

SHORT COMMUNICATION

Tree species do not influence local soil chemistry in a species-rich Costa Rica rain forest

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In a now classic study, Zinke (1962) showed that a single *Pinus contorta* tree growing on a sand dune along the coast of California modified the chemistry of the soil underneath its crown. He found distinct patterns of pH, exchangeable cations and nitrogen (N) content moving from the bole outward to the crown drip zone, because the acidic bark and stemflow were concentrated around the bole (Zinke 1962). Subsequent studies in temperate forests have also found tree species to affect soil chemical properties such as pH, organic carbon (C) and rates of N mineralization (Boerner & Koslowsky 1989, Boettcher & Kalisz 1990, Finzi *et al.* 1998). Presumably, these species-specific effects are caused by inter-specific differences in organic acid exudation, nutrient uptake, litter quality or quantity, decomposition rates or nutrient outputs (Binkley & Giardina 1998, Knops *et al.* 2002, Rhoades 1997). Regardless of the causes, species-generated soil heterogeneity has implications for stand-level estimates of biogeochemical processes such as soil C storage and N-cycling as well as implications for plant diversity and regeneration (Finzi *et al.* 1998). Although a number of studies have demonstrated that tree species modify soil environments in temperate forests or monospecific tree plantations in the tropics (Fisher 1995, Rhoades 1997), few studies have investigated these processes in species-rich tropical forests (but see Rhoades *et al.* 1994).

We investigated whether soil chemistry (total soil C, N, pH and extractable nutrients [Ca, Mg, K, P]) differs underneath the crowns of emergent rain-forest tree species at the La Selva Biological Station, Costa Rica. The climate at La Selva is wet (*c.* 4000 mm mean annual pre-

cipitation) and warm (26 °C mean annual temperature), and other site characteristics are described in McDade *et al.* (1994). We studied four species from different families: *Hyeronima alchorneoides* Allemão (Euphorbiaceae) and *Lecythis ampla* Miers (Lecythidaceae), and two legumes *Dipteryx panamensis* (Pittier) Record & Mell (Fabaceae), *Balizia elegans* Ducke (Mimosaceae). Soil chemical properties are known to vary over the 1500-ha reserve as a function of topography, parent material and soil age (Sollins *et al.* 1994), and tree species are distributed differentially over these gradients (Clark *et al.* 1998). In order to separate the effects of individual species from large-scale gradients in nutrient availability, we paired every sampled tree with the nearest *Pentaclethra macroloba* (Willd.) Kuntze (Mimosaceae) tree. *Pentaclethra* is the dominant tree species at La Selva, accounting for 36–38% of estimated aboveground biomass (Clark & Clark 2000a). Thus, we considered soil chemistry under the crowns of adjacent mature *Pentaclethra* trees as the ‘background’ local soil conditions and estimated species’ effects on soil chemistry by difference between each focal tree and its *Pentaclethra* neighbour.

Focal trees (> 70 cm diameter breast height; dbh) were identified using the TREES database (Clark & Clark 2000b). For each focal tree, we located the nearest *Pentaclethra* within 40 m and with a dbh of at least 50 cm. There were eight pairs for *Dipteryx*, *Hyeronima* and *Lecythis*, and nine for *Balizia*. At all trees, we collected eight soil samples. Samples were located by moving a random distance (from a random number table) between the bole and the crown drip line in each of eight cardinal directions from the bole (45° apart). Soil samples were collected from mineral soils (excluding the leaf litter layer) with a *c.* 2-cm-diameter soil probe to a depth of 15 cm, and

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Table 1. Means \pm 95% confidence intervals of soil variables (0–15 cm depth mineral soil) sampled underneath the crowns of four tree species and neighbouring *Pentaclethra* trees (data for the paired *Pentaclethra* trees are listed beneath each focal tree species).

	Ca	K	Mg	P ($\mu\text{g g}^{-1}$)	%C	%N	pH(CaCl ₂)
	(cmol(+)kg ⁻¹)						
<i>Albizia</i>	0.04 (0.02)	0.24 (0.03)	0.35 (0.05)	31.11 (7.98)	6.00 (0.79)	0.46 (0.05)	3.52 (0.18)
<i>Pentaclethra</i>	0.06 (0.05)	0.21 (0.03)	0.30 (0.04)	20.67 (4.38)	5.13 (1.07)	0.40 (0.07)	3.59 (0.17)
<i>Dipteryx</i>	0.13 (0.06)	0.26 (0.04)	0.46 (0.12)	28.51 (11.59)	5.72 (0.68)	0.45 (0.04)	3.66 (0.16)
<i>Pentaclethra</i>	0.08 (0.04)	0.51 (0.66)	0.42 (0.28)	26.06 (12.14)	5.14 (1.12)	0.42 (0.08)	3.72 (0.14)
<i>Hyeronima</i>	0.16 (0.10)	0.35 (0.14)	0.48 (0.15)	52.31 (48.54)	5.55 (1.15)	0.46 (0.09)	3.74 (0.20)
<i>Pentaclethra</i>	0.14 (0.23)	0.29 (0.08)	0.58 (0.40)	49.88 (31.15)	5.05 (0.87)	0.43 (0.09)	3.80 (0.26)
<i>Lecythis</i>	0.13 (0.07)	0.25 (0.03)	0.35 (0.10)	21.18 (6.17)	4.94 (0.48)	0.39 (0.03)	3.63 (0.20)
<i>Pentaclethra</i>	0.05 (0.04)	0.24 (0.08)	0.28 (0.13)	23.29 (6.96)	4.78 (0.58)	0.38 (0.04)	3.60 (0.23)

bulked by tree. pH was measured on field-moist soils in a 1:2.5 soil solution ratio of 0.01 M CaCl₂ (Öhlinger 1997). Soils were oven dried at 50 °C, passed through a 2-mm sieve, and taken to the United States for analyses. Total C and N were measured on ground samples in a Carlo Erba EA1108 CHN analyser. Cations and phosphorus (P) were extracted in Mehlich III solution (Kalycin & Newman 1999, Mehlich 1984) and quantified by atomic absorption and flame emission spectrophotometry and colorimetry. The Mehlich III solution consists of dilute acids, and presumably extracts labile or 'plant available' nutrients in acidic soils such as those at La Selva. We ran all analyses in duplicate and report average values on an oven-dry weight basis. For each species, paired t-tests were used to test for differences in soil chemical variables between focal trees and *Pentaclethra* neighbours.

The large differences in soil chemistry among the four species reflect the biased distributions of individual species toward different soil types (Table 1) (Clark *et al.* 1998). For example, the *Hyeronima* trees were consistently located on more nutrient-rich alluvial soils, which is reflected in higher average concentrations of extractable P under both focal trees and *Pentaclethra* neighbours (Table 1). In contrast, *Balizia* is more abundant on the residual Ultisols (Clark *et al.* 1998), which have higher organic C concentrations compared to the alluvial Inceptisols (Powers & Schlesinger 2002).

The paired t-tests evaluate the null hypothesis that the average differences between focal tree soil chemical properties and those of the paired *Pentaclethra* neighbours are not different from zero. There was only one difference significant at $\alpha = 0.05$, exactly what would be expected by chance when conducting 28 multiple comparisons (Table 2). This difference was not significant after a Bonferroni correction for multiple comparisons. Analyses of variance testing for differences in chemistry between focal trees and *Pentaclethra* neighbours (the response variable) among the focal tree species were also not significant (all $P > 0.30$).

Table 2. Results from paired t-tests and power analyses. Bonferroni-corrected P-value significance is $\alpha = 0.05/28 = 0.0018$. Units for Ca, K, and Mg are cmol(+)kg⁻¹, P is in $\mu\text{g g}^{-1}$, and C and N are expressed as percentages. There were eight pairs for *Dipteryx*, *Hyeronima* and *Lecythis*, and nine for *Albizia*.

Species and variable	Mean difference between pairs	P value	Power	Required mean difference between pairs for 80% power†
<i>Albizia</i>				
Ca	-0.019	0.354	0.179	0.055
K	0.029	0.066	0.540	0.039
Mg	0.050	0.158	0.323	0.090
P	10.4	0.033	0.255	11.4
C	0.864	0.105	0.448	1.327
N	0.052	0.111	0.433	0.081
pH	-0.07	0.147	0.363	0.123
<i>Dipteryx</i>				
Ca	0.052	0.065	0.580	0.066
K	-0.248	0.421	0.134	0.816
Mg	0.031	0.842	0.041	0.422
P	2.45	0.537	0.161	10.6
C	0.577	0.345	0.171	1.600
N	0.022	0.592	0.082	0.110
pH	-0.06	0.349	0.169	0.158
<i>Hyeronima</i>				
Ca	0.014	0.828	0.043	0.174
K	0.058	0.421	0.131	0.189
Mg	-0.091	0.580	0.082	0.131
P	13.6	0.851	0.161	32.0
C	0.499	0.388	0.149	1.523
N	0.031	0.566	0.089	0.142
pH	-0.06	0.520	0.100	0.227
<i>Lecythis</i>				
Ca	0.072	0.055	0.595	0.088
K	0.011	0.741	0.052	0.086
Mg	0.065	0.206	0.240	0.131
P	-2.11	0.637	0.025	12.0
C	0.161	0.609	0.078	0.841
N	0.010	0.618	0.076	0.053
pH	0.03	0.569	0.087	0.119

† Assuming the observed sample size and standard deviations.

It is surprising that we found no effects of emergent rain-forest trees on soil properties, given that these trees are likely to be at least 100 y old, differ in life history traits (e.g. shade tolerance, litter fall phenology, etc.) (Clark &

Clark 1992, Fichtler *et al.* 2003), and may also differ in N nutrition if *Pentaclethra* and *Albizia* host symbiotic N-fixing bacteria (there is no reported nodulation in the Dipterygeae; Corby 1988). One reason we may have not detected significant differences is power, i.e. the 'probability of correctly rejecting a false null hypothesis' (Zar 1996). High power provides confidence that the failure to reject the null hypothesis is appropriate, and a value of 0.80 or greater is desirable. We computed the power of each test, assuming a two-sided test with $\alpha = 0.05$. The power varied with species and soil property (Table 2), but in general was higher for the *Dipteryx* and *Balizia* analyses. This is due to larger mean differences between these species and the *Pentaclethra* pairs, not due to smaller standard deviations.

One reason we may not have found significant differences in species effects is lack of power. To explore this idea further we asked what the average difference between each species' soil properties and the *Pentaclethra* pairs would have to be to achieve a significant difference, assuming the sample sizes we used and the observed standard deviations ($\alpha = 0.05$, power = 0.80) (Table 2). These analyses show that the measured differences between soil properties under the focal species and *Pentaclethra* pairs would have to diverge from the differences that we observed by factors ranging from 1 to 12-fold in order to appear significant statistically (Table 2). In summary, our data suggest that if these four emergent tree species have direct effects on soil chemical properties, then those effects are small and many more samples than we collected may be needed to detect them.

Although power issues may have prevented us from detecting significant differences, there are also several biological reasons that may explain our failure to detect effects of tree species on soil properties. One possibility is that there is no difference in litter chemistry or nutrient use among these species, i.e. the focal species and *Pentaclethra* may all be affecting soil properties in similar ways. Although we cannot rule this out, the mean concentrations (%) of N and P in leaf litter for three of the study species (*Dipteryx* N = 1.75 ± 0.07 (standard error) and P = 0.094 ± 0.008 , *Balizia* N = 2.27 ± 0.24 and P = 0.071 ± 0.015 , and *Hyeronima* (composite sample from several trees) N = 0.99 and P = 0.046) suggest that is not the case (Powers unpubl. data). The concentrations of N and P in the leaf litter differ between the two legume species but are each approximately twice those in *Hyeronima*. Thus equivalent litter chemistry of the species is not a likely explanation for our results.

A second potential mechanism is the presence of plants with different life forms that grow interspersed with and underneath the crowns of emergent trees. Foliar N and P contents vary with life form and stature (Bigelow 1993), and thus the presence of other plants may disrupt

any localized effects of emergent trees on soil properties (Boettcher & Kalisz 1990). In particular, liana leaves are estimated to comprise 15% of the total foliage in La Selva primary forest (Werner 1985 cited in Clark 1994), and may have a special role in homogenizing patterns of soil properties. Lianas may serve to redistribute nutrients within tropical forests, because their canopies may be horizontally distant from the root zone (Putz 1984). Thus, nutrients that are acquired by roots in one patch of soil may be translocated tens of metres away through the stem, and later delivered to a distant patch of forest floor via litter fall. Finally, animal activity in these tropical forests may be much greater than in temperate forests. A diverse group of animals including termites, ants, anteaters, coatis and armadillos live in this forest and may homogenize soil by digging or burrowing. In summary, we conclude that although emergent tree species may affect soil chemistry and nutrient availability in this wet tropical forest, these effects cannot be generalized to all tree species and were undetectable in the four emergent tree species that we studied.

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LITERATURE CITED

- BIGELOW, S. W. 1993. Leaf nutrients in relation to stature and life form in tropical rain forest. *Journal of Vegetation Science* 4:401–408.
- BINKLEY, D. & GIARDINA, C. 1998. Why do tree species affect soils? The warp and woof of tree-soil interactions. *Biogeochemistry* 42:89–106.
- BOERNER, R. E. J. & KOSLOWSKY, S. D. 1989. Microsite variations in soil chemistry and nitrogen mineralization in a beech-maple forest. *Soil Biology and Biochemistry* 21:795–801.
- BOETTCHER, S. E. & KALISZ, P. J. 1990. Single-tree influence on soil properties in the mountains of eastern Kentucky. *Ecology* 71:1365–1372.
- CLARK, D. A. 1994. Plant demography. Pp. 90–105 in McDade, L. A., Bawa, K. S., Hespeneheide, H. A. & Hartshorn, G. S. (eds). *La Selva: ecology and natural history of a neotropical rain forest*. University of Chicago Press, Chicago.

- CLARK, D. A. & CLARK, D. B. 1992. Life history diversity of canopy and emergent trees in a neotropical rainforest. *Ecological Monographs* 62:315–344.
- CLARK, D. B., CLARK, D. A. & READ, J. M. 1998. Edaphic variation and the mesoscale distribution of tree species in a Neotropical rain forest. *Journal of Ecology* 86:101–112.
- CLARK, D. B. & CLARK, D. A. 2000a. Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management* 137:185–198.
- CLARK, D. B. & CLARK, D. A. 2000b. Tree growth, mortality, physical condition, and microsite in old-growth lowland tropical rain forest. *Ecology* 81:294.
- CORBRY, H. D. L. 1988. Types of rhizobial nodules and their distribution among the Leguminosae. *Kirkia* 13:53–123.
- FICHTLER, E., CLARK, D. A. & WORBES, M. 2003. Age and long-term growth of trees in an old-growth tropical rain forest, based on analyses of tree rings and ¹⁴C. *Biotropica* 35:306–317.
- FINZI, A. C., VAN BREEMAN, N. & CANHAM, C. D. 1998. Canopy tree-soil interactions within temperate forests: tree species effects on carbon and nitrogen. *Ecological Applications* 8: 440–446.
- FISHER, R. F. 1995. Amelioration of degraded rain forest soils by plantations of native trees. *Soil Science Society of America Journal* 59:544–549.
- KALICIN, M. H. & NEWMAN, M. E. 1999. *The effect of tree species on soil chemistry and nutrients in a tropical wet forest of Costa Rica*. Thesis. Department of Chemistry, Hartwick College, Onoenta, NY.
- KNOPS, J. M. H., BRADLEY, K. L. & WEDIN, D. A. 2002. Mechanisms of plant species impacts on ecosystem nitrogen cycling. *Ecology Letters* 5:454–466.
- MCDADE, L. A., BAWA, K. S., HESPENHEIDE, H. A. & HARTSHORN, G. S., (eds). 1994. *La Selva: ecology and natural history of a neotropical rain forest*. University of Chicago Press, Chicago. 486 pp.
- MEHLICH, A. 1984. Mehlich 3 soil test extractant: a modification of the Melich 2 extractant. *Communications in Soil and Plant Analysis* 15:1409–1416.
- ÖHLINGER, R. 1997. Acidity. Pp. 396–397 in Schinner F., Öhlinger, R., Kandeler, E. & Margesin R. (eds). *Methods in soil biology*. Springer, Berlin.
- POWERS, J. S. & SCHLESINGER, W. H. 2002. Relationships among soil carbon distributions and biophysical factors at nested spatial scales in rain forests of northeastern Costa Rica. *Geoderma* 109:165–190.
- PUTZ, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65:1713–1724.
- RHOADES, C. C. 1997. Single-tree influences on soil properties in agroforestry: lessons from natural forest and savanna ecosystems. *Agroforestry Systems* 35:71–94.
- RHOADES, C. C., SANFORD, R. L. & CLARK, D. B. 1994. Gender dependent influences on soil phosphorus by the dioecious lowland tropical tree *Simarouba amara*. *Biotropica* 26: 362–368.
- SOLLINS, P., SANCHO-M., F., MATA-CH., R. & SANFORD, R. L. 1994. Soils and soil process research. Pp 34–53 in McDade, L. A., Bawa, K. S., Hesperheide, H. A. & Hartshorn, G. S. (eds). *La Selva: ecology and natural history of a neotropical rain forest*. University of Chicago Press, Chicago.
- ZAR, J. H. 1996. *Biostatistical analysis*. (Third Edition). Prentice Hall, Inc., Upper Saddle River, New Jersey. 662 pp.
- ZINKE, P. J. 1962. The pattern of influence of individual forest trees on soil properties. *Ecology* 43:130–133.