

---

Gender Dependent Influences on Soil Phosphorus by the Dioecious Lowland Tropical Tree  
*Simarouba amara*

Author(s): Charles C. Rhoades, Robert L. Sanford, Jr. and David B. Clark

Source: *Biotropica*, Vol. 26, No. 4 (Dec., 1994), pp. 362-368

Published by: [Association for Tropical Biology and Conservation](#)

Stable URL: <http://www.jstor.org/stable/2389229>

Accessed: 16-12-2015 18:10 UTC

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Association for Tropical Biology and Conservation and Wiley are collaborating with JSTOR to digitize, preserve and extend access to *Biotropica*.

<http://www.jstor.org>

## Gender Dependent Influences on Soil Phosphorus by the Dioecious Lowland Tropical Tree *Simarouba amara*<sup>1</sup>

Charles C. Rhoades<sup>2</sup>

Department of Forest Sciences, Colorado State University, Fort Collins, Colorado 80523, U.S.A.

Robert L. Sanford, Jr.

Department of Biological Sciences, University of Denver, Denver, Colorado 80208, U.S.A.

and

David B. Clark

La Selva Biological Station, Organization for Tropical Studies, Puerto Viejo de Sarapiquí, Costa Rica

---

### ABSTRACT

We compared soil phosphorus levels below canopies of the lowland tropical rain forest tree species *Simarouba amara* Aubl. with soil sampled beyond the edge of *S. amara* canopies. Our data show that trees affect soil phosphorus concentrations and that differences below individual trees are related to gender for this dioecious species. Soil sampled adjacent to female trees had significantly higher soil phosphorus levels for several different indices of phosphorus availability than soil sampled beyond tree crowns. Male trees did not significantly modify soil phosphorus levels. Analysis of total mineral phosphorus (Total-phosphorus) below and beyond the canopies of male and female of *S. amara* found no differences in the total amount of phosphorus combined within bound and labile soil fractions. We measured a small increase in soil organic matter under tree canopies, but found no gender-related difference. Our results indicate that increased phosphorus availability beneath female *S. amara* arises from a gender-related modification in phosphorus cycling rather than from higher recruitment of females on sites rich in phosphorus or organic matter. We suggest that gender-dependent controls on soil phosphorus may include below-canopy enrichment of available phosphorus due to fruit and litter cycling or increases in phosphorus transformation from bound to labile forms.

---

### RESUMEN

Comparamos los niveles de fósforo en el suelo debajo de la copa de árboles de la especie *Simarouba amara*, con suelo muestreado fuera del borde de la copa de los mismos en las tierras bajas del bosque lluvioso tropical. Nuestros resultados mostraron que los árboles afectan la concentración de fósforo en los suelos y que diferencias encontradas debajo de árboles individuales están relacionadas al género, ya que esta especie es dioica. Suelos muestreados en lugares adyacentes a árboles femeninos presentaron niveles de fósforo significativamente más altos, en varios de los diferentes índices de disponibilidad de fósforo, que los suelos muestreados debajo de las copas. Árboles masculinos no modificaron los niveles de fósforo en los suelos significativamente. Análisis de fósforo mineral total (fósforo total), por debajo y fuera del borde de la copa de los árboles masculinos y femeninos de *S. amara*, no mostraron diferencias en la cantidad total de fósforo que combina las fracciones lábil y fija. Medimos un pequeño incremento en el nivel de materia orgánica debajo de la copa de los árboles, pero no encontramos diferencias relacionadas al género. Nuestros resultados indicaron que el incremento en la disponibilidad de fósforo debajo de *S. amara* femeninos surge de una modificación en el ciclo de fósforo relacionada al género, más que al establecimiento de los árboles femeninos en lugares con mayor contenido de fósforo y materia orgánica. Sugerimos que el control de fósforo en el suelo debido al género puede deberse al enriquecimiento debajo de la copa con fósforo lábil proveniente de frutos y hojarasca, o al incremento en la transformación de fósforo fijo a lábil.

*Key words:* Costa Rica; dioecy; lowland tropical rain forest; phosphorus; *Simarouba amara*; single-tree effects; soil nutrients.

THE EFFECT OF INDIVIDUAL TREES ON soil properties has been the focus of numerous studies in a variety

of temperate forest ecosystems (Zinke 1962, Alban 1969, Boettcher & Kalisz 1990, Beniamino *et al.* 1991, Klemmedson & Wienhold 1992). These efforts evaluate the spatial extent and magnitude of soil modification caused by different tree species. Nutrient levels, soil pH, and organic matter content were found to change as trees accumulated site re-

---

<sup>1</sup> Received 7 July 1993, revision accepted 28 January 1994.

<sup>2</sup> Corresponding author; current address: Institute of Ecology, University of Georgia, Athens, Georgia 30602-2202.

sources in tree biomass and returned it to the soil. Tree effects are species-specific due to differences in the quantity and chemical nature of litter components (Zinke 1962, Alban 1969, Boettcher & Kalisz 1990). For a single species, tree effects can vary on different sites or topographic aspects (Alban 1969, Klemmedson & Wienhold 1992).

In the species-rich rain forests of the lowland tropics, individual trees may leave long-term imprints on soils (Richter & Babbar 1991) that combine with the effects of canopy gaps (Vitousek & Denslow 1986) and other disturbances to produce the great spatial heterogeneity typical of tropical soils (Sánchez 1976). R. Sanford (pers. comm.) found that the tropical forest palm *Welfia georgii* increases soil potassium levels. Palms comprise 16 to 30 percent of the stems per hectare in several Neotropical forests (Janzen 1983); if other palms produce similar changes in soil nutrients, tree effects with reference to this taxa alone could significantly affect the mosaic of soil nutrients in tropical soils.

In the tropics, dioecious trees representing up to 21 percent of the tree flora (Bawa 1980), may contribute substantially to patterns of soil variability. Research on dioecious plants has focused on the relationship between gender-related distribution patterns and resource patchiness. For many dioecious species, females tend to occupy sites with higher resource levels (Bawa 1974; Freeman *et al.* 1976, Cox 1981, Dawson & Bliss 1989); males are more common on resource-poor sites (Bierzychudek & Eckhart 1986, Dawson & Ehleringer 1993). Niche differentiation between sexes is explained by the disparity in reproductive investment of the sexes and higher resource demand by females for seed production (Bawa & Opler 1975, Dawson & Ehleringer 1993). Gender-related niche partitioning based on total soil phosphorus levels was recorded for the tropical understory tree, *Trophis involuocrata* (Cox 1981). Female trees were found on soils containing significantly higher total P than male trees. Gender-specific differences in physiology and biomass allocation (Bullock 1984, Dawson & Ehleringer 1993) may affect nutrient cycling and influence tree effects on soil properties.

The objective of our study was to investigate the effect of the dioecious tree species *Simarouba amara* Aubl. (Simaroubaceae) on the availability of a limiting soil nutrient. In lowland tropical rain forest, soil P availability is extremely low due to losses of total P with intense weathering and rapid P adsorption by sesquioxide clays (Sánchez 1976, Vitousek & Sanford 1986). We measured inorganic and organic forms of soil P near male and female

trees to determine whether *S. amara* has a gender-related impact on P availability. Knowledge of species and gender-specific impacts on soil properties contributes to our understanding of soil heterogeneity and complexity within forest ecosystems.

## METHODS

The study site is located at La Selva Biological Station in the tropical wet and tropical premontane lifezones (Holdridge *et al.* 1971) of the Atlantic coast of Costa Rica (10°26'N, 83°58'W). Annual precipitation at La Selva averages 4000 mm. Mean annual temperature is 26°C (Organization for Tropical Studies, unpublished records). The dense, multistoried, primary forest is dominated by evergreen tree species; *Pentaclethra macroleoba* and *Welfia georgii* are most common (Holdridge *et al.* 1971). The soils at La Selva are variable and include residual soil originating from volcanic lava flows and alluvial soils that developed on terraced riverine alluvium (Sollins *et al.* 1993). Availability of soil P is low, (2.5  $\mu\text{g g}^{-1}$ ), but soil N is high due to the abundance of nitrogen-fixing trees (Vitousek & Denslow 1986).

Sample trees are part of a long-term study of the regeneration ecology of primary rain forest trees (Clark & Clark 1987, 1990, 1992). Along with annual growth and survival, flowering phenology was recorded and female and male individuals were identified. Sample trees occupy codominant positions in the forest canopy and are greater than 20 cm diameter at breast height (1.4 m). We selected eight individuals of each sex. Sample trees were located on the Matabuey and Jaguar soil consociations, derived from lava flows and the Arboleda consociation, a highly weathered, upper terrace soil (Table 1). Although the Matabuey and Jaguar soils originated from different lava flows, both are Typic Tropohumults and both possess very similar chemical and morphological properties (Sancho & Mata 1987). The Arboleda consociation is a very old alluvial soil (Sollins *et al.* 1993) found adjacent to the Jaguar soils; the two soil consociations have been grouped together in recent investigation (Vitousek & Denslow 1987). Trees sampled on the Arboleda consociation were located near the border of the mapping unit, adjacent to the Jaguar soil type.

Soil was sampled within 20 cm of each tree stem (adjacent sample), and 1 to 2 m beyond the edge of the canopy drip line (control sample), but not below the canopy of another *S. amara*. Mineral soil cores were sampled from the 0–10 cm depth after removing forest floor debris. Soils were refrig-

TABLE 1. Selected chemical and physical characteristics of soils (0–15 cm depth) in this study. All data from Sancho and Mata (1987) except for  $\text{NH}_4$ ,  $\text{NO}_3$  and  $\text{P}^{(1)}$  which were measured in each of the study plots.  $\text{P}^{(1)}$  is available phosphorus as determined by dilute acid-fluoride extraction (Bray I) while  $\text{P}^{(2)}$  is sodium bicarbonate extractable phosphorus (modified Olsen).

Series name	Classification	pH (H <sub>2</sub> O)	O.M. %	NO <sub>3</sub> µg/g	NH <sub>4</sub> µg/g	P <sup>(1)</sup> µg/g	P <sup>(2)</sup> µg/g	Ca	Mg	K	Bulk density Mg/m <sup>3</sup>	Sand %	Silt %	Clay %
								cmol/kg						
Arboleda	Typic Humitropept	5.3	4.03	5.86	7.82	0.98	4.7	11.00	2.96	0.41	0.55	82	12	6
Jaguar	Typic Tropohumult	4.5	6.75	4.00	6.86	0.89	6.4	0.54	0.53	0.29	0.69	44	15	41
Matabuey	Typic Tropohumult	5.0	7.13	4.01	8.88	0.61	7.7	0.59	0.46	0.35	0.80	46	13	41

erated immediately after sampling and transported from Costa Rica to Colorado in an insulated cooler. Laboratory analyses were completed within two weeks of sampling.

Different forms of soil phosphorus of increasing chemical stability were removed by sequential extraction (Hedley *et al.* 1982). Resin extractable phosphorus (resin-P) was removed by shaking soils and anion exchange resins (Dowex 1 × 8–50, >30 mesh, bicarbonate form) for one hour in distilled water (Hedley *et al.* 1982). The sodium bicarbonate-extractable inorganic fraction (Pi) was extracted with 0.5 M NaHCO<sub>3</sub> at pH = 8.5 (Bowman & Cole 1978). A subsample of the filtrate was then digested by acidified ammonium persulfate oxidation to release the organically-bound P in the bicarbonate extract (Po). The total bicarbonate extractable P (Pt) contained in the digested samples includes both Po and Pi; Po was calculated as the difference between Pt and Pi (O'Halloran *et al.* 1985). Orthophosphate concentrations in the filtered extracts and the neutralized digests were measured using the method of Murphy and Riley (1962).

Resin-P indexes the most biologically active plant available fraction (Hedley *et al.* 1982). Pi is moderately labile, plant available P, that is adsorbed to soil exchange sites (Tiessen *et al.* 1984). The Po fraction contains labile, plant available organic forms (Bowman & Cole 1978). In Ultisols, resin-P is highly correlated with Po (Tiessen *et al.* 1984). Together resin-P and Po represent a labile pool of P, available to plants in soil solution and replenished by mineralization of labile organic matter.

Total mineral soil-P (Total-P) was recovered after fusion of samples with Na<sub>2</sub>CO<sub>3</sub> in nickel crucibles (Olsen & Sommers 1982). Total P combines the organic and inorganic forms of P that are adsorbed on exchange sites (bicarbonate extractable-P) with those that are tightly fixed by Al and Fe

oxides and any P residing within the primary soil minerals. Soil organic matter content was analyzed using the Walkley-Black method (1934).

Statistical analysis tested for differences in treatment means with one-way and two-way analysis of variance (ANOVA), two sample *t*-tests, LSD pairwise comparisons, and linear correlation (Steel & Torrie 1980). Comparisons evaluated differences in soil properties based on tree sex (sex effect) and sample location (tree effect). Calculations were completed using SPSS/PC (SPSS 1988) setting the probability of a Type I error at 0.05.

## RESULTS

SOIL PHOSPHORUS.—In general, soil adjacent to female *S. amara* trees had higher extractable phosphorus levels than soil adjacent to male trees or the control samples (Fig. 1). This indicates that not only does *S. amara* influence soil P, but that tree gender has an additional influence. Soil P, indexed by resin-P and bicarbonate extractable Pi, Po, and Pt, was higher below canopies of female *S. amara* than in control soils (two-way ANOVA, *P* values = 0.036, 0.048, 0.335, 0.222; *N* = 8). Correlation analysis found that with the exception of total mineral P content, no clear relation existed between soil P fractions adjacent to trees and those beyond tree canopies (*F*-test, *P* = 0.489, 0.577, 0.753, 0.403, 0.013; Pearson's coefficient, *r* = -0.186, 0.151, 0.086, 0.224, 0.606; for Pi, Po, Pt, Resin-P, and Total mineral P; *N* = 16). This lack of relation allows female and male, adjacent and control samples to be treated independently in a two-way ANOVA analysis.

No significant differences were found between control samples of the male and female trees for any of the phosphorus fractions (Table 2). For the following statistical analyses, female and male con-

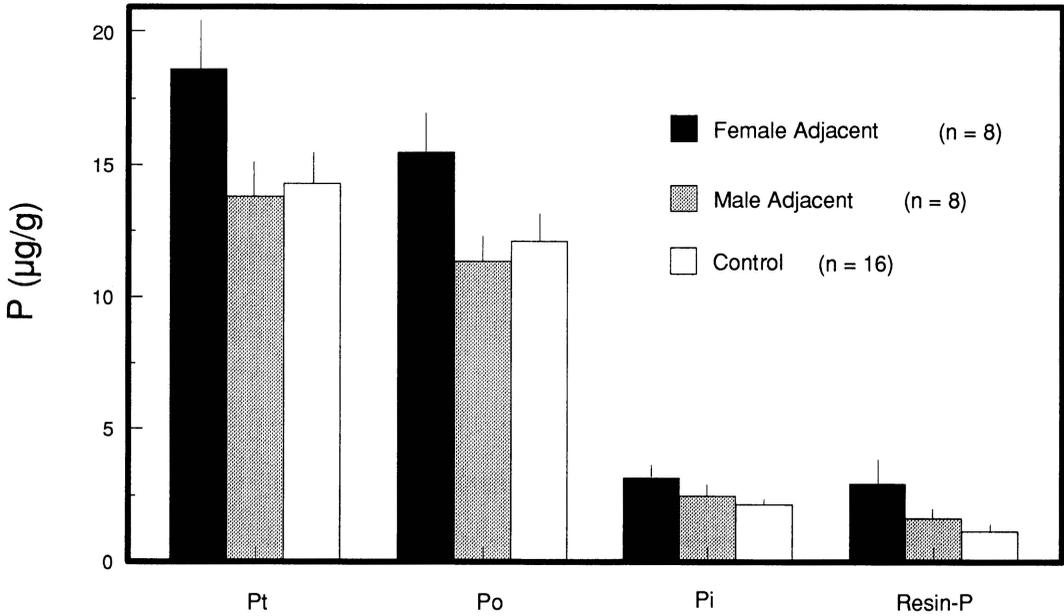


FIGURE 1. Phosphorus fraction means and standard errors ( $\mu\text{g}^{-1}$  oven dry soil). Pt, Po, and Pi are bicarbonate extractable total, organic, and inorganic phosphorus fractions, respectively.

control samples were combined into a single control group. Resin-P was 2.5 times higher adjacent to female trees ( $2.93 \mu\text{g}^{-1}$ , SE = 0.88,  $N = 8$ ) than in control samples ( $1.13 \mu\text{g}^{-1}$ , SE = 0.21,  $N = 16$ ). The combination of the most labile P forms (resin-P and Po) was 40 percent higher beneath female trees ( $18.4 \mu\text{g}^{-1}$ , SE = 2.2,  $N = 8$ ) compared to controls ( $13.2 \mu\text{g}^{-1}$ , SE = 1.1,  $N = 16$ ). No clear tree effect occurred beneath male trees; resin-P and Pi were slightly higher adjacent to male trees, but Po, Pt and the labile pool were lower than controls. Below tree canopies, gender-related differences existed for bicarbonate extractable Pt, Po, and the labile pool ( $t$ -test,  $P = 0.048, 0.036,$  and  $0.045, N = 8$ ). Resin-P and labile P were 80 and 42 percent greater adjacent to females compared to

male trees. Total mineral P (Total-P) did not differ among the treatments (one-way ANOVA,  $P = 0.9809$ , Table 3).

SOIL ORGANIC MATTER.—Organic matter content was 17 percent higher adjacent to trees (15.8%) compared to control samples (13.5%). Soil organic matter beneath male and female trees was not significantly different ( $t$ -test,  $P = 0.596, N = 8$ ). Neither

TABLE 2. Statistical comparison of soil phosphorus fractions for control soils sampled beyond the canopy drop line of male vs. female trees.

Extraction	Student's $t$	$P$ -value
Resin P	0.25	0.81
Bicarb Pi	1.48	0.16
Bicarb Po	0.86	0.41
Bicarb Pt	0.95	0.36
Total P	0.42	0.68

TABLE 3. Total mineral phosphorus by fusion extraction (Olsen & Sommers 1982) and soil organic matter (Walkley & Black 1934).  $N = 8$  for Adjacent samples,  $N = 16$  for Control samples.

	Mean	SE	ANOVA $P$ -value
Total P ( $\mu\text{g P g}^{-1}$ oven dry soil)			
Female Adjacent	560.0	65.98	0.9809
Male Adjacent	563.8	72.77	
Control	550.0	38.01	
Organic Matter (%)			
Female Adjacent	7.47	0.91	0.3299
Male Adjacent	8.34	1.33	
Control	6.45	0.32	

tree nor gender effects were statistically significant (Table 3). Comparison of the weathered alluvial soil (Arboleda; 7.69%) and the two soils derived from lava flows (Jaguar and Matabuey; 7.12%) revealed no difference in organic matter content (ANOVA,  $P = 0.530$ ).

## DISCUSSION

Our data suggest that female *S. amara* increase the availability of soil P. It is necessary, however, to consider the possibility that the results relate to *a priori* soil conditions or other causes (*e.g.*, tree diameter) before concluding that gender-related traits of *S. amara* are the cause. Prior research at La Selva (Cox 1981) discovered gender-specific niche partitioning for an understory shrub based on total soil P content. Female *Trophis involucreta* were more abundant on soils with higher total P. Our analysis of Total-P showed that males and females occurred on similar soils (*t*-test,  $P = 0.970$ ) and that neither sex modified Total-P content compared to surrounding soil (Table 3).

The amount of P cycled through plant biomass and soil organic matter is an important determinant of P availability, so variation in soil organic matter levels could explain differences in P cycling and influence tree effects (Klemmedson & Weinhold 1992). In highly weathered acidic Ultisols, total P is often quite low, and organic P may account for up to 80 percent of the total soil P (Sánchez 1976, Duxbury *et al.* 1989). In this study, the organic-bound  $P_o$  comprised 85 percent of the total amount of P extracted with sodium bicarbonate. We found that soil organic matter content was the same under male and female trees (Table 3).

Finally, the magnitude and spatial extent of tree effects on soil properties increase with tree size (Bernard-Reversat 1982, Rhoades 1993) due to cumulative additions of organic matter and modification to the surrounding microenvironment as tree canopies expand (Joffre & Rambal 1993). The diameters of female sample trees were slightly larger than those of male trees ( $47.7 \pm 3.3$  cm vs  $40.9 \pm 3.0$  cm), though the differences were not significant ( $P = 0.340$ ). Correlation analysis, however, did not explain a significant amount of the variation in below canopy soil properties (*F*-test,  $P = 0.333$ , 0.249, 0.242, 0.062; Pearson's coefficient,  $r = 0.259$ , 0.306, 0.310, 0.474 for  $P_i$ ,  $P_o$ ,  $P_t$ , and Resin-P;  $N = 16$ ).

After examining *a priori* soil conditions and tree size, we conclude that the increase in available P is due to gender-related traits of *S. amara*. Further

investigation is required to isolate the controls on P cycling beneath *S. amara*. Flowering and fruiting are the only known morphological distinctions between sexes of *S. amara*. For a dioecious palm Bullock (1984) found that with the exception of fruit and seed on female trees, N and P content were similar for male and female biomass structures. For *S. amara*, neither the elemental composition nor the biomass production of flowers, fruits, or pollen is known. If *S. amara* fruit is rich in P, deposition and decomposition of fruit beneath female tree canopies could augment soil P levels. Reproductive structures may influence P cycling indirectly if vertebrate and invertebrate frugivores concentrate P beneath female canopies by defecating during feeding visits. Gender-specific physiological differences in water and carbon balance have been shown for a dioecious shrub (*Salix*: Dawson & Bliss 1989, 1993) and a dioecious tree (*Acer*: Dawson & Ehleringer 1993). Such traits may extend to nutrient cycling and help to explain our findings.

Another area deserving research on *S. amara* is the impact of plant defense compounds on nutrient cycling. Secondary compounds extracted from *S. amara* bark and roots have known antimicrobial properties used in the manufacture of anti-moebics (Wright *et al.* 1988). Root exudates could affect herbivory or microbially mediated mineralization of organic material (Coley *et al.* 1985). The presence of secondary compounds in the rooting zone may affect microbial populations and alter plant-microbe competition for soil nutrients. Organism-specific defense compounds may favor beneficial microbial associations, such as vesicular arbuscular mycorrhizae, and increase P uptake. If plant defense compounds influence soil microbes, it is possible that they may also alter nutrient cycling near dioecious species, since sex-related differences in production of terpenoid secondary compounds are common in dioecious species (Bawa & Opler 1975). The occurrence of increased soil P beneath female *S. amara* has important implications for management of soil fertility on low P tropical soils. It is impossible to predict if female *S. amara* trees will have the same effect on soils in plantation or agroforestry systems as they do in undisturbed rain forest, but the pattern encountered in this study should encourage future research on *S. amara*.

## ACKNOWLEDGMENTS

Long-term studies on *Simarouba* have been supported by grants from the National Science Foundation to D. B. Clark, D. A. Clark, and S. F. Oberbauer. We are grateful

for laboratory and field assistance from the staff at La Selva Biological Station, and from A. Bratt, X. Zou, and C. Camberdella at Colorado State University. Thanks to

R. M. Gordillo for the Spanish translation. We thank T. Dawson, S. Miller and an anonymous reviewer for helpful comments on the manuscript.

## LITERATURE CITED

- ALBAN, D. H. 1969. The influence of western hemlock and western redcedar on soil properties. *Soil Sci. Soc. Am. Proc.* 33: 453–457.
- BAWA, K. S. 1974. Breeding systems of tree species of a lowland tropical community. *Evolution* 28: 85–92.
- . 1980. Evolution of dioecy in flowering plants. *Annu. Rev. Ecol. Sys.* 11: 15–39.
- , AND P. A. OPLER. 1975. Dioecism in tropical forest trees. *Evolution* 29: 167–179.
- BENIAMINO, F., J. F. PONGE, AND P. ARPIN. 1991. Soil acidification under the crown of oak trees. I. Spatial distribution. *For. Ecol. Manage.* 40: 221–232.
- BERNARD-REVERSAT, F. 1982. Biogeochemical cycle of nitrogen in a semi-arid savanna. *Oikos* 38: 321–332.
- BIERZYCHUDEK, P., AND V. ECKHART. 1986. Spatial segregation of the sexes in dioecious plants. *Am. Nat.* 132: 34–43.
- BOETTCHER, S. E., AND P. J. KALISZ. 1990. Single-tree influence on soil properties in the mountains of eastern Kentucky. *Ecology* 71: 1365–1372.
- BOWMAN, R. A., AND C. V. COLE. 1978. Transformations of organic phosphorus substrates in soils as evaluated by NaHCO<sub>3</sub> extraction. *Soil Sci.* 125: 49–54.
- BULLOCK, S. H. 1984. Biomass and nutrient allocation in a neotropical dioecious palm. *Oecologia* 63: 426–428.
- CLARK, D. A., AND D. B. CLARK. 1987. Population ecology and microhabitat distribution of *Dipteryx panamensis*, a neotropical rain forest emergent tree. *Biotropica* 19: 236–244.
- , AND ———. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecol. Monog.* 62: 315–344.
- CLARK, D. B., AND D. A. CLARK. 1990. Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. *J. Trop. Ecol.* 6: 321–331.
- COLEY, P. D., J. P. BRYANT, AND F. S. CHAPIN III. 1985. Resource availability and plant antiherbivore defense. *Science* 230: 895–899.
- COX, P. A. 1981. Niche partitioning between sexes of dioecious plants. *Am. Nat.* 117: 295–307.
- DAWSON, T. E., AND L. C. BLISS. 1989. Patterns of water use and the tissue water relations in the dioecious shrub, *Salix arctica*: the physiological basis for habitat partitioning between the sexes. *Oecologia (Berlin)* 79: 332–343.
- , AND ———. 1993. Plant mosaics: leaf-, ramet-, and gender-level variation in the physiology of the dwarf willow, *Salix arctica*. *Funct. Ecol.* 7: 293–304.
- , AND J. R. EHLERINGER. 1993. Gender-specific physiology, carbon isotope discrimination, and habitat distribution in boxelder, *Acer negundo*. *Ecology* 74: 798–815.
- DUXBURY, J. M., M. S. SMITH, AND J. W. DORAN. 1989. Soil organic matter as a source and a sink of plant nutrients. In D. C. Coleman, J. M. Oades, and G. Uehara (Eds.), *Dynamics of soil organic matter in tropical ecosystems*, pp. 33–68. Univ. of Hawaii Press, Honolulu, Hawaii.
- FREEMAN, D. C., L. G. KLIKOFF, AND K. T. HARPER. 1976. Differential resource utilization by the sexes of dioecious plants. *Science* 193: 597–599.
- HEDLEY, M. J., J. W. B. STEWART, AND B. S. CHAVHAN. 1982. Changes in inorganic and organic soil phosphorus fractions induced by cultivation practices and by laboratory incubations. *Soil Sci. Soc. Am. J.* 46: 970–976.
- HOLDRIDGE, L. R., W. C. GRENKE, W. H. HATHEWAY, T. LIANG, AND J. A. TOSI, JR. 1971. *Forest environments in tropical life zones: a pilot study*. Pergamon Press, Inc., New York, New York.
- JANZEN, D. H. 1983. *Costa Rican natural history*. Univ. of Chicago Press, Chicago, Illinois.
- JOFFRE, R., AND S. RAMBAL. 1993. How tree cover influences in the water balance of mediterranean rangelands. *Ecology* 74: 570–582.
- KLEMMEDSON, J. O., AND B. J. WIENHOLD. 1992. Aspect and species influences on nitrogen and phosphorus accumulation in Arizona chaparral soil-plant systems. *Arid Soil Res. and Rehab.* 6: 105–116.
- MURPHY, J., AND J. N. RILEY. 1962. A modified single solution method for the determination of phosphate in natural waters. *Anal. Chimica Acta* 27: 31–36.
- O'HALORAN, I. P., R. G. KACHANOSKI, AND J. W. B. STEWART. 1985. Spatial variability of soil phosphorus as influenced by soil texture and management. *Can. J. Soil Sci.* 65: 475–487.
- OLSEN, S. R., AND L. E. SOMMERS. 1982. Phosphorus. In A. L. Page, R. H. Miller, and D. R. Keeney (Eds.), *Methods of soil analysis. Part 2*. 2nd edition, pp. 403–430. ASA, Madison, Wisconsin.
- RHOADES, C. 1993. Seasonal pattern of nitrogen mineralization and soil moisture beneath *Acacia albida* on the Lakeshore Plain of Malawi. In E. Bonkoungou (Ed.), *Proceedings of Parc Land Agroforestry Symposium, October 25–27, 1993*. Ouagadougou, Burkina Faso. ICRAF, Nairobi, Kenya.
- RICHTER, D. D., AND L. I. BABBAR. 1991. Soil diversity in the tropics. *Adv. Ecol. Res.* 21: 315–389.
- SÁNCHEZ, P. A. 1976. *Properties and management of soils in the tropics*. John Wiley & Sons, New York, New York.

- SANCHO, F., AND R. MATA. 1987. Estudio detallado de suelos. Estacion Biologica "La Selva," Organizacion para Estudios Tropicales, San Jose, Costa Rica.
- SANFORD, R. L., JR., J. LUVALL, P. PAABY, AND P. PHILLIPS. 1993. The La Selva ecosystem: climate geomorphology, and aquatic systems. In L. A. McDade, K. S. Bawa, G. S. Hartshorn, and H. A. Hespenheide (Eds.). *La Selva: the ecology and natural history of a neotropical rainforest*, pp. Univ. of Chicago Press, Chicago, Illinois.
- SOLLINS, P., F. M. SANCHO, R. CH. MATA, AND R. L. SANFORD, JR. 1993. Soils of La Selva Biological Station. In L. A. McDade, K. S. Bawa, G. S. Hartshorn, and H. A. Hespenheide (Eds.). *La Selva: the ecology and natural history of a neotropical rainforest*. Univ. of Chicago Press, Chicago, Illinois.
- SPSS INC. 1988. SPSS/PC+™ V2.0 base manual. SPSS Inc. Chicago, Illinois.
- STEEL, R. G. D., AND J. H. TORRIE. 1980. Principles and procedures of statistics: a biometrical approach. 2nd edition. McGraw-Hill Publishing Company, New York, New York.
- TIESSEN, H., J. W. B. STEWART, AND C. V. COLE. 1984. Pathways of phosphorus transformations in soils of differing pedogenesis. *Soil. Sci. Soc. Am. J.* 48: 853-858.
- VITOUSEK, P. M., AND J. S. DENSLOW. 1986. Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *J. Ecol.* 74: 1167-1178.
- , AND ———. 1987. Differences in extractable phosphorus among soils of the La Selva Biological Station, Costa Rica. *Biotropica* 19: 167-170.
- , AND R. L. SANFORD, JR. 1986. Nutrient cycling in moist tropical forest. *Annu. Rev. Ecol. Syst.* 17: 137-167.
- WALKLEY, A., AND I. A. BLACK. 1934. An examination of the Degtjareff method for determining soil organic matter and a proposed modification of the chromic acid titration method. *Soil Sci.* 37: 29-38.
- WRIGHT, C. W., M. J. O'NEILL, J. D. PHILLIPSON, AND D. C. WARHURST. 1988. Use of microdilution to assess *In Vitro* antimicrobial activities of *Brucea javanica* fruits, *Simarouba amara* stem, and a number of quassinoids. *Antimicrob. Agents Chemother.* 32: 1725-1729.
- ZINKE, P. J. 1962. The pattern of individual forest trees on soil properties. *Ecology* 43: 130-133.