



## Do legumes and non-legumes tree species affect soil properties in unmanaged forests and plantations in Costa Rican dry forests?

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### ABSTRACT

Legume tree species, which are abundant in tropical dry forests, may be a critical regulator of soil nutrient dynamics because of their high foliar nitrogen (N) and potential for symbiotic N fixation. We investigated whether three legume tree species (*Acosmium panamense*, *Dalbergia retusa*, and *Gliricidia sepium*) have distinct soil chemistry under their crowns compared to nearby non-legume species (*Rehdera trinervis*, *Swietenia macrophylla*, and *Quercus oleoides*) when grown in two habitats: a diverse secondary forest or in 18-yr old monoculture plantations in northwestern Costa Rica. We quantified soil moisture, pH, labile carbon (C), inorganic N (NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>), net N mineralization rates, total C and N, δ<sup>15</sup>N signature and enzyme activity. We predicted that legumes would have higher soil nutrient availability under their crowns, but that this effect would be more pronounced in plantations, where tree species diversity is low. In the forest, soils under *Dalbergia* had the highest values of total C and N, and extractable nitrate, whereas soils under *Acosmium* the highest N mineralization rates. The activity of acid phosphatase enzymes varied among the soils under different species in both habitats, with the highest activity in the soils under the legume *Acosmium* at the forest site. In the plantations, *Acosmium* had the highest values for total soil C and N, labile C, and potential N mineralization rates. We conclude that 1) the legume species did not have consistent effects as a functional group, possibly due to different amounts of nodulation in individuals within species, and 2) as hypothesized, the magnitude of the species effect was more pronounced in the plantations than in the diverse secondary forest.

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### 1. Introduction

Variation in nutrient pools in above- and below-ground litter from different tree species helps determine nutrient availability in the soil, as well as the quality of the substrate for soil microbes (Hobbie, 1996; Rhoades, 1997; Ushio et al., 2010), and can contribute to species generated soil heterogeneity (Zinke, 1962). In turn, the existence of plant-generated soil heterogeneity, or patches of distinct soil conditions beneath tree canopies, can impact nutrient fluxes into, out of, and within ecosystems (Rhoades, 1997). In their review, Hutchings et al. (2003) predicted that heterogeneous conditions in the soil change competitive processes and their outcome, with greater competition in nutrient-rich patches and less diversity as fast-growing species eliminate slow-growing species, compared to nutrient-poor patches. Nutrient-rich and nutrient-poor soil patches are important in determining local and

regional nutrient reserves and thus can potentially affect species composition at the community level (Rhoades, 1997; Binkley and Giardina, 1998; Hutchings et al., 2003; Vivanco and Austin, 2008).

Individual trees are known to influence soil physicochemical properties, creating a zone of influence under the tree canopy (Zinke, 1962). These “species effects” have been extensively studied in comparatively low-diversity systems such as temperate forests or tropical plantations, where different tree species have significant impacts on soil properties (e.g. pH, exchangeable cations, water content), on substrate quality for microbes (e.g. total C, N and P concentrations, and C:N ratio), and on nutrient availability (N mineralization, organic P concentration) (Hobbie, 1992; Finzi et al., 1998a,b). One common mechanism invoked to account for these effects is the amount of nutrients recycled in each species’ leaf litter, which in turn is affected by leaf nutrient concentration, the degree of nutrient resorption prior to leaf abscission, litterfall mass, or even by nutrients captured by tree canopies (McClougherty et al., 1985; Rhoades, 1997; Binkley and Giardina, 1998).

Legumes (Fabaceae, Leguminosae) are a good test case for individual species effects on tropical soils as they are potential

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regulators of ecosystem nutrient dynamics (Fisher, 1995; Franco and De Faria, 1997; Wang et al., 2010). Legumes are the most diverse and widespread group of plants with the capacity of N<sub>2</sub> fixation (Sprent, 1995; Sprent and Parsons, 2000), and are particularly abundant in tropical dry forests (Gentry, 1995; Gillespie et al., 2000; Pennington et al., 2009). Irrespective of their ability to fix atmospheric N<sub>2</sub>, most members of this family have high foliar N (Fyllas et al., 2009). Moreover, in the dry forests of Costa Rica, legume trees stand out as a different plant functional group since they have high leaf C and N concentrations and greater wood density, than non-leguminous species (Powers and Tiffin, 2010). Despite a general understanding of legumes as drivers of N dynamics, the magnitude of the effects of this group of species in tropical forest soils is poorly quantified. Defining the effects that legumes have on soils is a required first step toward understanding how community composition and functional group assemblages influence soil processes and particularly N dynamics. While a few studies have quantified the influence of tree species on soil characteristics in diverse tropical forests (Powers et al., 2004; Reed et al., 2008), or plantations (Montagnini and Sancho, 1990, 1994; Fisher, 1995; Powers et al., 1997; Warren and Zou, 2002) to date no studies have included species effects in both habitats.

This study was designed to elucidate the effect of legume tree species on soil chemistry and nutrient availability in both diverse secondary dry forest or alone in monoculture plantations. We focused on three legume species and compared their effects to nearby non-legume species. Because legumes typically have higher foliar and litter N concentrations compared to other species (McKey, 1994; Townsend et al., 2007), we predicted that legumes would have higher soil N availability under their crowns. A corollary to this prediction is that if legume trees are indeed increasing soil N availability under their crowns, the cost of the investment in the production of N-rich enzymes like acid phosphatases should be reduced (Houlton et al., 2008). Acid phosphatases hydrolyze the ester bonds of organic P compounds releasing phosphate in forms available to plants (Malcolm, 1983; Olander and Vitousek, 2000). Thus we hypothesized that acid phosphatase activity would be higher under legume species compared to under non-legume species. In addition, we compared the stable N isotope composition ( $\delta^{15}\text{N}$ ) of the soils under each species, expecting to find soils with  $^{15}\text{N}$  values closer to zero under N<sub>2</sub>-fixers that would reflect inputs of atmospheric N<sub>2</sub>. Alternatively, a relative enrichment in  $^{15}\text{N}$  in soils under the N<sub>2</sub>-fixers could imply greater losses of N through trace gas emissions and hence fractionation or discrimination against the heavy N isotope, suggesting that N is in relative excess to microbial N requirements (Högberg, 1997; Martinelli et al., 1999). Finally, we predicted that the effect of legume species on soils under their crowns would be more pronounced for trees in the plantations compared to the forest, where a diversity of N-demanding non-leguminous species might be rapidly recycling the N resulting from the decomposition of legume species litter.

## 2. Materials and methods

### 2.1. Site description

This study was carried out in Sector Pocosol and in Estación Experimental Horizontes of Área de Conservación Guanacaste (ACG; 10.84°N, 85.62°W) in northwestern Costa Rica. Established in 1971, ACG currently comprises 147,000 ha of protected land (<http://www.gdrcf.org>). This region has a mean annual temperature of 25 °C and a mean annual precipitation of 1575 mm with a large inter-annual range from 880 to 3030 mm and a 6 month dry season (Gillespie et al., 2000). Pocosol is a mosaic of old pastures and dry forest of various ages and has been protected from cattle grazing since 1988 (Gerhardt, 1993). Tree species richness (stems > 10 cm diameter at breast height) in 0.1 ha forest inventory plots in the region ranges from 1 to 21 species (Powers, unpub. data). Horizontes is located ~20 km from Pocosol and was established in 1991 as an experimental area of ACG for research in restoration and silviculture; it has 74 ha of forest plantations of native tree species embedded in ~7300 ha of lowland deciduous forest directly connected to ACG. Before 1991, Horizontes was a farm that had rice, sorghum and cotton fields, with cattle pastures as well (Gutiérrez, pers. comm.). In Pocosol, most of the soils are Entisols, Inceptisols, or Vertisols of volcanic origin overlying bedrock of volcanic ashes and pumice (Gerhardt, 1993). In Horizontes, soils are Inceptisols and of volcanic origin as well (Czarnowski, 2002).

### 2.2. Species selection and soil sampling

Species were selected based upon local abundance and presence in the Horizontes plantations. In the forested areas of Pocosol, we identified five individuals of each of the following tree species from the Fabaceae family: *Acosmium panamense* (Benth.) Yakovlev, *Dalbergia retusa* Hemsl., and *Gliricidia sepium* (Jacq.) Kunth ex Walp.. In the same area, we chose five individuals of each of the following non-legume species: *Quercus oleoides* Schltdl. & Cham. (Fagaceae), *Rehdera trinervis* (S.F. Blake) Moldenke (Verbenaceae), and *Swietenia macrophylla* King (Meliaceae). All species are henceforth referred to by genus name only. The three legume species are known for their potential for nodulation and hence potential capacity to fix N<sub>2</sub> (Corby, 1988; Sprent, 2001). Functional traits for these species have been previously collected (Powers and Tiffin, 2010) (Table 1). Non-legume species were chosen for their high foliar C:N ratios and were located in the same area as legume focal trees but at least two tree crowns away from any of them. Previous work has shown that many plant functional traits for these species, with the exception of the legumes, are not phylogenetically conserved (Powers and Tiffin, 2010). All individuals were chosen within a 20 ha area. To standardize for light environments, only individuals with direct access to light were included. In Horizontes, we targeted focal trees in 18-yr old monoculture plantations (1 ha in size) of the same three legume species sampled in the forest site,

**Table 1**  
Leaf characteristics and functional traits of six tree species found in Costa Rican tropical dry forests.

Species	Leaf habit	Functional type	SLA (cm <sup>2</sup> g <sup>-1</sup> )	Wood density (g <sup>1</sup> cm <sup>-3</sup> )	Leaf water (%)	Leaf $\delta^{15}\text{N}$ (‰)	Leaf $\delta^{13}\text{C}$ (‰)	Leaf P (g kg <sup>-1</sup> )	Leaf N (g kg <sup>-1</sup> )	Leaf C (g kg <sup>-1</sup> )	Decay rate <sup>a</sup> (yr <sup>-1</sup> )
<i>Acosmium panamense</i>	Semideciduous	Legume	92.19	0.77	58.26	-2.48	-27.86	0.7	29.3	489.6	n.a.
<i>Dalbergia retusa</i>	Deciduous	Legume	67.70	0.80	55.19	-1.70	-27.76	0.8	24.3	476.4	0.6
<i>Gliricidia sepium</i>	Deciduous	Legume	137.82	0.78	71.34	-1.06	-28.52	1.3	35.3	475.6	2.2
<i>Quercus oleoides</i>	Evergreen	Non legume	63.80	0.80	49.49	0.37	-28.27	0.7	14.6	478.9	0.5
<i>Rehdera trinervis</i>	Deciduous	Non legume	74.86	0.74	61.83	-0.55	-28.45	0.7	14.5	444.4	4.6
<i>Swietenia macrophylla</i>	Deciduous	Non legume	68.72	0.67	54.48	-0.79	-27.95	0.8	15.7	471.2	0.8

Data collected in 2008 from individuals in Área de Conservación Guanacaste (ACG). Values represent means of 1–7 trees, adapted from Powers and Tiffin (2010).

<sup>a</sup> Powers, unpublished data, decomposition rates are from one-pool models fit to data from a litterbag study. SLA: specific leaf area, n.a.: data not available.

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