



# Microbial Enzymatic Activities and Community-Level Physiological Profiles (CLPP) in Subsoil Layers Are Altered by Harvest Residue Management Practices in a Tropical *Eucalyptus grandis* Plantation

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## Abstract

Harvest residue management is a key issue for the sustainability of *Eucalyptus* plantations established on poor soils. Soil microbial communities contribute to soil fertility by the decomposition of the organic matter (OM), but little is known about the effect of whole-tree harvesting (WTH) in comparison to stem only harvesting (SOH) on soil microbial functional diversity in *Eucalyptus* plantations. We studied the effects of harvest residue management (branches, leaves, bark) of *Eucalyptus grandis* trees on soil enzymatic activities and community-level physiological profiles in a Brazilian plantation. We measured soil microbial enzymatic activities involved in OM decomposition and we compared the community level physiological profiles (CLPP) of the soil microbes in WTH and SOH plots. WTH decreased enzyme activities and catabolic potential of the soil microbial community. Furthermore, these negative effects on soil functional diversity were mainly observed below the 0–5 cm layer (5–10 and 10–20 cm), suggesting that WTH can be harmful to the soil health in these plantations.

**Keywords** Tropical forest soil · Forest residue management · *Eucalyptus grandis* · Enzyme activities · CLPP

## Introduction

Areas of planted forests are expanding in tropical regions contributing to supply the growing demand in wood and wood-

derived products [24]. High amounts of nutrients exported with tree biomass harvested every 6–10 years rise the issue of the sustainability of *Eucalyptus* plantations [1]. Recent meta-analyses confirmed negative impacts of intensive forest management practices, such as whole-tree harvesting (WTH), on soil properties and tree productivity [2, 39]. Nevertheless, in comparison to stem only harvesting (SOH), the effect of WTH on tree and soil properties remains in debate regarding *Eucalyptus* plantations. Indeed, independent studies have shown either negative impacts [11, 18, 22, 37] or no effect of whole-tree harvesting on tree growth and soil properties [7, 10, 14, 20, 21]. Changes in tree productivity and soil properties after residue management might result from disturbances of the decomposition processes in the soil. The link between soil organic matter (OM) and tree productivity is mainly due to the activity of soil microorganisms, which contribute through degradation mechanisms to supply plant-available nutrients [36]. Microorganisms deploy extracellular enzymes to break down organic compounds into shorter assimilable molecules and therefore they participate to carbon and other nutrient cycles in soil [6, 38, 40]. In comparison to SOH,

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WTH practices might weaken these recycling key processes in soil by decreasing the availability of soil carbon and nutrients at planting, then tree growth and litter production.

A negative effect of WTH in *Eucalyptus* plantations on soil microbial biomass was shown in Australia by Mendham et al. [20], but potential effect on soil microbial functions remains unknown. To understand how WTH influence soil microbial functions, we compared the effects of WTH and SOH forest practices on soil microbial functional diversity, in an experimental *Eucalyptus grandis* plantation in South East of Brazil. As most of previous studies focused on forest floor, or topsoil (0–5 cm), we chose to examine additionally whether residue management practices influence deeper soil layers (5–10 and 10–20 cm). First, we hypothesized that residue removal would alter the functional potential of the soil microbial community. We also hypothesized that the soil microbial functional diversity decreases in response to residue removal, with higher impacts in the topsoil than in subsoil.

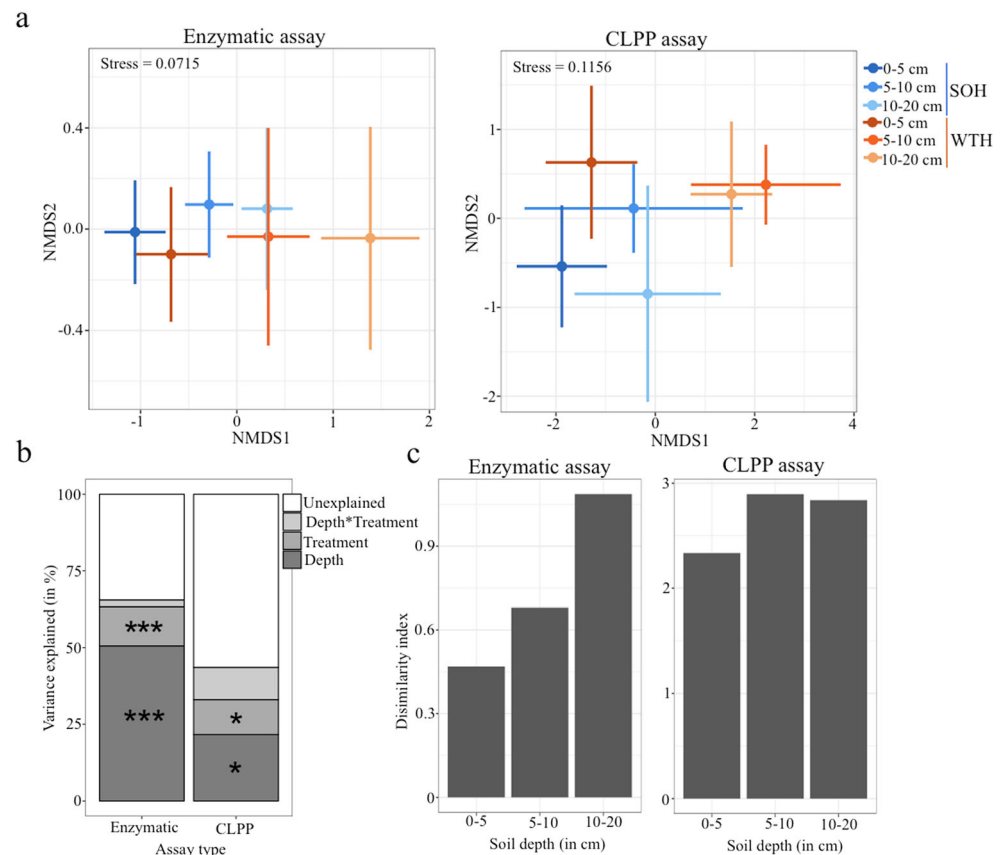
The study site is an experimental plantation located at Itatinga, São Paulo state (23° 17' S and 48° 28' O). The native savannah was replaced by *Eucalyptus* spp. The soil was a very deep Ferralsol [13]. We compared two treatments with contrasting harvest residue management during the inter-rotation period. The two different residue management treatments were applied at the end of the first rotation. *Eucalyptus* trees were cut and only the stem wood was harvested. Forest residues (i.e., leaves, branches, bark, and stem tops) were let for decomposition on the soil. We called this treatment stem-only harvesting (SOH). In the second treatment, the whole-tree was harvested including leaves, branches, bark, and stem tops. This treatment was called whole-tree harvesting (WTH) and was considered as a more intensive forestry practice than SOH due to the greater amount of tree biomass harvested. Our study was carried out 4 years after replanting *Eucalyptus grandis* trees in plots submitted to SOH or WTH. We collected soil samples in three plots for each WTH and SOH treatment on 16 November 2016 at the Itatinga *Eucalyptus grandis* experimental plantation. Sampling was conducted at this time of the year when soil moisture was relatively elevated as it is the maximum of soil microbial activity period [4, 15]. Each plot (24 × 18 m) comprised 81 trees in 9 rows of 9 trees, with a double row buffer separating the adjacent plots. Surface litter was removed before sampling and six soil cores (5 cm diameter) were withdrawn per plot: five on a diagonal transect through the 5 × 5 tree inner plots and one random inside this plot (Figure S1). Soil cores were divided in three layers 0–5, 5–10, and 10–20 cm, sieved at 2 mm, homogenized, and then stored in cold room (+ 4 °C) until analyses. To study the microbial functional diversity, we applied enzymatic activities and CLPP

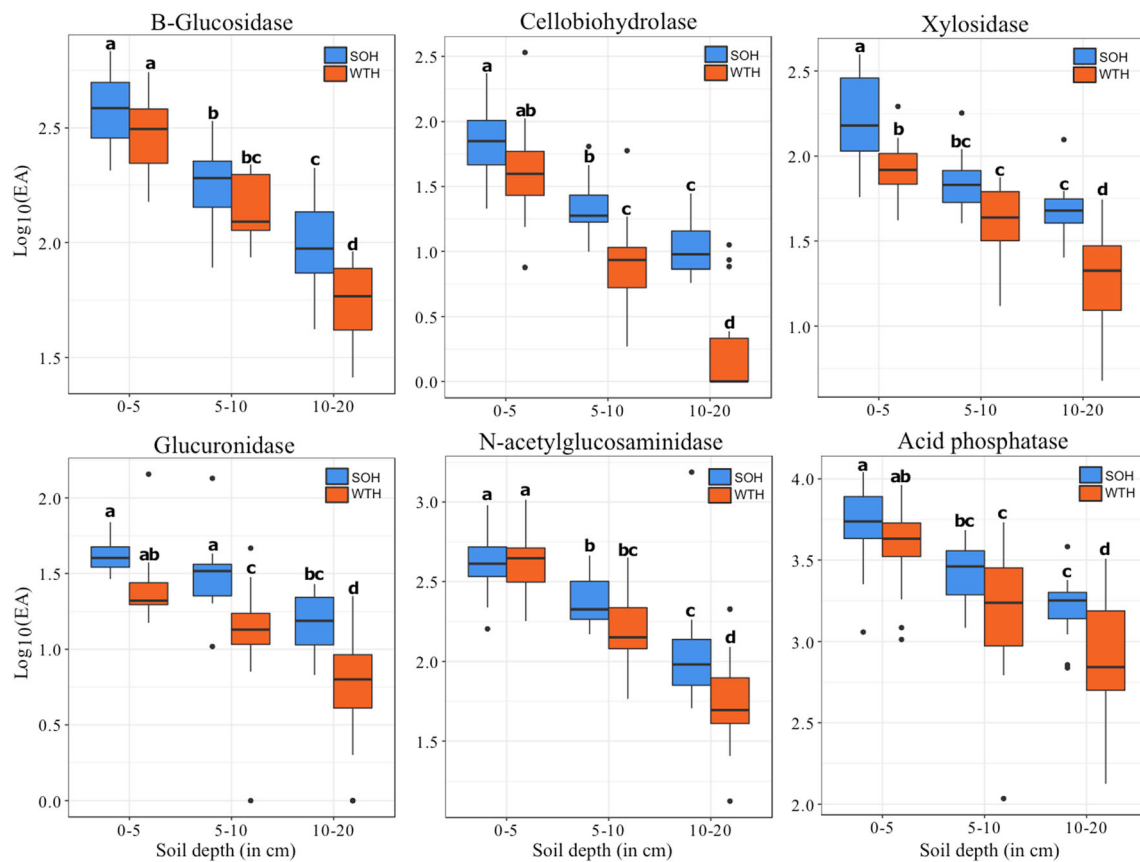
approaches. Enzymatic activities approach mostly reveals a direct in situ measurement of fungi OM degradation ability while CLPP approach mainly highlights bacterial community carbon substrates metabolization potential, which makes these two complementary approaches [3, 19, 26, 29]. First, we measured activities of six enzymes involved in soil OM degradation and mobilization of C, nitrogen (N) and phosphorus (P):  $\beta$ -glucosidase, cellobiohydrolase, xylosidase, glucuronidase, for polysaccharide degradation; N-acetylglucosaminidase for chitin decomposition and N mobilization; and acid phosphatase, as functional indicator of P mobilization. Protocol was adapted from Saiya-Cork et al. [29]. Briefly, 1 g of soil ( $n = 18$  soil samples per treatment per depth) was weighted and added to 20 ml of acetate buffer (pH = 5, 28.82 mL of 1 M acetic acid, 273.3 mL of 0.3 M sodium acetate and adjusted to 1 L with distilled water) to give a final concentration of 1:20 w/v. These soil suspensions were incubated at 4 °C for one night under agitation. For microplate assays, in each well of a clear flat-bottom 96-well plate (Sarstedt, Newton, NC, USA), 200  $\mu$ L of the soil suspension were added to 50  $\mu$ L of the respective substrate solution. After incubation at 25 °C, the plate was centrifuged at 4500 g for 5 min and 50  $\mu$ L of the clear solution was transferred in a black opaque 96-well microplate (Perkin-Elmer, Life Sciences) containing 50  $\mu$ L of stopping buffer (Tris 2.5 M pH 10–11) in each well. Measurements were carried out using a Victor3 microplate reader (Wallac Perkin-Elmer Life Sciences, Villebon-sur-Yvette, France) with an excitation wavelength of 360 nm and an emission wavelength of 450 nm. Enzymatic activity (EA) was expressed in picomoles of methylumbelliferone formed per gram of dry soil per minute. Secondly, we pooled soil samples per plot and applied a physiological profile approach (CLPP) using BIOLOG Ecoplates™ on each composite soil ( $n = 3$  soil composites per treatments per depths) as described by Uroz et al. [35]. CLPP approach is based on the measurement of the ability of the microbial community to metabolize 31 different carbon sources. The OD 590 nm of the reference well was subtracted from the other wells containing carbon sources. These corrected absorbances were used for the subsequent analysis. Statistical analyses and data representations were performed using R software [28]. Soil enzymatic data were log transformed to ensure normality. Soil enzymatic and CLPP data were analyzed using nonmetric multidimensional scaling analysis (NMDS) and permutational multivariate analysis of variance (PERMANOVA) based on Euclidean distance matrix using Vegan package [23]. Soil enzymatic activities and soil CLPP were compared using analysis of variance (Two-way ANOVA with depth and treatment as factor).

Nonmetric multidimensional scaling (NMDS) analysis of the soil extracellular enzymatic activities and the CLPP data show that SOH and WTH treatments were closely clustered for the organic soil layer (0–5 cm). By contrast, the two other soil layers (i.e., 5–10 cm and 10–20 cm) segregated in function of treatment (Fig. 1a). PERMANOVA using Euclidean distance matrix confirms that soil depth ( $P \leq 0.001$ ) and treatment ( $P \leq 0.001$ ) significantly influenced the soil extracellular enzymatic activities (Fig. 1b). Soil depth and treatment explained 50.6% and 12.7% of the variation in distances, respectively. This analysis confirms a treatment effect on CLPP profiles ( $P = 0.024$ ), treatment explaining 11.4% of the total variance (Fig. 1b). PERMANOVA shows that soil depth impacted significantly CLPP profiles ( $P = 0.016$ ). For both enzymatic and CLPP approaches, dissimilarity index increased with soil depth (Fig. 1c), indicating that harvest management practices impacted more the deeper soil horizons studied here (i.e., 5–10 cm and 10–20 cm) than the topsoil (i.e., 0–5 cm). The activities of acid phosphatase and cell wall degrading enzymes decrease from the 0- to 5-cm to the 10- to 20-cm layers (Fig. 2). It is well known that soil potential enzyme activities generally decline with soil depth [32–34]. In the upper soil layer (0–5 cm), only the xylosidase

activity is significantly influenced by harvest management practices ( $P \leq 0.05$ ), decreasing by 13.6% in WTH treatment in comparison to SOH treatment. In the 5- to 10-cm layer, cellobiohydrolase and glucuronidase activities were 32.3% and 25.5% lower in WTH than in SOH, respectively. WTH treatment disrupted all enzyme activities in the 10- to 20-cm soil layer. Indeed, the six enzyme activities measured were significantly ( $P < 0.05$ ) lower in WTH than in SOH in the 10- to 20-cm layer (decreasing by 78.2% for cellobiohydrolase, 35.9% for glucuronidase, 23.5% for xylosidase, 14.7% for N-acetylglucosaminidase, 12.5% for  $\beta$ -glucosidase, and 10.3% for acid phosphatase). In the same way, if rate of substrate utilization based on CLPP approach appeared to be slightly impacted by harvest management practices in the topsoil (0–5 cm), overall substrate utilization decreased respectively by 16% and 15% in the 5- to 10-cm and 10- to 20-cm layers in the WTH plots by comparison with the SOH plots (Fig. 3). This decrease of total microbial catabolic potential in WTH treatment was mainly explained by the following substrates: L-serine, alpha-D-lactose, D-cellobiose, glycyl-L-glutamic acid, D-erythritol, and N-acetyl-D-glucosamine. Shift in CLPP profiles in function of treatment and depth could be due to change in bacterial biomass and/or bacterial

**Fig. 1** **a** First two axes for the nonmetric multidimensional scaling analysis (NMDS) of the six enzymes activities and the 31 substrates of the CLPP approach based on Euclidean distance dissimilarity matrix between groups (i.e., SOH 0–5 cm, SOH 5–10 cm, SOH 10–20 cm, WTH 0–5 cm, WTH 5–10 cm, and WTH 10–20 cm). **b** Variances explanation based on permutational multivariate analysis of variance using Euclidean dissimilarity matrix for enzymatic and CLPP approaches ( $P \leq 0.05^*$ ,  $P \leq 0.01^{**}$ ,  $P \leq 0.001^{***}$ ). **c** Dissimilarity index calculated for the six enzymes activities and the 31 substrates of the CLPP approach based on Euclidean dissimilarity matrix between WTH and SOH treatments in function of depth (i.e., 0–5, 5–10, and 10–20 cm)





**Fig. 2** Soil enzyme activities (i.e., acid phosphatase, cellobiohydrolase, glucosidase, glucuronidase, N-acetylglucosaminidase, and xylosidase) in function of depth (i.e., 0–5, 5–10, and 10–20 cm) and treatment (i.e., SOH

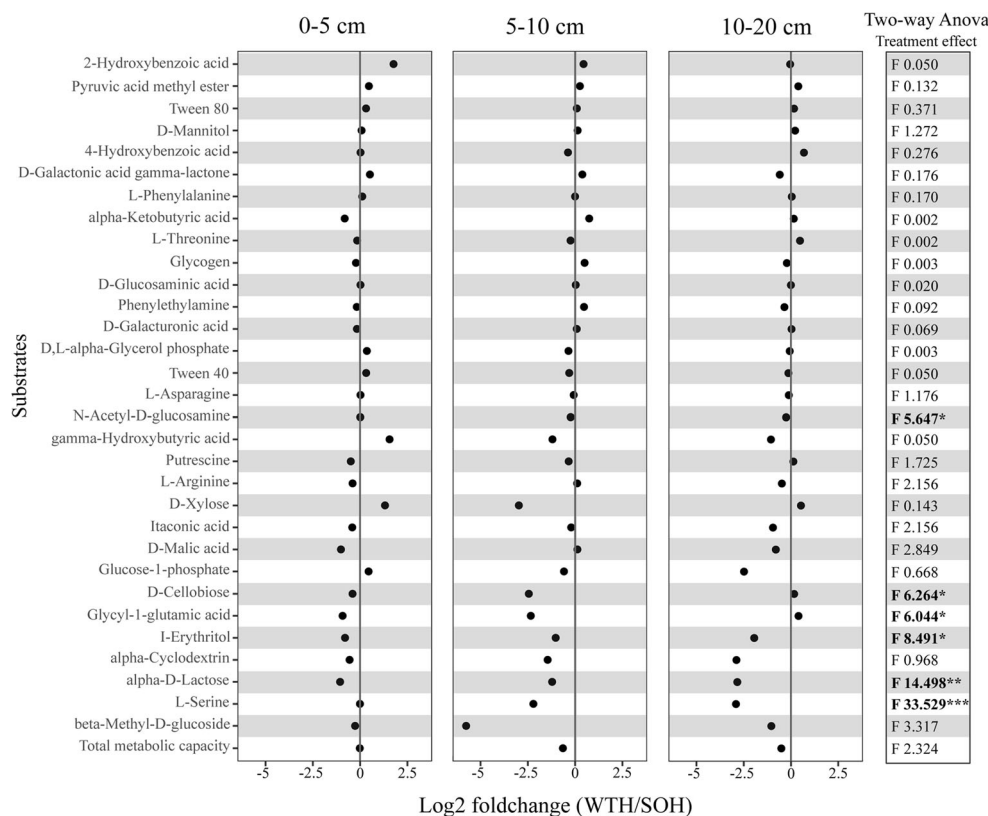
and WTH). Different letters denote significant differences within each group ( $P \leq 0.05$ , two-way ANOVA and Tukey's test,  $n = 18$ )

community composition which are described as potential drivers of substrates metabolism capacity based on BIOLOG approach [19, 26]. Both enzymatic activities and CLPP approach revealed a negative impact of WTH by comparison with SOH respectively on the effective functions and the functional potential of the soil microbial community. Such decreases in soil functional diversity resulting from forest intensification practices, as whole-tree harvesting, have already been observed [5, 17, 41]. As soil OM degradation occurs mainly in the topsoil, only this horizon is commonly sampled to investigate soil microbial response to OM manipulation [3, 9, 16, 25, 30, 31, 41]. In our study, the soil microbial response to harvest residue management was higher below 5 cm depth than in the topsoil. In a meta-analysis comparing WTH to SOH, Achat et al. [2] reported that soil properties of deep layers were more negatively impacted than in topsoil. Chen and Xu [8], in a subtropical pine plantation, showed that microbial biomass was relatively more negatively affected in subsoil than in topsoil in response to WTH harvesting. Taken together, these results revealed that soil properties, microbial biomass

and microbial functions might be more negatively impacted in subsoil layer than in topsoil layer in response to intensive forestry. Consequently, the monitoring of these parameters, only targeted in the topsoil layer, cannot be considered as complete indicators of possible impact of intensive forest management. Changed in microbial functions, we measured in response to WTH could be due to the direct impact of intensive forestry on soil OM and nutrients content or indirect impact such as modification of soil compaction, moisture and temperature that we have now to explore and bridge with soil microbial functions [12, 21, 27].

In conclusion, we demonstrate that whole-tree harvesting negatively impacted the functional diversity of soil microbes in comparison to stem only harvesting, resulting in a decrease in microbial enzymatic activities involved in C, N, and P cycling. Nevertheless, the functional gaps measured between these two treatments exhibited opposite responses to our prediction. Indeed, residue-removing effects were more pronounced in the deepest studied layers, providing a lasting imprint of intensive harvest management practices in subsoil horizons. Our findings highlight

**Fig. 3** Effect of WTH on metabolization capacity of the 31 substrates measured with CLPP approach [ $\log_2$  (fold change WTH over SOH)] in function of depth (i.e., 0–5, 5–10, and 10–20 cm). Differences in metabolization capacity was assessed using two-way ANOVA ( $P \leq 0.05^*$ ,  $P \leq 0.01^{**}$ ,  $P \leq 0.001^{***}$ )



the need to explore the consequences of forest management on the functioning of the relatively deep soil horizon under tropical climate.

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## Compliance with Ethical Standards

**Conflict of Interest** The authors declare that they have no conflict of interest.

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