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Impact of superficial lateral drainage on tree root distribution and forest community structure in French Guiana

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Abstract
This study investigates the impact of drainage barriers on tree root distribution and forest structure in Paracou, French Guiana. Using the depth at which a horizon high in silt (HSD, high silt depth) occurs as a proxy for drainage barrier, the study explores the relationship between drainage barriers, topography, and forest community structure. Despite expectations of reduced root density in soil horizons with high silt content, no significant reduction of root density was found. Species richness and tree density showed a slight but significant decrease with increasing HSD, while diameter at breast height (DBH) exhibited minimal variation. The strong association between silt and mica content suggests the potential use of mica as a practical proxy for silt in future studies, streamlining data collection. These findings contribute valuable insights into the complexity of soil-root interactions in tropical ecosystems. 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

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1. Introduction

In tropical ecology, the relationship between root distribution and soil abiotic factors is crucial to forest community structure (Schlesinger, 1991; 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 a 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 drainage barriers restrict 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 Transition 2022-2025).

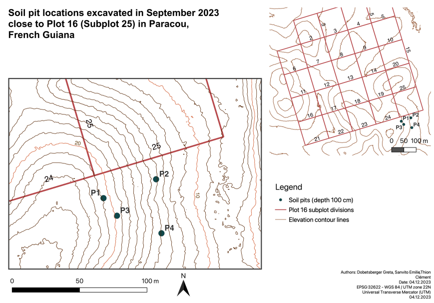

Figure 1. Study site and Pit locations at Paracou research station. P1-4 represent pit 1-4.

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, next to the subplots 24-25 (Fig. 1), to avoid disturbances on inventoried trees.

We implemented a standardized 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%, characterized 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 C Fig. @ref(fig:pitPlot_TextureProfile)) on one side of the pit (Ferry et al., 2003). For each horizon, the depth was measured, mica content was visually estimated from 0 (no mica) to 3 (high mica content), and soil samples were moistened to estimate the texture by touch (Jahn et al., 2006). We used 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 A, 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 Dogny Piette and Corbera Serrajordia (Dogny Piette and Corbera Serrajordia). 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 causes leadsus to an underestimation ofe the total root biomass but although it remains valuable is still useful for pit comparison. $RI_d = \sum_{i=1}^{4} r_i n_i$, with d the layer depth (cm), i the indice of the diameter class (< 2 mm, 2-5 mm, 5-10 mm and 10 mm), $r_i \in [1, 2, 5, 10]$ the minimum root diameter, n_i the count of root in diameter class i. The minimum root diameter of the first class (<2mm) is set to 1mm 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, 2002; 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, 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 A 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 (m2) of each HSD class was also determined. Only slopes were considered during further analysis. Topographical data comes from Dourdain (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 m2 (HSD 40-50 cm) and 5494 m2 (HSD 90-100 cm), with the total area considered being 21055 m2 . To take into account that some HSD classes cover a bigger 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 and 3d), 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

In contrast to our expectations, the four pits show similar root index variations with depth, regardless the variation in silt content. Focussing on the specific depth range of 60-80 cm, it becomes evident that P3 (pit 3) root index exceeds that of P2 (pit 2), even though P3 shows high silt content and P2 intermediate silt content. A similar observation is made when using mica content as a proxy of silt content. Figure 1b shows a general decrease of root index with depth, from 60 roots at a depth of 10 cm to 10 roots at 50 cm.

3.2 Auger data

A significant negative correlation was found between elevation (m) and HSD (cm) (rho = - 0,634; p-value = 0.0002246). A higher position along the topographical gradient therefore indicates lower HSD.

Among all HSD classes, the range of 40 to 50 cm stands out with notably higher species richness. This range contains the uppermost observed HSD. A significant but small decrease (p-value = 0.00245; Estimate = -0.0044) in species richness with HSD class can be observed (see Fig. 2a). Species rich-

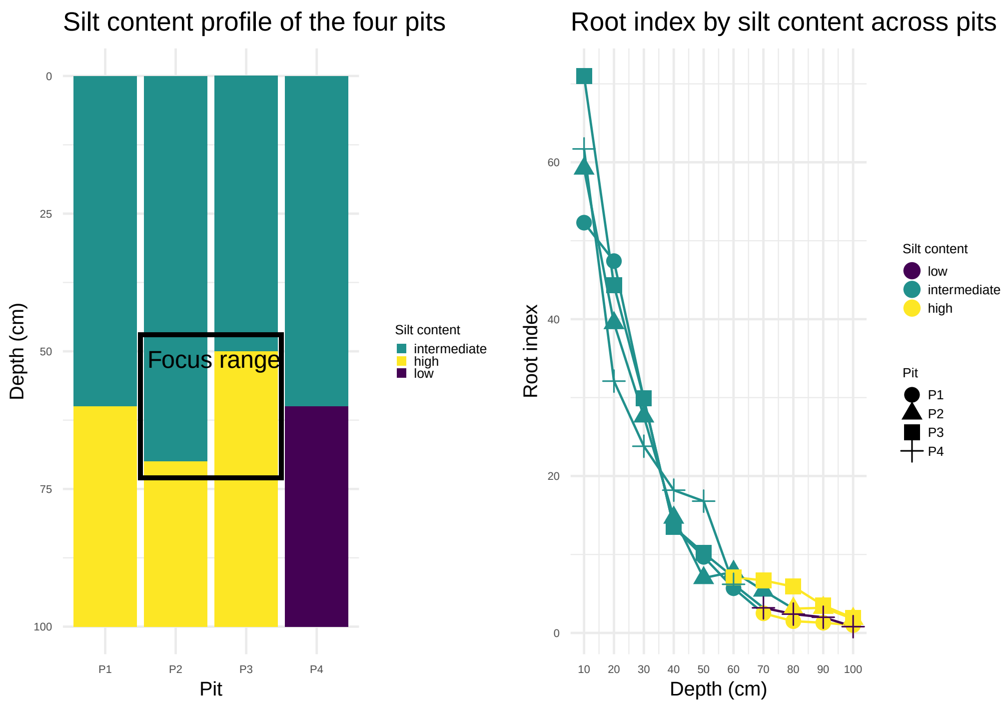

Figure 2. a) Silt content and b) root index across pits excavated in September 2023. F1-4 correspond to pits 1-4.

ness and tree density is lowest for the 90 to 100 cm HSD range. For areas with no horizon high in silt, species richness was higher than for the HSD classes 70-100 cm, but lower than for horizons where silt appears closer to the surface. Tree density also significantly decreases with HSD class (p-value $<$ 2e-16; Estimate = -0.013), although there is still an increase visible for the first HSD classes in the plot (see Fig. 2b). Samples without horizons high in silt show very low tree density of less than 5000 trees per ha. Fig. 2c and 2d illustrate the relationship between the DBH and HSD classes. The mean DBH values and quantiles are very similar over all classes, only a small pattern is visible in the maximum value of the outliers, which increases with the HSD class.

Figure 2 Forest structure indicators relation with HSD (high silt depth) class. 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 function of HSD classes, d) DBH filtered (max value = 10 cm) in function of HSD classes

3.3 Mica as a proxy for silt

The chi-squared test assessing the association between silt and mica content in the auger samples was highly significant (^{2} = 49.994, df = 6, p = 4.715e-09). Cramer's V was 0.574, supporting a strong positive association. The Kruskal-Wallis showed a similar significance (^{2} = 39.456, df = 2, p = 2.706e-09) and a Kruskal's (x,y)= 0.561, 0.231, which also confirms a strong association. The association is depicted in a mosaic plot in Appendix 2 (Fig. 1). illustrating an increase of silt content with rising mica content.

4. Discussion

4.1 Root distribution with HSD and depth

Our findings align with literature, illustrating that most roots are present within the first 30 cm of the soil (Freshet, 2021; Schenk and Jackson, 2002). HSD range across the pits, spanning from 50 cm to 70 cm (Fig. 1a), coincides with the depth range (60-80 cm) of the drainage barrier identified by Epron et al. (2006).

We expected the HSD to act as a barrier for roots, and therefore to find less roots

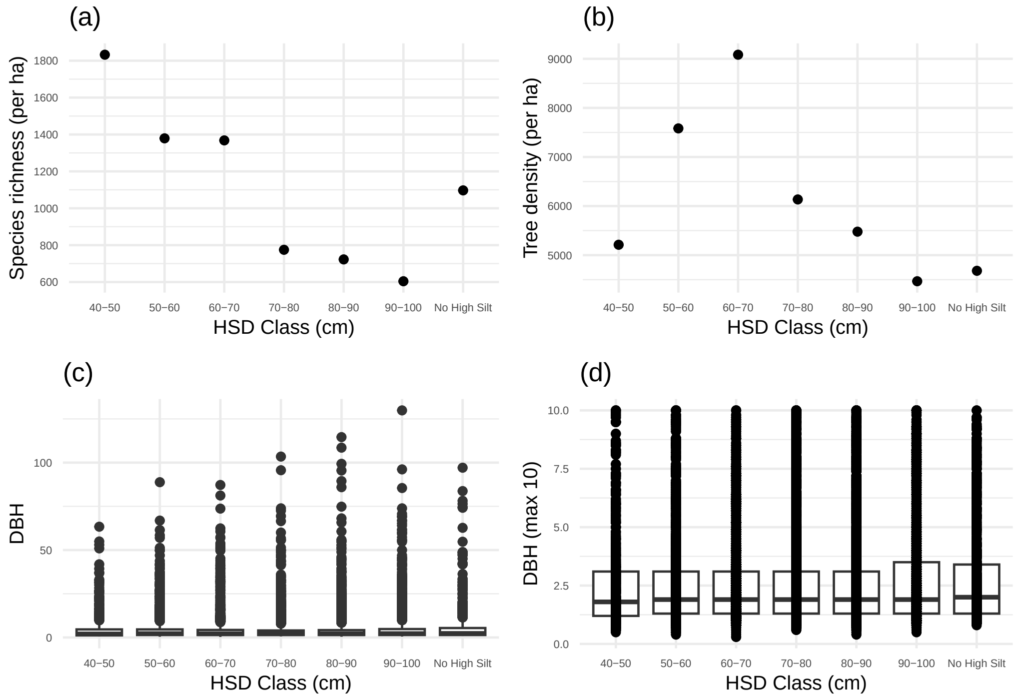

Figure 3. Forest structure indicators relation with HSD (high silt depth) class. a) Species richness (per ha) in function of HSD classes, b) Tree density (per ha) in function of HSD classes, c) DBH (diameter at breast height) in function of HSD classes, d) DBH filtered (max value = 10 cm) in function of HSD classes

below the HSD, as was observed by Humbel (1978). However, there is no discernible effect of HSD on the vertical root distribution (Fig. 1b), no matter the root diameter observed (Appendix 2 Fig. 2). Roots of certain species can penetrate the drainage barrier and might be adapted to the drought constraints this can pose (Ferry, 2003). The absence of an observed effect may also be due to the narrow depth range of 20 cm, within which the two pits exhibited differences in silt content. Additionally, the restricted 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. However, soil pit profiles are a very time-consuming and destructive method, despite the essential insights they provide for root and soil analysis.

4.2 Predicting forest structure indicators with HSD

No linear dependency was found between HSD and DBH measurements (Fig. 2c). The mean DBH values appear consistent over all HSD classes (Fig. 2d). A trend can be observed in the outliers per class, where the maximum DBH value increases with HSD class. This observation might indicate that trees can achieve a larger DBH in soils with fewer drainage restrictions. As DBH did not vary significantly between different HSD classes, tree density variation indirectly indicates variations in basal area. We found a significant negative effect of HSD on density, with a maximum tree density per ha observed at a medium HSD between 60 and 70 cm. This indicates that as the drainage barrier is closer to the surface, tree density is higher. Sabatier (1998) found no effect of drainage type, and therefore no effect of the appearance of HSD, on tree density. But they only looked at trees with a DBH > 10 cm, in contrast to this study (DBH > 1 cm). Tree density increases significantly by considering also smaller trees. Therefore, considering smaller trees might show that in that case there is an effect of HSD on tree density. Small trees can benefit from the drainage barrier, as the barrier prevents water from "percolating?"

deep into the soil, making it easier for them to take up water. Bigger trees have deeper roots and therefore might not be affected by the HSD, as seen in Sabatier (1998). 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 densities between different HSD classes. Species richness also decreases with HSD class (Fig. 2a). This trend is confirmed by Sabatier (1998), who found that there are more species present on soils with SLD. We observed a robust correlation (rho = - 0,634) in our data between elevation and HSD, which is similar with the study of Epron (2006) on the same research station. As elevation increases, the depth of the restricting layer also increases. This is not surprising, as the drainage barrier defines the drainage type, and topography and drainage type are strongly linked (Allié et al., 2015). This can also help to explain the decreasing trend of species richness with HSD as Allié et al. (2015) showed that species richness is higher in mid-slope positions. This correlation makes it difficult to distinguish drainage barrier effect on community structure from other effects associated with the topography, like the nutrient content (source) or the inclination. The study of drainage barrier depth variation may contribute to the study of forest structuration as it characterises microenvironment, particularly for the response to drought (Schwartz, 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 test relies 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. 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 linkage between botanical data and HSD values.

4.3 Mica-silt correlation

Our findings indicate a strong association between silt and mica content. Therefore, we can deduct that with high silt content we have a high mica content. Given the easy to detect micas due to their shiny nature, defining the HSD by looking at high mica content instead of high silt might simplify and expedite the data collection process. This approach may offer a more efficient means of assessing drainage barrier depth in Paracou.

With our study, we showed that soil-root 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 hope to/try to/provided? provide insights on how drainage barriers might affect forest communities (in Paracou). However, further studies on a larger scale are needed to gain a clearer picture of how Amazonian forests will develop in the future (are we allowed to say this, although ALT is already trying to do that?).

5. Appendix

Le temps passe et la mort approche.

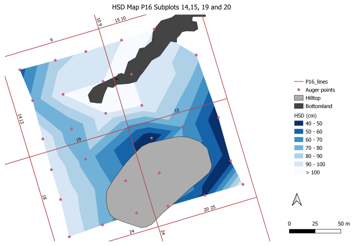

Figure 4. HSD contour line map of subplots 14, 15, 19 and 20 of the P16.

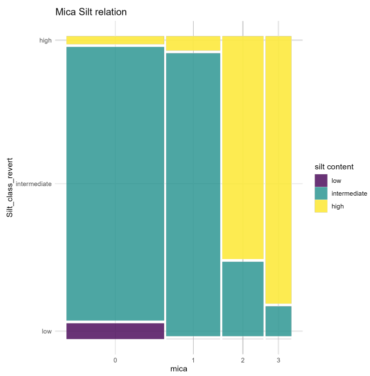

Figure 5. Mosaic plot displaying the relationship between mica and silt content. Dark grey represents high silt content, grey represents moderate silt content, and light grey signifies low silt content. Mica content ranges from 0 to 3, denoting low (0) to high (3) levels.

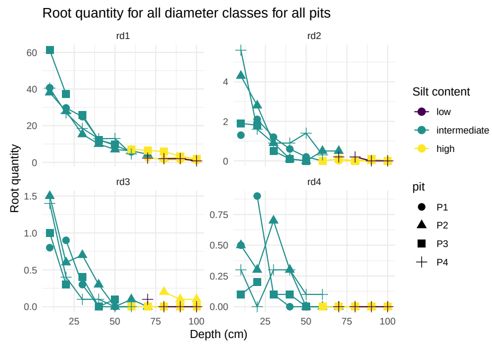

Figure 6. Root quantity for all diameter classes for all pits. rd1, rd2, rd3, rd4 correspond respectively with diameter classes of < 2 mm, 2-5 mm, 5-10 mm and 10 mm. For silt content, hight is LSA or LAS, intermediate is SL or SA, and low is AS or A.

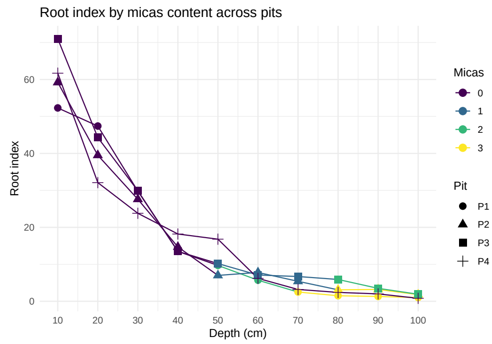

Figure 7. Root index across soil depths in different pits, considering varying levels of mica content ranging from low (0) to high (3).

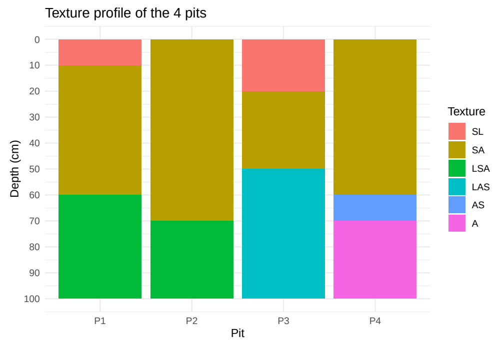

Figure 8. Soil texture profiles of the four pits.

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