meta-analysis ($I^2=99.74\%$; 95% CI: 99.48 to 99.87%; df=20; $p \le 0.01$) did not change when considering moderator variables. That means heterogeneity caused the most variability among studies, and moderators could not fully explain it. Five of 22 studies represented 86.30% of the overall summary effect size.

Particle size distribution (sand, silt, and clay) and AI^{3+} presented publication biases because the findings were not evenly distributed on both average sides, and many studies were plotted marginally or outside the funnel shape (Supplemental Material, Figure 5a-d). Regarding meta-analysis balance, the trim and fill method suggested that, for sand, three studies may be added to the left side of the average, adjusting I^2 to 99.03% and the effect size to -7.54% (Supplemental Material, Figure 5a), and five studies to the right side of the average for AI^{3+} , adjusting I^2 to 99.82% and the effect size to 98.40% (Supplemental Material, Figure 5d).



Figure 2. A - Rhizosphere summary effect size of particle size distribution and B - Al³⁺. Bars represent the response ratio (%) \pm 95% confidence interval. The numbers in parentheses indicate the number of studies (*n*). Significance occurred at * $p \le 0.1$; ** $p \le 0.05$; *** $p \le 0.01$; *ns*: not significant.

Available P, K⁺, Ca²⁺, and effective CEC

The concentration of available phosphorus (P_{av}) was higher in the rhizosphere than in the bulk soil (18.53%, n=32) (Figure 3a). However, this rhizosphere effect was significant only for naturally regenerated stands, increasing by 32.31% compared to the bulk soil.

Potassium (K^+) showed a positive rhizosphere effect, with a 69.89% increase (n=18) relative to bulk soil (Figure 3b). The increase in the coniferous rhizosphere was higher (80.40%) than the broadleaved trees (69.90%), and the regeneration rhizosphere effect was even higher (203.44%) than monoculture (24.61%), even though the K^+ increase in the monoculture was insignificant.

Calcium (Ca²⁺) in the rhizosphere did not differ from the bulk soil (Figure 3c). The large confidence interval (-30.23% to 29.69%) indicates high data dispersion, reducing estimate precision. The significant reduction (15.63%) was unreliable for monoculture because only one study recorded it.

Effective cation exchange capacity (*e*CEC) increased by 22.14% (*n*=41) in the rhizosphere compared to the bulk soil (Figure 3d). Coniferous trees had a higher *e*CEC (24.61%) than the respective broadleaved species (17.35%). Despite the few studies (*n*=4), the regeneration rhizosphere presented higher *e*CEC (34.99%) than monoculture (20.93%).

The overall meta-analysis showed high heterogeneity for these four attributes, as demonstrated by the high I^2 (93.54% for P_{av}, 98.92% for K⁺, 99.55% for Ca²⁺, and 85.65% for *e*CEC), suggesting inconsistency across studies. The attempt to explain part of heterogeneity through moderator variables was frustrated. However, the lower heterogeneity for P_{av} and K⁺ in regeneration sites was because all or almost all studies were from the same publications and performed in equivalent conditions. Regarding *e*CEC, the heterogeneity of the regeneration subgroup decreased to zero, probably due to the small number of studies (*n*=4). The same occurred in the Ca²⁺ monoculture subgroup (*n*=1).

The publication bias analysis through funnel plot visual interpretation showed that P_{av} , K^+ , and Ca^{2+} studies presented publication biases because they were not evenly distributed on both average sides, as more than 40% were plotted marginally or outside the funnel shape (Supplemental Material, Figure 6a-d). Therefore, the trim and fill method suggested adding five studies for Ca^{2+} , three for K^+ , and 17 for *e*CEC. The Ca^{2+} studies were plotted on the right side of the average, and K^+ and *e*CEC on the left side. These additional studies adjusted I^2 and reduced the rhizosphere effect size: for Ca^{2+} , I^2 =99.57% with a negative effect size of -22.79%; for K^+ , I^2 =98.86% with a positive effect size of 53.97%; and for *e*CEC, I^2 =91.24% with a positive effect size of 9.63%.

The contribution of studies on P_{av} shows that five of 32 investigations represented over 50% of the overall effect size. Three of 18 studies on K⁺ explain 77.02% of the overall effect size, four of 17 studies on Ca²⁺ explain 61.82%, and one of 41 studies on *e*CEC justify 76.92%.

Correlation analysis

pH was significantly correlated with MAP for the rhizosphere and bulk soil but not with MAT. However, TOC in the rhizosphere and bulk soil was significantly correlated with MAP and MAT, and *e*CEC did not significantly correlate with either MAP or MAT (Table 3).

Table 3. Pearson's correlation coefficients (*r*) between pH, total organic carbon (TOC), effective cation exchange capacity (*e*CEC), and the climatic factors of mean annual precipitation (MAP) and mean annual temperature (MAT).

			MAP	MAT	п
рН Total TOC еСЕС	۶U	Rhizosphere	-0.47 **	0.02 ^{ns}	116
	рп	Bulk soil	-0.36 **	0.02 ^{ns}	110
	Rhizosphere	0.62 **	-0.51 **	93	
	Bulk soil	0.36 **	-0.38 **		
	0050	Rhizosphere	-0.23 ^{ns}	-0.16 ^{ns}	41
	ELEL	Bulk soil	-0.03 ^{ns}	-0.26 ^{ns}	41



** Significant at $p \le 0.05$; *ns*: not significant. *n*: the number of studies.

Figure 3. A - Rhizosphere summary effect size on available P (P_{av}), B - exchangeable K (K^+), C - exchangeable Ca²⁺, and D - effective cation exchange capacity (*e*CEC). Bars represent the response ratio (%) ± 95% confidence interval. The numbers in parentheses indicate the number of studies (*n*). Significance occurred at * $p \le 0.1$; ** $p \le 0.05$; *** $p \le 0.01$; *ns*: not significant.

4. Discussion

The rhizosphere effect of coniferous and broadleaved trees

Coniferous trees caused a higher rhizosphere effect than broadleaved ones. The rhizosphere changes the soil solution composition, and its impact depends on the specific functioning of different plant species, the related microbial community, and soil mineralogy (McGahan et al. 2014; Sokolova et al. 2019). Adjacent soils with the same land-use history under a uniform tree coverage may present diverse soil microbial communities, especially when comparing exotic species to native ones (Kourtev et al. 2002), but also when comparing the rhizosphere of coniferous to broadleaved trees (Sokolova et al. 2019). Regardless of the species, numerous studies have demonstrated that Ca, Mn, K, Fe, Mn, and Al saturations, proton activity, N, C, and BS are usually higher in the rhizosphere than in the bulk soil (Séguin et al. 2004; Turpault et al. 2005; Calvaruso et al. 2011; Collignon et al. 2012).

This meta-analysis showed that the pH of the coniferous rhizosphere decreased more (2.96%) than in the broadleaved rhizosphere (1.98%), and Al³⁺ increased more in coniferous (197.43%) than in the broadleaved (50.68%) rhizospheres. Therefore, the risk of Al toxicity is higher under coniferous than broadleaved species and agrees with the lower pH observed under conifers (Firn et al. 2007; Collignon et al. 2012). In acid soils, the rhizosphere plays an ecological role in Al detoxification by nutrient accumulation and Al complexation with organic compounds (Collignon et al. 2012). Sokolova et al. (2019) found similar changes in soil acidity due to forest species, reporting a lower pH in the rhizosphere and enclosing soil of the Norway spruce conifer (*Picea abies*) than in the Norway maple broadleaved tree (*Acer platanoides*). Also, the clay fraction showed smaller quantities of mica, kaolinite, and illite - more labile minerals associated with higher nutrient availability - under spruce than maple trees. These authors partially attributed the differences to the woody species and associated microbial community and partially to the clay fraction composition.

The higher H⁺ activity in coniferous than broadleaved rhizospheres was followed by higher P_{av}, K⁺, TOC, and *e*CEC. The increased proton activity (H⁺) in the rhizosphere was most attributed to low-molecularweight organic acids (LMWOAs) released by the microbiota, primarily ectomycorrhizal fungi (Sokolova 2011), as a plant nutrition mechanism through the balance charge (Wang et al. 2001; Churchman and Lowe 2012; Korchagin et al. 2019). Soil acidification affects base cation pools and implicates mineral weathering and forest sustainability (Rosenstock et al. 2019). For instance, the strategy of growing *Ericaceae* in very acid soil is to modify the rhizosphere pH from close to neutral to acid levels in the bulk soil, potentially related to the ability of Ca²⁺ accumulation in the root zone (Álvarez et al. 2011). pH reduction followed by an increase in soluble Al³⁺ and *e*CEC in the rhizosphere indicates the action of dissolution mechanisms (Wang et al. 2001). Also, the higher K⁺ in the rhizosphere may be inferred to dissolution mechanisms followed by mineral transformation, with probable K⁺ loss from illite interlayers, transforming it into vermiculite (Bortoluzzi et al. 2012).

These results indicate a higher impact on soil from coniferous than broadleaved trees, as mentioned in the literature (Firn et al. 2007; Collignon et al. 2012; Sokolova et al. 2019). However, considering the concentration of studies in temperate zones, the impact of botanical groups and tree species cannot be extrapolated to tropical and subtropical regions.

Changes in the rhizosphere due to establishment forms

The rhizosphere effect on naturally regenerated forest soils where trees grow spontaneously in a mixed-forest stand was higher than on monoculture sites. Despite the lack of pH differences, Al³⁺, TOC, K⁺, available P, and *e*CEC levels were higher in the rhizosphere of regeneration than in monoculture sites. These findings confirm the positive relationship between soil nutrient availability and species diversity. Considering that naturally regenerated woody environments favor the recolonization of species from the native flora, the diversity of organic materials promotes a similar nutrient availability to natural secondary forests and the maintenance of original edaphic conditions (Firn et al. 2007), with higher soil fertility (Malysz and Overbeck 2018). Also, replacing the monoculture with a mixed-specie forest promotes soil

nutrient availability (Bu et al. 2020), and higher organic matter and K^+ contents were found in secondary forest soils than in artificial forests under the same geological conditions (Fan et al. 2019).

Organic mineral nutrient turnover is a relevant P source (Clevelário Junior 1996; Chen 2003) and K (Turpault et al. 2008) and the largest source of plant nutrients, especially in forests that have reached their climax (Uhlig and Von Blanckenburg 2019; Uhlig et al. 2020). However, the large nutrient inventory is geogenic, replenishing the reservoir through chemical weathering and sustaining forest ecosystem nutrition from centuries to millennia (Uhlig and Von Blanckenburg 2019; Dawson et al. 2020). The high biological activity in the rhizosphere increases nutrient recycling efficiency (Collignon et al. 2011), even though soil fertilization reduces microbial activity and nutrient availability due to fertilization (Phillips and Fahey 2008). For instance, P-deficient soils may enhance the phosphatase activity and organic acid production in the rhizosphere (Chen 2003; Fujii et al. 2012; Hofmann et al. 2016), and soil acidification dissolves apatite, the primary source of soil mineral P. Soil acidification may also transform micas and illite into chloritized structures and labile minerals (Sokolova 2011), releasing K from illite interlayers into the soil (Bortoluzzi et al. 2012).

The rhizosphere showed higher TOC than the bulk soil, and the significant correlation with MAP and MAT confirms the influence of climatic factors on soil carbon stocks. Warming and higher precipitation stimulate soil respiration and ecosystem photosynthesis. That increases aboveground biomass and productivity (Sullivan et al. 2008; Luo et al. 2009; Wu et al. 2011), with expressive responses in woody ecosystems (Rustad et al. 2001) as a consequence of higher microbial activity (Sardans et al. 2008), enhanced C inputs and net C uptake (Luo et al. 2009; Wu et al. 2011), and soil nutrient mineralization (Hartley et al. 1999). Precipitation is the only factor influencing soil pH, with a higher correlation between rhizosphere pH and MAP than the bulk soil. Effective CEC cannot be directly correlated to MAP and MAT because it depends on several cations related to different soil properties. Furthermore, ecosystems are less responsive to the interaction of warming and precipitation than expected from single-factor effects (Luo et al. 2008; Wu et al. 2008; Wu et al. 2008; Wu et al. 2011).

5. Conclusions

Timber production from coniferous and naturally regenerated tree stands affected soil properties more than broadleaved species and monocultures. This meta-analysis evidenced a higher rhizosphere effect on soil properties than the surrounding bulk soil. The coniferous rhizosphere effect was higher than broadleaved trees, and the same occurred for regeneration sites compared to monocultures. Soil fertility was higher in naturally regenerated mixed stands, favoring tree establishment and development and organic nutrient turnover. Knowledge of the rhizosphere effect on soil is crucial for better understanding forest system dynamics for biomass production, especially in a low-input perspective, as soil nutrients can be depleted and threaten soil sustainability. However, further research is required on the tropics (the new agricultural frontier) to assess the impact of botanical groups and tree species on soil quality worldwide, considering the concentration of previous studies in temperate zones. The reasons for choosing specific tree species and forest management practices must be revisited, and the replacement of monoculture with mixed species stands where naturally regenerated woody species are managed for timber production must be considered to meet the demand for renewable energy sources while protecting the environment.

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