Impact of Superficial Lateral Drainage on Tree Root Distribution and Forest Community Structure in Paracou, French Guiana — A Study on Drainage Barrier Depth

SANVITO Emilie[1*]
DOBETSBERGER Greta[2]
THION Clément[3]

Abstract

As tropical forests will experience more droughts in the coming decades, understanding their response to drought stress is crucial. This study investigates the impact of drainage barriers on root vertical distribution of trees and forest community structure in Paracou, French Guiana. Using the depth at which a horizon high in silt (HSD) occurs as an indicator for the drainage barrier, our study explores the relationship between drainage barrier, topography, and forest community structure. Our results confirm that drainage barrier influences tropical forest community structure, however the effect of a drainage barrier on vertical root distribution remains unclear. Mean species richness and tree density per hectare showed a slight but significant decrease with increasing HSD, while diameter at breast height (DBH) of trees (DBH >1 cm) on the studied plot exhibited minimal variation. However, the maximum DBH values were found in areas with a deeper drainage barrier. These findings contribute valuable insights into the soil-tree interactions and the effect of a drainage barrier in tropical ecosystems and complement earlier research by including DBH > 1 cm. Our results confirm that drainage barrier influences tropical forest community structure, however the effect of a drainage barrier on vertical root distribution remains unclear. Further research with increased sampling density and direct data collection is recommended to refine and expand upon these initial observations.

Keywords

root, tropical forest, community structure, drainage, pedology, drought, Paracou, French Guyana, silt, superficial horizontal drainage

[1]Tropimundo
    Avenue Franklin Roosevelt 50, 1050, Belgium.
[2]Université des Antilles
    Campus de Fouillole - BP250, 97157, France.
[3]AgroParisTech Montpellier
    648 Rue Jean François Breton, 34090, France.
*Corresponding author: emilie@sanvito.be,

1. Introduction

In tropical ecology, the relationship between root distribution and soil abiotic factors is crucial to forest community structure (Bardgett et al., 2014). Roots are essential for the nutrition and water uptake of trees (Hutchings et al., 2003; Hodge, 2009). Their distribution is driven by factors like soil texture, nutrient content, topography, and water content (Freschet et al., 2021).

A large part of the forests in French Guiana features a topography alternating between hills and valleys (Ferry et al., 2003). Acrisol (WRB, 2022), characterised by superficial lateral drainage (SLD), is the typical soil type on slopes (Fan et al., 2017). Acrisol is characterised by a silty texture horizon with low permeability that functions as a drainage barrier in the soil (Ferry et al., 2003; Humbel, 1978).

Drainage type, and to a lesser extent topography, are the main factors influencing forest community structure (Pélissier et al., 2002; Sabatier et al., 1997). Root vertical distribution (RVD) is the distribution of roots in units of biomass over sequential soil layers (Freschet et al., 2021). In soil with superficial lateral drainage, root development is inhibited by the drainage barrier (Ferry et al., 2003).

Tree roots are therefore concentrated in the

uppermost layers of the soil (Humbel, 1978), characterised by low water reserves. Consequently, roots in this soil type may undergo drought stress during the dry season. During the rainy season, this impermeable silty horizon will cause a temporary water table in the soil (Humbel, 1978; Pélissier et al., 2002), which creates anoxic stress for tree roots (Sabatier et al., 1997).

Our study takes place at Paracou research station in French Guiana. Epron et al. (2006) confirmed the presence of SLD in this area. They found that the depth of the drainage barrier on slopes depends on the topographical position, with deeper barriers at higher elevation. However, the specific ways in which drainage barriers influence both roots and forest structure remain understudied. Therefore, we examined whether a drainage barrier restricts tree roots on slopes in Paracou, exploring their role in shaping forest community structure. We investigated the effect of the depth, at which the drainage barrier occurs, on root vertical distribution and on 3 different forest structure indicators (DBH, species richness and tree density). Our main hypotheses are: (1) root density not only decreases with depth, but is also negatively influenced by the drainage barrier; (2) the depth at which the drainage barrier appears can be a predictor of DBH, species richness and tree density.

2. Material and method

2.1 Study site

The study took place at Paracou research station in French Guiana (5°18'N; 52°53'W), a 40000 ha domain owned by CNES (National Centre for Space Studies) containing 16 permanent plots studied by the French research centre CIRAD for over 35 years. Elevation ranges from 5 to 50 m, and the mean annual temperature is 26 °C, with an annual range of 1–1.5 °C. Rainfall averages 2980 mm per year with a 3-month dry season (< 100 mm month) from mid-August to mid-November. The landscape is characterised by a patchwork of low hills (100–300 m wide and 20–35 m high) separated by narrow streams. The soil type in this area is mostly Acrisol (WRB, 2022) and soil depth is restricted by a poorly draining, loamy saprolite, typically encountered at a depth of around 1 m (Epron et al., 2006). Sampling was carried out as part of the ALT-project (Amazonian Landscapes in
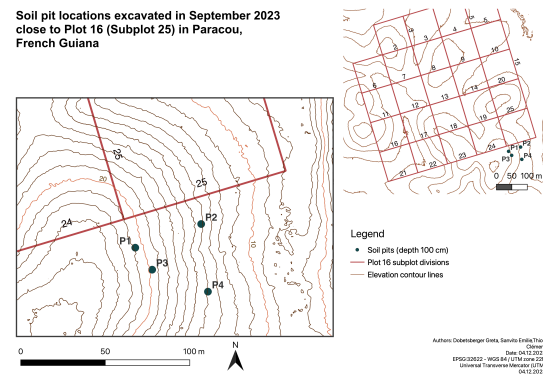

Figure 1. Study site and Pit locations at Paracou research station. P1-4 represent pit 1-4.

Transition 2022-2025).

2.2 Pit data collection

Pit excavation allows the collection of root distribution data (Freschet et al., 2021). Four pits were sampled between September 11 and 16, 2023, just outside of plot 16 (P16), next to the subplots 24-25 (Fig. 1), to avoid disturbances on inventoried trees.

We implemented a standardised experimental design, ensuring uniform topographical conditions for the soil pits. All pits were excavated at a mid-slope position with a consistent inclination of 17-18%, characterised by superficial lateral drainage. Potential pits were prospected using an auger in order to dig pits with maximum HSD variability. Based on (Epron et al., 2006) we expected the HSD to be between 60 cm and 80 cm deep. Rectangular pits, 100 cm deep and 50 cm wide, were dug with pickaxes and spades.

After cleaning the exposed soil surface in the pits by scraping, colour and texture changes were used to identify horizons (Appendix Fig. 8) on one side of the pit (Ferry et al., 2003). For each horizon, the depth was measured, mica content was visually estimated from 0 (mica absence) to 3 (high mica content), and soil samples were moistened to estimate the texture by touch (Jahn et al., 2006). We used the Jamagne et al. (1977) soil texture triangle. For two sides of the pit, we counted the roots using a 100 x 50 cm grid subdivided in squares of 10 x 10 cm (Freschet et al., 2021), to characterise RVD. In each square, roots were counted and classified by diameter (< 2 mm, 2-5 mm, 5-10 mm and 10 mm).

2.3 Auger and botanical data

In addition to our pit data, we used 36 auger samples collected during a 2022 data collection campaign on the P16 of Paracou, in the subplots 14, 15, 19 and 20 (Appendix Fig. 4). The auger samples were positioned with a spacing of 33 meters between each sampling point. In contrast to the pit data collection, root abundance was not sampled. For the complete auger collection method, we refer to **?**. The botanical data corresponds to the 2020 inventory of the GUYAFOR tree database, which monitors trees of Diameter at Breast Height (DBH) superior to 10 cm. In our study area, this data was completed with data from the ALT project, which also included trees of DBH > 1 cm.

2.4 Data analysis

2.4.1 Pit data analysis

We regrouped the soil textures into a categorial variable "silt content", identified using the texture triangle (Jamagne et al., 1977): low (A, Alo, AS), intermediate (SL, SA, S), and high (LSA, LAS, LS). We defined the depth (cm) at which the silt content changed to high for each pit, which we refer to as "high silt depth" (HSD). HSD is used to determine the depth of the drainage barrier, which is characterised by a silty texture (Ferry et al., 2003; Humbel, 1978). Given the small sample size (4 pits), we chose to only conduct visual analysis of HSD effect on RVD. As roots were counted per layer of 10 cm, and soil texture was determined per soil horizon, we assigned a texture class to every 10 cm layer of the soil.

In order to approximate root biomass, a root index was calculated by weighing each root count with its corresponding minimum diameter class and summing the totality weighted count. Using the minimum diameter leads to an underestimation of the total root biomass, although it remains valuable for pit comparison. $RI_d = \sum_{i=1}^{4} r_i n_i$, with d layer depth (cm), i index of the diameter class (< 2 mm, 2-5 mm, 5-10 mm and 10 mm), $r_i \in [1, 2, 5, 10]$ minimum root diameter, n_i count of root in diameter class i. The minimum root diameter of the first class (<2 mm) is set to 1 mm as we assume it is the smallest diameter detectable by bare eye.

We then assessed the relation between root index and silt content. Root index was compared between pits 2 and 3 at the depth of 50-70 cm. This depth range is where maximum HSD variation between two pits occurs. Fixing the depth accounts for the effect that root index decreases exponentially with depth. We calculated the decrease of root index in the selected depth range (total root index at 50-70 cm divided by total root index at 0-50 cm) for pits 2 and 3 and compared them.

2.4.2 Auger and botanical data analysis

Out of the 36 auger measurements available, we focused our analysis on the subset of 29 measurements that contained texture class data. The auger points were located using the coordinates of the closest inventoried tree on the plot. As for the pit data, soil textures in the pits were grouped into "high", "intermediate", and "low" silt content, and HSD was defined for each auger point following the same methodology as employed for the pit data. We defined the depth (cm) at which the silt content changed to high for each auger sample, which we refer to as "high silt depth" (HSD). HSD is used to indicate the depth of the drainage barrier, characterised by a silty texture (Ferry et al., 2003; Humbel, 1978). For auger points without any horizons high in silt, we defined HSD to be 100 cm, which is the maximum depth of the auger measurements. As topography, besides drainage type, strongly influences forest community structure (Baldeck et al., 2013; Ferry et al., 2010) and can be correlated with soil texture and drainage (Epron et al., 2006), we did a correlation test (Spearman method due to non-normality of HSD) between elevation (m) and HSD (cm).

We mapped the area where auger samples were taken and created contour lines based on the values of HSD of the different auger points (Appendix Fig. 4). The contour lines were created with the Contour Plugin in QGIS. We employed 10 cm contour line intervals, resulting in the formation of seven distinct HSD classes, from 40 cm to 100 cm deep. With this approach, we interpolated HSD values spatially across nearly the entire 4 ha study area. Every tree on the map could therefore be linked to a certain HSD class and the corresponding coverage area (m^2) of each HSD class was also determined.

Only slopes were considered during further analysis. Topographical data comes from (Dourdain et al., 2022), which defines slope as the zone with a slope > 25 % and the absence of a permanent water table, no deeper than 1 m in the middle of the dry season. For each HSD class species richness was extracted from the botanical

data by counting the number of species present in the area. The total number of trees was extracted by counting the number of trees present in the area. Due to the ordinal nature of the different HSD classes, they cannot be considered as a categorical variable. Hence, we assigned a specific intermediate HSD value to each HSD class. For example, an HSD class from 40 cm to 50 cm was designated the value of 45 cm. This creates a continuous HSD-value, allowing us to perform a Poisson regression for both species richness and number of trees (HSD continuous values as predictor, species richness or number of trees as response). The areas covered by a specific HSD class varied between 1015 m^2 (HSD 40-50 cm) and 5494 m^2 (HSD 90-100 cm), with the total area considered being 21055 m^2. To take into account that some HSD classes cover a larger area than others, offset is set to logarithm of area per HSD class in the model. This way the number of trees and species richness per area are modelled. The relationship between DBH (cm) and HSD (cm) did not show linear dependency (Fig. 3c), making it difficult to construct a precise model.

Muscovite (white mica) degrades into kaolinite (Nicolini et al., 2009) with a particle size classified as silts. Thus, to complement our detection of the drainage barrier, we try to use mica content as a complementary indicator of silt content. A chi-squared test was done to quantitatively assess the association between silt content (categorical variable) and mica content (categorical variable) in the different horizons of the auger data. Cramer's V was calculated to indicate the strength and direction of the association. We tried to replace silt content by mica content for the pit data analysis, and verified whether the results were similar.

All analyses were performed in R (version 4.2.2) (R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/) and QGIS (version 3.28 Firenze).

3. Results

3.1 Pit data
HSD ranges across the pits, spanning from 50 cm to 70 cm (Fig. 2a). In contrast to our expectations, the four pits show similar root index variations with depth, regardless the variation in silt content. Fig. 2b shows a general decrease of root index with depth, from 60 roots at a depth of 10 cm to 10 roots at 50 cm. Focussing on the specific depth range of 50-70 cm, it becomes evident that the root index of P3 (pit 3) does not exceed that of P2 (pit 2), even though P3 shows high silt content and P2 intermediate silt content. The ratio of root index in the focus range (50-70 cm) (Fig. 2a) and root index in the depth range above (0-50 cm) between P2 and P3 also showed no difference (0.137 for P2 and 0.142 for P3).

3.2 Mica as an indicator for silt
The chi-squared test assessing the association between silt and mica content in the auger samples was highly significant ($x^2 = 57.154$, p-value < 0.001). Cramer's V, assessing the strength and direction of the association, was 0.58, supporting a strong positive relationship. The association is depicted in a mosaic plot in Appendix Fig. 5, illustrating an increase of silt content with rising mica content. By replacing mica content with silt content in the pit data analysis where the relation between root index and silt content are assessed, we found a similar result (Appendix Fig. 7).

3.3 Auger data
A significant but small decrease (p-value = 0.00245; Estimate = -0.0044) in species richness with HSD class was detected. Among all HSD classes, the range of 40 to 50 cm stands out with notably higher species richness per ha (Fig. 3a). This range contains the uppermost observed HSD. Species richness per ha is lowest for the 90 cm to 100 cm HSD range. For HSD class "No high silt" species richness was higher than for the HSD classes 70-100 cm. Tree density significantly decreases with HSD class (p-value $< 2e-16$; Estimate = -0.013), although Fig. 3b shows that the tree density first increases between HSD 40 cm to 70 cm. Tree density increases a little when the HSD is not detected, the lowest tree density being present at HSD 90 cm to 100 cm range.

Fig. 3c and 3d illustrate the relationship between the DBH and HSD classes. The mean DBH values and quantiles are very similar over all classes (mean = 4.9 cm), primarily due to the high representation of trees with small diameter (minimum diameter count > 1 cm). A pattern is visible in the maximum values of the outliers, representing trees with a DBH > 50 cm, which increases with HSD class.

A significant negative correlation was found between elevation (m) and HSD (cm) (rho = -
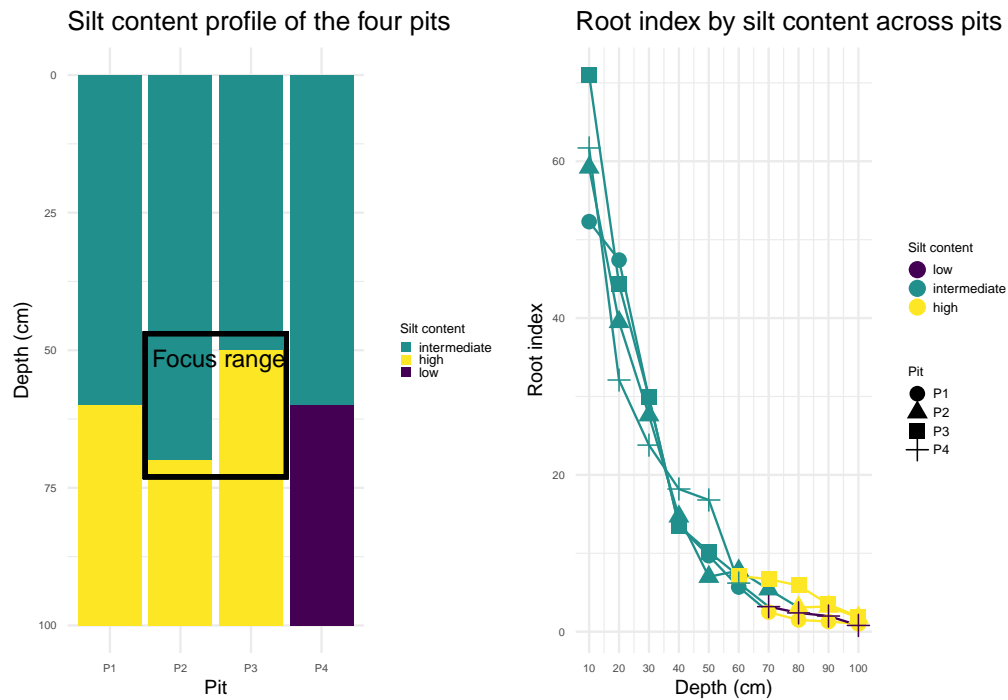
Figure 2. a) Silt content (low, intermediate, high) and b) root index, calculated by weighing each root count with its corresponding maximum diameter class, per layer of 10 cm across pits excavated in September 2023. P1-4 correspond to pits 1-4.
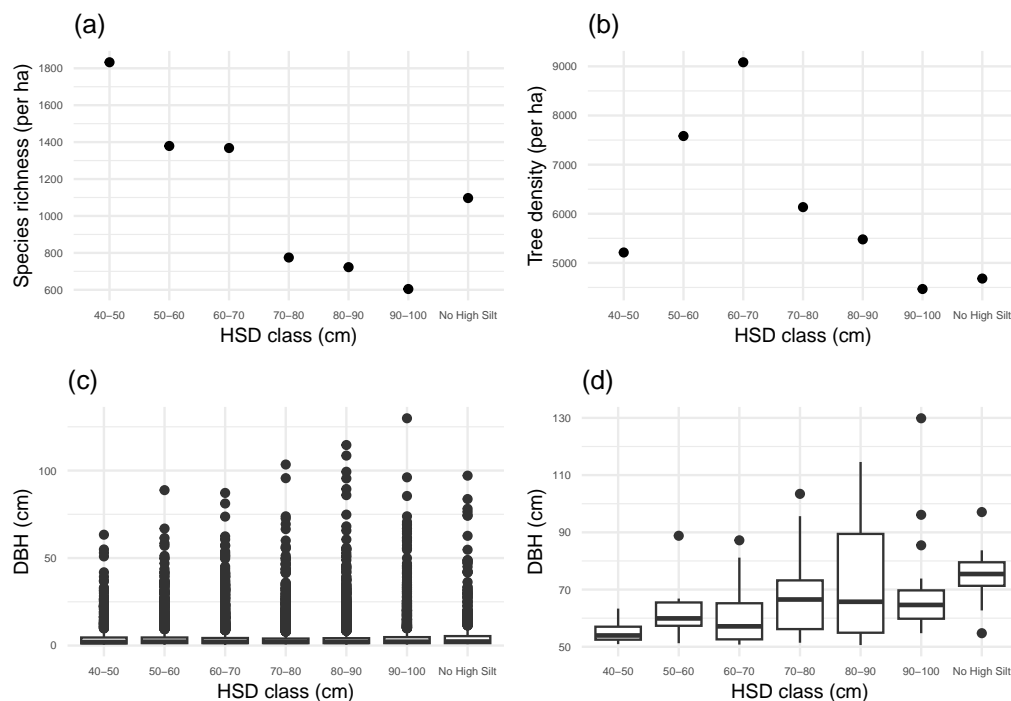

Figure 3. Forest structure indicators relation with HSD (high silt depth) class (cm). a) Species richness (per ha) in function of HSD classes, b) Tree density (per ha) in function of HSD classes, c) DBH (diameter at breast height in cm) in function of HSD classes, d) DBH filtered (max value = 50 cm) in function of HSD classes

0.634; p-value = 0.0002246). A higher position along the topographical gradient therefore indicates lower HSD.

4. Discussion

4.1 Root distribution with HSD and depth

Our findings on RVD align with the literature, illustrating that most roots are present within the first 30 cm of the soil (Freschet et al., 2021; Schenk and Jackson, 2002). HSD ranges across the pits, spanning from 50 cm to 70 cm (Fig. 2a), coincides with the depth range (60-80 cm) of the drainage barrier identified by Epron et al. (2006). This strengthens our choice to use of HSD as an estimator of the drainage barrier depth.

We expected that the drainage barrier restricts roots, and therefore to find less roots below the HSD, as was observed by Humbel (1978). However, there is no visually discernible effect of HSD on vertical root distribution (Fig. 2b), no matter the root diameter (Appendix Fig. 6). The absence of an HSD effect might be because roots of certain species can penetrate the drainage barrier, which suggests a deeper water uptake and therefore higher drought resistance (Ferry et al., 2003). The absence of an observed effect may also be due to the small HSD variation between the sampled pits (maximum variation of 20 cm). Additionally, the small sample size of 4 pits precluded the performance of a statistical test. More soil pits would be needed to study root distribution in additional soil profiles.

4.2 Mica-silt correlation

Our findings indicate a strong association between silt and mica content. Given that mica is shiny and easily detectable, identifying HSD by high mica content instead of high silt content might simplify and expedite the data collection process. This approach may offer a more efficient means of assessing drainage barrier depth in Paracou.

4.3 Forest structure indicators with HSD

Species richness decreases when HSD increases (Fig. 3a). Sabatier et al. (1997) found higher species richness on soils with a thinner permeable soil layer. This indicates a higher species richness on SLD, which present on slopes. Allié et al. (2015) confirmed that the species richness is the highest on mid-slope. As HSD is negatively correlated with topography, an increase in HSD indicates a decrease in elevation (more downslope),

and therefore explains the decrease in species richness. The decrease in drought stress with increasing HSD might also explain this declining trend in species richness (Sabatier et al., 1997). The estimate (-0.0044) indicates that the detected significant decrease is relatively small. It is likely that a difference in HSD of 60 cm has a minor effect on species richness.

Tree density varies with DBH, with lower tree density in areas with high DBH. Since the mean DBH remains consistent across the different HSD classes (Fig. 3c), we can compare our tree densities between the different HSD classes. We found that tree density is higher when the drainage barrier is closer to the surface. This result contradicts Sabatier et al. (1997) who found no effect of drainage type, and therefore SLD, on tree density. This contradiction may result from the small minimum diameter count used in our botanical data (>1 cm) compared with Sabatier et al. (1997) who considered only trees with DBH >10 cm. Trees of small diameter which might benefit from the presence of a drainage barrier, as it retains water closer to the surface, making it more accessible for their roots. If the drainage barrier is too high, this might increase stress for small tree roots during the rainy season (anoxic stress), explaining the highest densities at intermediate drainage barrier depth (HSD) (Fig 3b). Moreover, the varying species composition across different HSD classes and their adaptability to soil constraints and water availability may contribute to the observed differences in tree density between different HSD classes.

While the mean DBH remains consistent across the different HSD classes, a pattern can be observed in the outliners (Fig. 3c). Trees of DBH >50 cm increase in DBH with increasing HSD class (Fig. 3d). This result suggests that the drainage barrier affects trees throughout their lifespan and becomes only visible in trees with higher diameter. Therefore, deeper HSD contributes to higher diameter growth when the drainage barrier is deeper in the soil.

We observed a robust negative correlation (rho = -0.634) in our data between elevation and HSD . As elevation increases, the depth of the restricting layer decreases. This finding contradicts Epron et al. (2006) discovery of deeper drainage barriers at higher elevations. The difference in results can be attributed to the differences in the elevation range considered. Epron et al.

(2006) solely focused on the depth of drainage barriers on slopes, whereas our correlation test encompassed hilltops and bottomlands. In our study, the maximum elevation difference between two auger points was 12 m, going from 8 m to 20 m. Fewer auger points were situated on hilltops (Appendix Fig. 4) which skews our data towards an elevation range predominantly covering a topographic gradient from slopes to bottomlands. Knowing that SLD is typically present on slopes (Fan et al., 2017; Pélissier et al., 2002), the impermeable silty texture horizon likely disappears towards the bottomlands (Boulet et al., 1982), which accounts for the observed decrease in HSD with elevation. The correlation between topography and drainage type makes it difficult to distinguish the drainage barrier effect on community structure from other effects associated with topography, like nutrient content (Peguero et al., 2023; Van Langenhove, 2020).

Caution is necessary when interpreting these results. Firstly, we chose to use only seven classes to keep significant HSD variation, thus with only one value per class the tests rely on seven values only. Secondly, HSD was spatially extrapolated over 4 ha based on auger measurements distanced 33 m from each other. Diverse soil textures and soil profiles can be found within a short geographical distance, which was also observed with our pits. Microtopography is known to influence forest structure (Schwartz et al., 2020). To improve our study design, an autocorrelation test for short distance HSD measurements could have been valuable to determine the maximum extrapolation distance of HSD. This would allow a more precise connection between botanical data and HSD values.

With our study, we showed that tree-soil interactions are highly relevant and influence tree community structure. By exploring the connections between superficial lateral drainage on slopes, forest structure indicators and root density, we provide insights on how the depth of a drainage barrier might affect forest communities in French Guiana. For pits sampled next to the P16 in Paracou 2023, no effect of drainage barrier on root vertical distribution has been found. Species richness decreases and maximum DBH increases when the drainage barrier occurs deeper in the soil, complementing earlier findings regarding drainage type effects. For smaller diameters, no difference in DBH for
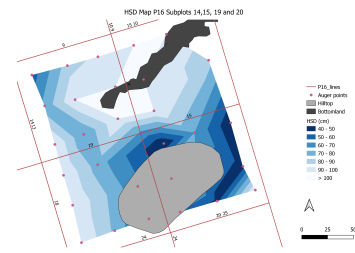

Figure 4. HSD contour line map of subplots 14, 15, 19 and 20 of the P16.

the different HSD classes was observed. Tree density was higher for intermediate HSD classes (50-70 cm), allowing young trees to profit from superficial water tables. Sample size for this study was small, especially for the soil pits, and analyses were possible only to a limited extent. Despite these limitations, this study provides lead information on drainage barriers and their effect in Paracou. Further studies on a larger scale are needed to gain a clearer picture of how soil structural constraints affect roots and forest structure in Amazonia.

5. Acknowledgements

6. Appendix

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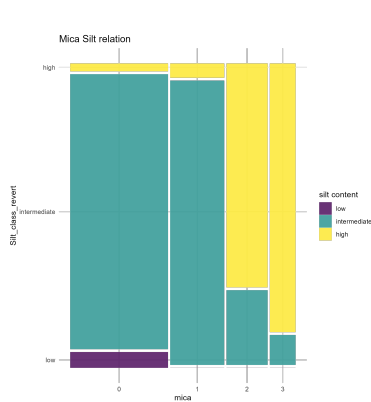
Figure 5. Mosaic plot displaying the relationship between mica and silt content. Dark grey represents high silt content, grey represents moderate silt content, and light grey signifies low silt content. Mica content ranges from 0 to 3, denoting low (0) to high (3) levels.
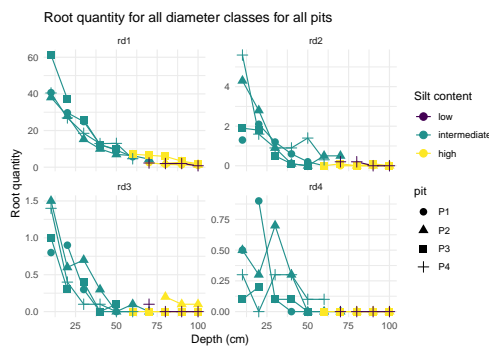

Figure 6. Root quantity for all diameter classes for all pits. rd1, rd2, rd3, rd4 correspond respectively with diameter classes of < 2 mm, 2-5 mm, 5-10 mm and 10 mm. For silt content, hight is LSA or LAS, intermediate is SL or SA, and low is AS or A.
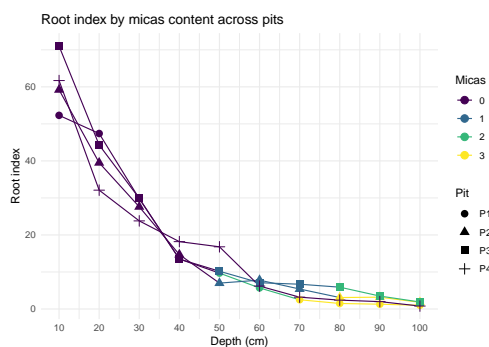

Figure 7. Root index across soil depths in different pits, considering varying levels of mica content ranging from low (0) to high (3).
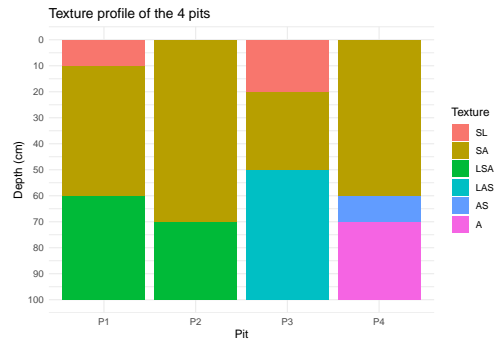

Figure 8. Soil texture profiles of the four pits.

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