



# Lagging Response of Belowground Functional Traits to Environmental Cues in a Mature Amazonian Tropical Rainforest

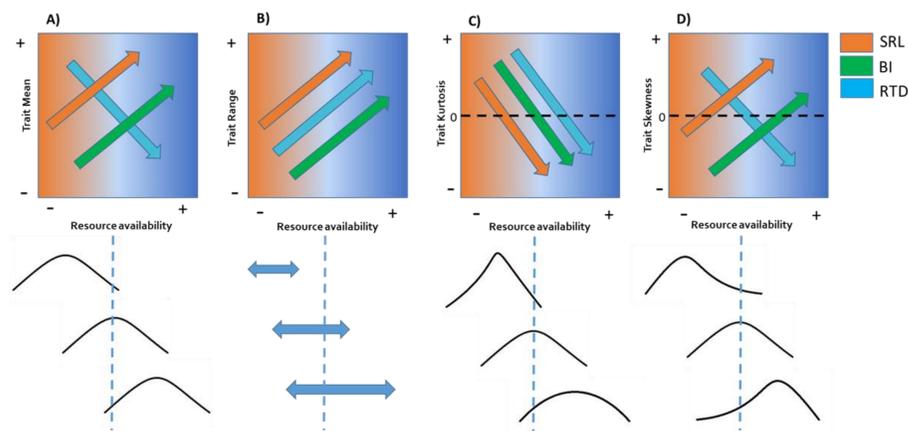
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## INTRODUCTION

The stress-dominance hypothesis (SDH) is a model of community assembly predicting that the relative importance of environmental filtering increases and competition decreases along a gradient of increasing environmental stress. Therefore, communities adapted to stressful environmental conditions exhibit lower trait diversity and the distribution is skewed to traits that reflect stress tolerance. In contrast, in more benign conditions the influence of biotic interactions is more important, increasing trait diversity and the evenness of traits within communities (Hille et al 2012). Previous research focused mostly on aboveground measurements showed that trait dispersion remains constant despite decreases in fertility, suggesting that trait competition does not decrease with resource scarcity (Coyle et al 2014). However, competition belowground is considered more even and intense than aboveground due to the symmetric access to resources for all individuals and the fast response of root systems to resource pulses (Cahill & Casper 2000, Valverde-Barrantes et al 2015, Chen et al 2016). The acute limitation in nutrients and rain seasonality in the Amazon basin could imply strong morphological responses belowground for nutrient competition with the onset of the rainy season. Nonetheless, few studies have monitored the morphological changes in the root community of tropical forest over time, limiting our understanding of the ways trees compete for nutrients in tropical forests.

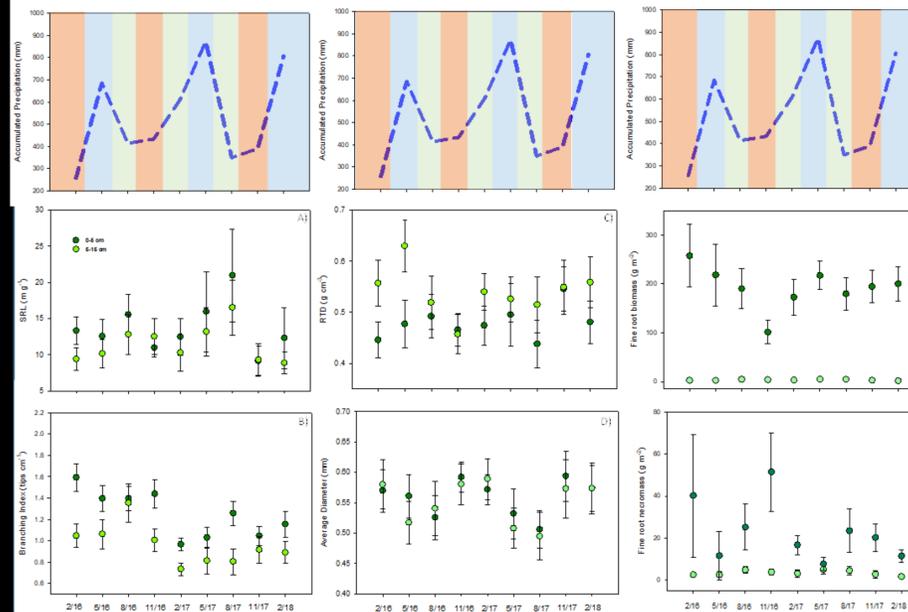
**This study is a first attempt to understand phenological changes in the morphological appearance of fine roots in a mature tropical forest. We expected a synchronous response between resource pulses and shifts in functional traits with mean values for traits associated with acquisition capabilities (SRL, diameter and tip abundance) will increase as environmental conditions (i.e. soil moisture) became less stressful for the community, whereas tissue investment (root tissue density, RTD) would do the opposite. Moreover, we expect an increase in the range and evenness of functional trait diversity with moisture conditions, and a positive association between range and evenness with a shift of the community to more acquisitive traits.**



**Fig 1.** Expected shifts in root community trait values along temporal changes in resource availability under the stress-dominance hypothesis (SDH).

## METHODS

The study in a tropical forest was carried out in the Cuieiras Reserve at ZF2, ca. 60 km north of Manaus, Amazonas, Brazil (latitude S 2 ° 35'40", longitude W 60 ° 12'28"). For the studied period, there was an increase in precipitation from March to May 2016 and January to May 2017, and dry periods from September to December 2016 and from July to November 2017, which is typical of the rain seasonality in the area (Fig 2, Cordeiro et al 2020). Soils were sampled repeatedly from 18 locations along a 500 m transect between February 2016 to February 2018 in three-monthly collections, adding up to a total of nine soil collections. On average 7±2 root systems per core (for a total of 1295 individual root systems) were scanned and weighted to calculate changes over time on specific root length (SRL), root tissue density (RTD), average diameter, specific root tip abundance (SRTA), and branching intensity (BI, Fig 2) at the community level. We also estimated root biomass and necromass over time.



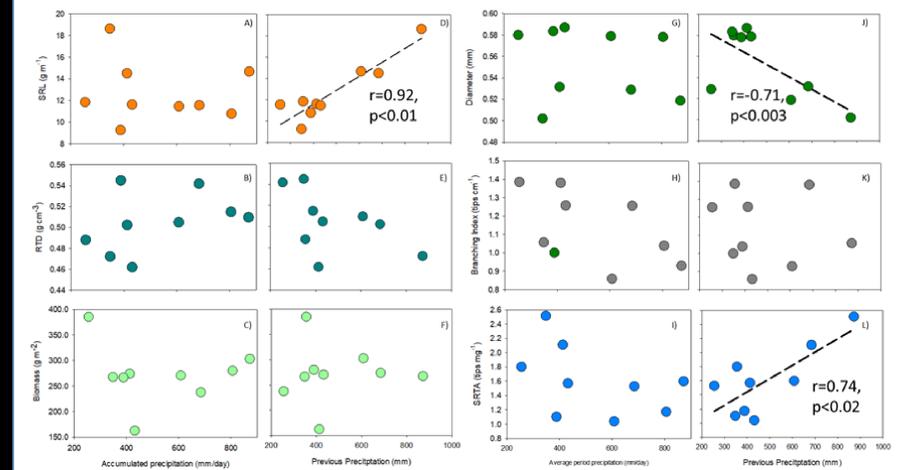
**Fig. 2.** Temporal changes in functional root traits compared to rainfall seasonality at two different depths (0-5 and 5-15 cm deep). Upper panels describe changes in precipitation over time, with orange lines representing the onset of the dry season, blue lines represent the onset of the wet season. Bars represent 95% CI.

## RESULTS

Factor	Biomass (g/m <sup>2</sup> )	SRL (m/g)	Diameter (mm)	RTD (g/cm <sup>3</sup> )	SRTA (tips/mg)	Branch Index (tips/cm)
Date	9.78***	5.76***	6.43***	2.32*	6.34***	10.89***
Feb-2016/Feb-2018	(13.1)	(13.7)	(14.1)	(5.48)	(12.9)	(17.6)
Depth (0-5/5-15 cm)	205.58***	8.01***	0.87	18.84***	35.89***	84.75***
	(34.4)	(2.4)	(NS)	(5.58)	(9.13)	(16.60)
Date * Depth	1.62	0.62	0.48	1.03	0.77	1.56
	(NS)	(NS)	(NS)	(NS)	(NS)	(NS)

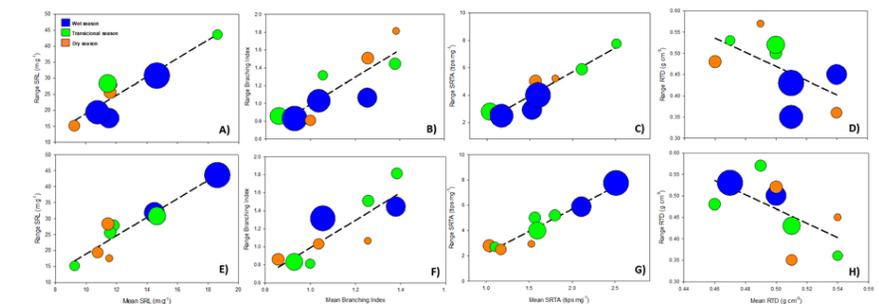
We found a substantial seasonality in root biomass and morphological change over time.

## Effect of precipitation on mean values of root morphology



Morphological traits associated with acquisition were positively associated with rainfall patterns. However, the association was significant for rain events of the previous trimester.

## Shifts in root trait mean and range community variation as a function of precipitation



Community range of traits associated with acquisition were positively associated with the mean values, whereas traits associated with stress tolerance showed a negative correlation. Variation in traits for SRL and SRTA were more strongly associated with precipitation of the previous trimester (lower panels) than the immediate precipitation at the time of sampling (upper panels).

## CONCLUSION

Our study confirms a dynamic interaction between rain patterns and root morphological changes in the tree community of a mature tropical forest in Central Amazon. Besides the expected differences in morphology between the organic and mineral horizons in the soil, we found significant morphological variations over time, unrelated to changes in root biomass. As predicted, these changes showed a correlation between resource availability and acquisition strategies, with roots showing higher acquisition capabilities and higher divergence with increases in moisture. However, these changes appeared after several months of the rainy season onset, suggesting a delay between the cue and the community response.