Ethnobotany of Woody Species in Second-Growth, Old-Growth, and Selectively Logged Forests of Northeastern Costa Rica

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Abstract: *We assessed quantitatively the woody species used for timber, medicine, and other products in 10 tropical wet-forest stands with different land-use histories in the Atlantic lowlands of northeastern Costa Rica. Species were classified into 20 use categories based on regional ethnobotanical studies. Three size classes of woody vegetation were sampled in nested, contiguous plots along transects: trees (≥5 cm diameter at breast height [dbh]), saplings (>1 m high, <5 cm dbh), and seedlings (>20 cm high, <1 m high). Our study included five second-growth stands, three old-growth stands, and two selectively logged stands. Of the 459 woody species surveyed, 70% of the species and 86% of the total number of individuals had at least one use. Overall, species richness was highest for medicinal species (167 species). Absolute and relative abundance of medicinal and timber trees was significantly higher in second-growth stands than in old-growth and selectively logged stands. For 8 of the 15 use categories examined statistically, stem density showed no significant differences across forest types for any stem size class. Young, tropical, second-growth forests and selectively logged forests have high utilitarian as well as conservation value and will likely become important sources of forest products. The success of secondary forest regeneration, however, depends critically upon conservation of genetically diverse source populations in forest fragments and protected old-growth stands.*

Etnobotánica de Plantas Leñosas en Bosques de Crecimiento Secundario, Bosques Maduros, y Bosques Talados Selectivamente en el Noreste de Costa Rica

Resumen: *Evaluamos cuantitativamente las especies leñosas utilizadas para maderas, medicina y otros productos en 10 bosques tropicales húmedos con diferente historia de uso en las tierras bajas del Atlántico del Noreste de Costa Rica. Las especies fueron clasificadas en 20 categorías de uso en base a estudios etnobotánicos regionales. Tres clases de vegetación leñosa fueron muestreadas en lotes contiguos anidados a lo largo de transectos: árboles (≥5 cm dbh), árboles jovenes (≥1m de altura; <5 cm dbh) y plántulas (>20 cm de altura, <1m de altura). Nuestro estudio incluyó cinco áreas de bosque de crecimiento secundario, tres áreas de bosque maduro y dos áreas con tala selectiva. De las 459 especies leñosas muestreadas, 70% de las especies y 86% del número total de individuos tuvieron por lo menos un tipo de uso. En general, la riqueza de especies fue mayor para especies medicinales (167 especies). La abundancia absoluta y relativa de árboles medicinales y maderables fue significativamente mayor en áreas de crecimiento secundario que en las de bosque maduro y las de tala selectiva. Para ocho de las 15 categorías de uso examinadas estadísticamente, la densidad de tallos no mostró diferencias signficativas entre los tipos de bosque para ninguna clase de tamaño de tallo. Bosques tropicales jóvenes de crecimiento secundario y bosques talados selectivamente tienen un valor utilitario alto, además de un valor de conservación y posiblemente se conviertan en fuentes importantes de productos forestales. El éxito de la regeneración del bosque secundario, sin embargo, depende críticamente de la conservación de poblaciones genéticamente diversas en fragmentos de bosque y áreas protegidas de bosque maduro.*

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Introduction

Throughout the world's tropical regions, secondary and degraded forests are increasing in extent and importance as old-growth forests become exploited, fragmented, or converted to agricultural uses (Brown & Lugo 1990; Whitmore 1997). The utilitarian value of old-growth tropical forests as sources of timber and nontimber products has been widely appreciated and has been used as a strong argument for conservation and sustainable management (Prance et al. 1987; Peters et al. 1989; Bennett 1992; Panayotou & Ashton 1992; Phillips et al. 1994; Prance 1998). Recently, an increasing number of studies have emphasized the potential of second-growth or logged tropical forests for timber and nontimber products (Wadsworth 1987; Balée & Gély 1989; Dubois 1990; Finegan 1992; Grenand 1992; Lugo 1992; Salick 1992; Salick et al. 1995; Toledo et al. 1995). Compared to old-growth forests, tropical secondary forests and selectively logged forests are generally poorly studied, despite the variety of useful plant species they support (Toledo et al. 1992; Toledo et al. 1995). For future generations, it is likely that secondary and selectively logged forests will become the primary source of timber and nontimber products throughout the tropics.

Ethnobotanical studies in the Neotropics confirm that second-growth flora is rich in medicinal species and may be utilized far more intensively by traditional (indigenous and nonindigeous) peoples than old-growth forests in the same vicinity (Grenand 1992; Kohn 1992; Toledo et al. 1995; Voeks 1996). Moreover, many fast-growing second-growth tree species are recognized for their timber value (Wadsworth 1987; Finegan 1992). Our study is the first to compare quantitatively the species richness, abundance, and size-class distribution of useful woody species found in old-growth, second-growth, and selectively logged forests within the same region. We also assessed regeneration of useful woody species in these forests. These data are critical to evaluation of the management and conservation potential of different types of forest cover and land-use practices for both timber and nontimber forest products. We considered 20 categories of use (Fig. 1), including timber and nontimber uses, and traditional and commercial uses.

Methods

Stand Selection and Vegetation Inventory

All study areas were located in the Atlantic lowland rain forest of Sarapiquí, Costa Rica, in the premontane wet-forest life zone (Table 1; Holdridge et al. 1975). This region is a mosaic of active pasture land, small- and large-scale agriculture, second-growth forest, selectively logged forest, and old-growth forest in protected areas (Butterfield 1994). The land-use history of each stand was determined by a combination of historical records (Pierce 1992), aerial photographs, satellite images, and interviews with local residents, farm staff, and landowners (Table 1). Second-growth stands were cleared for pasture in the early to mid-1970s, actively managed for 4–6 years, and subsequently abandoned in the late 1970s or early 1980s. Remnant canopy trees were found in all second-growth stands (Guariguata et al. 1997). In the two selectively logged stands, commercial tree species >70 cm dbh were removed 15–20 years before the study. When we conducted our survey, study sites were surrounded by areas of second-growth or old-growth forest ranging from 10 ha to >1000 ha.

Overall vegetation structure did not differ significantly among the three stand types (Table 2). The five second-

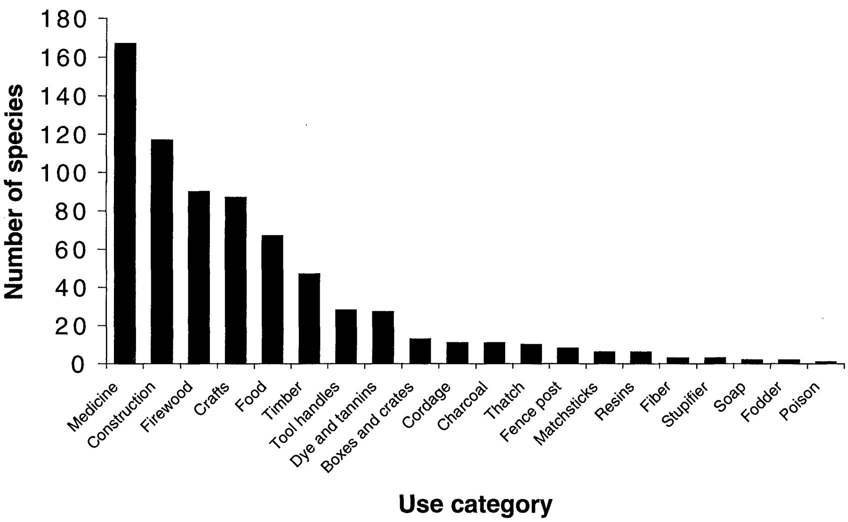

Figure 1. Species richness distribution among 20 use categories, based on the complete database from 10 forest stands in Sarapiquí, Costa Rica.

Table 1. Site characteristics of 10 forest stands in the Caribbean lowlands of Costa Rica.

Site name	*Forest type*	*Location, latitude, longitude*	*Recent land-use history*	*Estimated time since disturbance (years)*
Lindero Occidental	second growth	La Selva Biological Station, 10°26′N; 84°01′W	cleared in 1971–1973; pasture for 6 years; regrowth cleared before pasture abandoned	15–17
Peje	second growth	La Selva Biological Station, 10°26′N; 84°02′W	cleared in 1972–1974; pasture for 5 years; regrowth cleared before pasture abandoned	15–17
La Martita	second growth	Chilamate, 10°27′N; 84°04′W	cleared in 1971–1972; pasture for 4–5 years; then abandoned	17–20
Cuatro Rios	second growth	La Virgen, 10°23′N; 84°08′W	cleared in mid 1970s; then abandoned	15–20
Sendero Holdridge	second growth	La Selva Biological Station,10°25′N; 84°01′W	cleared in 1950s; pasture abandoned in 1967	25
La Selva	old growth	La Selva Biological Station,10°25′N; 84°03′W	no apparent or recorded human disturbance	
Chilamate	old growth	Chilamate, 10°27′N; 84°04′W	no apparent or recorded human disturbance	
Cay Rica	old growth	El Roble, 10°26′N; 84°04′W	no apparent or recorded human disturbance	
Intervenido	selectively logged	La Selva Biological Station, 10°25′N; 84°02′W	logged for more than 10 years until the late 1970s; approximately 3–4 stumps/ha	15–17
Kelady	selectively logged	Pueblo Nuevo, 10°29′N; 84°09′W	logged for more than 10 years until the early 1980s; approximately 8–9 stumps/ha	12–14

growth stands had tree densities and basal areas similar to those of old-growth stands, and the two selectively logged stands had recovered their basal area. Moreover, all stands showed similar densities of regenerating saplings and woody seedlings (Table 2). Species richness, floristics, seedling and sapling growth forms, and vegetation structure in six of these stands are described in detail by Guariguata et al. (1997) and Chazdon et al.

Table 2. Vegetation structure of 10 forest stands in the Caribbean lowlands of Costa Rica.*

Site	*Tree density (no./ha)*	*Tree basal area (m^2/ha)*	*Sapling density (no./ha)*	*Seedling density (no./ha)*
Second growth				
Lindero Occidental	1235	33.4	7363	13271
Peje	927	32.7	5396	11667
La Martita	1115	26.8	7971	11625
Cuatro Rios	1356	33.6	7674	10889
Sendero Holdridge	1091	35.5	6619	16313
mean	1145	32.4	7004	12753
Old growth				
La Selva	1015	27.8	6121	17271
Chilamate	870	32.8	7740	12395
Cay Rica	900	31.1	5153	13170
mean	928	30.6	6338	14279
Selectively logged				
Intervenido	986	31.9	5856	12467
Kelady	971	32.0	7143	18901
mean	979	32.0	6500	15684
p	0.114	0.687	0.693	0.459

**Stands with different land-use history did not differ significantly in stand structure characteristics.*

(1998). Nicotra et al. (1999) describe woody seedling regeneration and light conditions in eight of these stands.

In each stand, vegetation was sampled in nested, contiguous quadrats along three parallel transects 100–160 m in length. Trees ≥5 cm dbh were sampled in 10 × 10 m quadrats (total area sampled per stand = 0.24 −0.48 ha); saplings (stems >1 m high and <5 cm dbh) were sampled in 5 × 5 m quadrats (total area sampled per stand = 0.135 - 0.24 ha); and seedlings (stems 20–100 cm high) were sampled in 1 × 1 m quadrats (total area sampled per stand = 270 - 480 m^2). Transects did not traverse any steep slopes or known environmental gradients. Species were identified in the field by project staff assisted by an expert local naturalist; in questionable cases, specimens were collected, dried, pressed, and used to identify species by comparison with specimens in the La Selva Herbarium or the Costa Rican National Herbarium. Vegetation data were entered into a specimen-based, relational database (Biota; Colwell 1996). Species names follow those of Wilbur (1994).

Ethnobotanical Survey

Although local residents use some nontimber forest products from these stands, such as palm heart, the study areas have been protected from logging and other forms of use. Indigenous peoples have not lived in the Sarapiquí region for hundreds of years. Ethnobotanical information about these species therefore must be obtained from traditional peoples (indigenous and nonindigenous) currently living in neighboring areas within this floristic zone. We use the term *useful* to refer to those species documented in the field, through observations and interviews, and from the literature as having medicinal, timber, or nontimber value to traditional peoples. We recognize, however, that virtually any species can have some potential use. The selection of a species for use is a complex process, involving personal preference or bias, knowledge level, cultural beliefs, abundance, familiarity, access, and the amount of processing required prior to use (Phillips & Gentry 1993).

Ethnobotanical uses of species found within our vegetation inventory were compiled by F. G. C. based largely on detailed ethnobotanical studies of the Garífuna, Sumu, and Miskitu of eastern Nicaragua, who live in the same rainforest zone found in northeastern Costa Rica, just north of the Rio San Juan (Coe & Anderson 1996*a*, 1997, 1999). The territory of the Sumu and Miskitu indigenous groups at one time included parts of northeastern Costa Rica. In the case of the Miskitu, their territory reached as far south as Bocas del Toro, Panama (Conzemius 1932; Smutko 1985; Bell 1989). The Garífuna people, descendants of the Arawaks and Red Carib Islanders, are relative newcomers to the Atlantic coast of Nicaragua and learned ethnobotanical uses from the Sumu and Miskitu (Coe & Anderson 1996*a*). Species utilized by these groups are of wide taxonomic diversity. Complete accounts of these species and their uses are provided by Coe and Anderson (1996*a*, 1997, 1999).

Additional information on the uses of woody species in our inventory was compiled from 20 published accounts of species used by other indigenous and nonindigenous peoples throughout the lowland wet forest life zone of Costa Rica and Panama (list available from authors upon request). For broadly distributed species used differently throughout their range, only Costa Rican uses were considered here. Species with timber uses reach diameters sufficiently large to mill into boards; these are extracted for commerce as well as local use and are mostly species of high-quality wood. Timber species currently used in local or international commerce in Costa Rica were considered of commercial value; others were classified as traditional value only. The commercial value of timber and nontimber forest products varies greatly among regions and countries and is subject to market demand. Species used for construction were distinguished from timber species in their extraction for noncommercial purposes, primarily for local use in construction of dwellings and dugouts. Use values (high, moderate, low) were recorded for each species for each of 20 use categories (Fig. 1). Use categories and use values were entered as auxiliary fields in the species table of the Biota database (Colwell 1996). Specimen data were then exported by site, size-class, and use value for subsequent tabulation and statistical analysis. Raw abundance data for each stand were converted to density based on the actual areas sampled. A complete listing of species and their uses can be obtained upon request from the senior author or at http://viceroy.eeb.uconn.edu/usefulspecies.

Statistical Analysis

Differences among stand types in the percentage of useful species and individuals and on the densities of useful trees, saplings, and seedlings were examined by one-way analysis of variance (ANOVA). For density comparisons, Tukey's Honest Significant Difference post-hoc tests were used only when differences among stand types were significant ($p > 0.05$). To compare the relative abundance of timber and medicinal species among stand types, we used a Kruskal-Wallis nonparametric test. One-way ANOVA was used to compare basal area of timber species among stand types.

Results

Species Richness and Uses

In total, 24,769 specimens were recorded in the vegetation inventory, representing 459 woody taxa. We identified 382 species, representing 81 families. Of these, 320 were useful species, constituting 70% of the total number of species (including unidentified taxa) and 86% of the total individuals found within the study area. Within each stand and size class, the mean percentage of identified species with at least one use was higher for trees than for seedlings and saplings and did not differ significantly among stand types (Table 3). Because unidentified taxa were excluded, these figures were larger than those based on the total number of species and individuals present. The percentage of useful woody individuals (specimens) was higher for trees as well, reaching an average of 97% in the logged forests. Stand types differed significantly in the percentage of useful individuals for saplings only (one-way ANOVA, $p = 0.047$; Table 3). Of the 139 species with no known human use, 21 (15%) remained unidentified at the genus or family level, suggesting that we likely underestimated the number of useful woody species within the study region.

Across the entire vegetation inventory, the medicinal use category contained the largest number of species (167; Fig. 1), followed by construction (117 species), firewood (90), crafts (87), food (67), and timber (47). Less species-rich use categories were tool handles, dyes or tannins, boxes and crates, cordage, thatch, fence posts, matchsticks, and resins. The remaining five categories (fiber, stupifier, soap, fodder, and poison) contained fewer than 5 species; densities of species in these categories were not statistically compared among stand types (Fig. 1).

Four families dominated the set of useful species. The Fabaceae contained the largest number of useful species (33), followed by the Rubiaceae (30), the Melastomataceae (25), and the Arecaceae (23). These also were the most common families with woody taxa occurring in the study area (Hartshorn & Hammel 1994). Half of the useful species observed in the vegetation inventory were found in only 8 plant families; these 8 families comprised 48% of the total number of woody species sampled. Of the 17 families with 5 or more species in the study area, on average, 83% of the species had at least one use.

Many species had multiple uses; six species had seven different uses. For example, *Pouteria campechiana* and *P. glomerata* ssp. *stylosa* (Sapotaceae) were used for food, medicine, tool handles, construction, firewood, charcoal, and crafts. *Virola koschnyi* (Myristicaceae), a species widely planted in reforestation projects throughout Sarapiquí, has 6 uses (timber, medicine, boxes and crates, construction, resins, and soap).

Medicinal Species

For trees ≥5 cm dbh, density of medicinal species ranged from 353 to 913 stems/ha. The second-growth stands had a significantly higher density of medicinal trees (mean of 740 stems/ha) compared to both old-growth (mean of 434 stems/ha) and selectively logged stands (mean of 542 stems/ha; one-way ANOVA, $p < 0.022$; Fig. 2). Mean medicinal sapling density ranged from 2152 stems/ha in the old-growth stands to 3483 stems/ha in the second-growth stands (Fig. 3). In the seedling size class, mean density of medicinal species ranged from 6742 stems/ha in the second-growth stands to 9087 stems/ha in the selectively logged stands (Fig. 4). For these smaller size classes, density of medicinal species did not differ significantly among stand types (one-way ANOVA, $p > 0.05$; Figs. 3 & 4).

The greater density of medicinal trees in the second-growth stands reflected a higher relative abundance of medicinal species. In the second-growth stands, 65% of the trees ≥5 cm dbh had medicinal value, compared to 48% in the old-growth and 56% in the selectively logged forests. Second-growth forests showed significantly higher relative abundance of medicinal trees and saplings compared to old-growth stands (Kruskal-Wallis, $p = 0.041$ [trees] and $p = 0.049$ [saplings]; Fig. 5a). Relative abundance of medicinal species did not vary significantly among stand types for seedlings (Kruskal-Wallis, $p = 0.56$; Fig. 5a).

Table 3. The percentage of identified species and individuals of these species with at least one use (mean % ±1 SD), grouped by stand type and size class.*

	Stand type		
Size class	*Old growth* (n = 3)	*Second growth* (n = 5)	*Logged* (n = 2)
Percentage of species			
trees	90.0 ± 2.3	87.1 ± 4.6	93.4 ± 0.5
saplings	84.7 ± 4.0	84.9 ± 2.5	84.9 ± 1.3
seedlings	81.1 ± 1.5	81.7 ± 5.5	80.6 ± 0.5
Percentage of individuals			
trees	95.4 ± 1.9	91.5 ± 4.1	97.4 ± 0.5
saplings	87.5 ± 4.6	81.0 ± 8.2	91.7 ± 0.3*
seedlings	83.3 ± 5.6	75.9 ± 10.6	83.4 ± 1.6

**One-way analysis of variance across stand types,* p *< 0.05.*

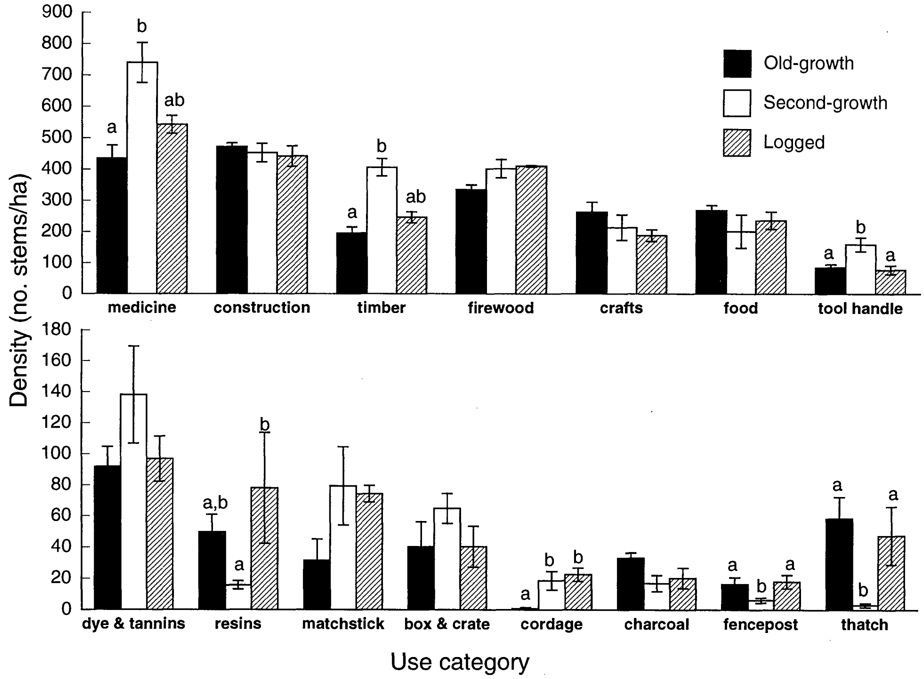

*Figure 2. The mean density of trees ≥5 cm dbh ±1 SE for 15 use categories in old-growth, second-growth, and selectively logged stands. Letters indicate significantly different means across stand types based on Tukey's HSD post-hoc test (*p *< 0.05).*

Timber Species

DENSITY AND RELATIVE ABUNDANCE

Second-growth forests also showed significantly higher density of timber trees ≥5 cm dbh than both old-growth and selectively logged forests (one-way ANOVA, $p = 0.002$; Fig. 2). On average, second-growth forests contained 406 stems/ha, whereas old-growth forests contained 195 stems/ha and selectively logged forests contained 246 stems/ha for tree species with timber value. Density of timber species in the sapling and seedling size class varied greatly across forests and did not differ significantly among stand types (Figs. 3 & 4). Two second-growth forests showed high sapling densities, up to 1533 stems/ha in La Martita. This forest has excellent regeneration of timber species such as *Brosimum guianensis*, *Dendropanax arboreus*, *Dipteryx panamensis*,

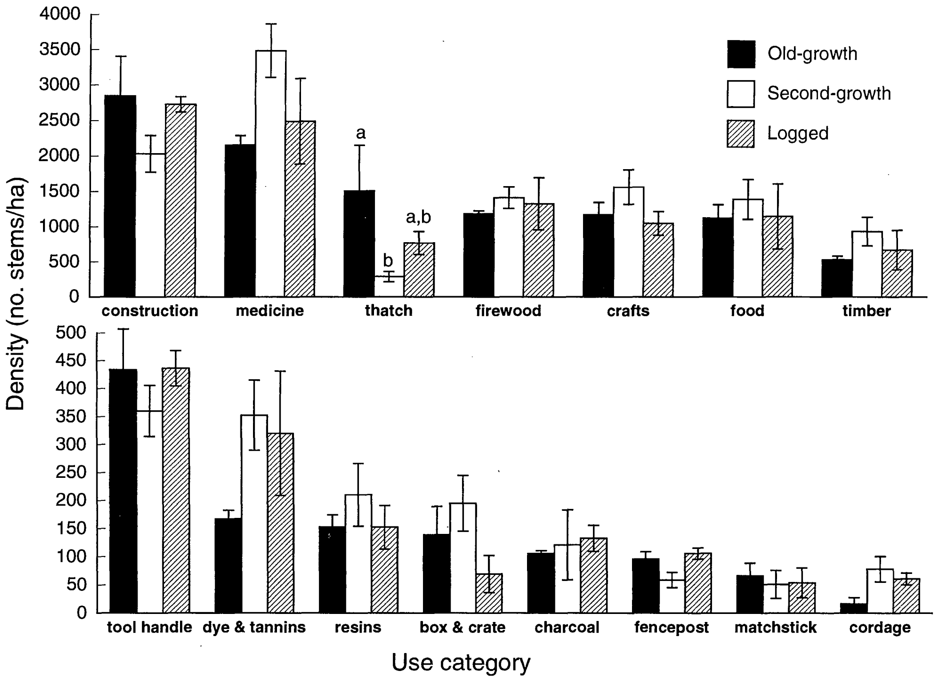

*Figure 3. The mean density of saplings <5 cm dbh ±1 SE for 15 use categories in old-growth, second-growth, and selectively logged stands. Letters indicate significantly different means across stand types based on Tukey's HSD post-hoc test (*p *< 0.05).*

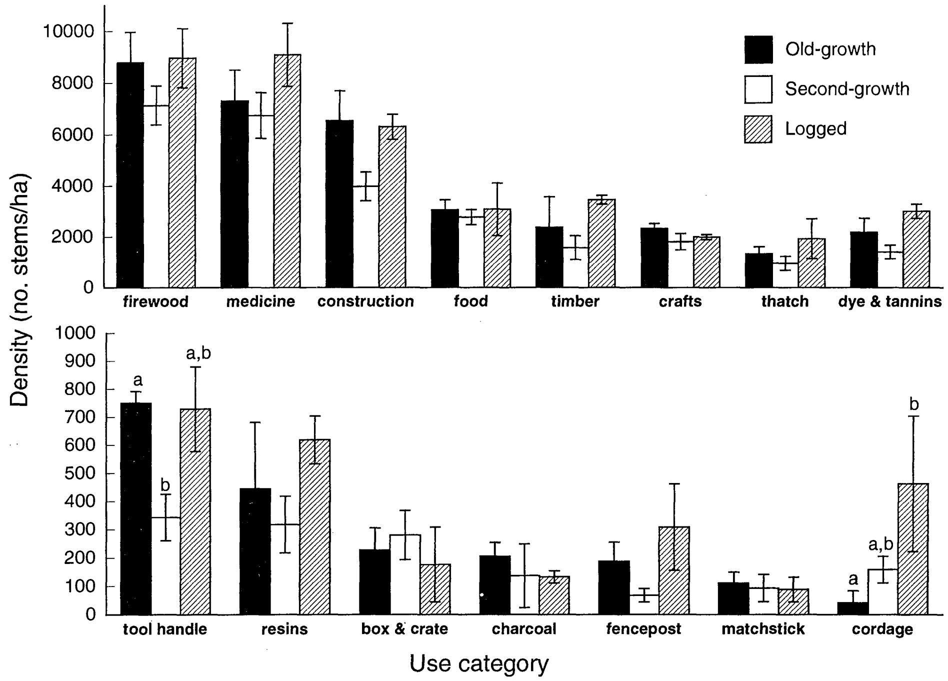

Figure 4. The mean density of seedlings <1 m high ±1 SE for 15 use categories in old-growth, second-growth, and selectively logged stands. Letters indicate significantly different means across stand types based on Tukey's HSD post-hoc test (p < 0.05).

Minquartia guianensis, *Pentaclethra macroloba*, and *Vochysia ferruginea*. These long-lived species also occupy the canopy of old-growth stands. The relative abundance of timber species was significantly higher in the second-growth forests (mean of 35%) than in old-growth (mean of 22%) and selectively logged forests (mean of 25%; Fig. 5b). Saplings and seedlings showed no significant difference in the relative abundance of timber species among stand types (Fig. 5b).

BASAL AREA OF TIMBER SPECIES

Although density is a useful comparative measure, the basal area of stems above some marketable diameter is a better measure of site occupancy by timber species. When only high-quality (commercial) timber species are considered, no significant difference is observed in the basal area of trees ≥30 cm dbh or between 10 and 30 cm dbh between second-growth and old-growth forests, although selectively logged forests clearly showed previous removal of virtually all high-quality timber (Fig. 6a). *Vochysia ferruginea*, a common second-growth canopy dominant, is a high-quality timber species that contributes substantially to the basal area in several of the forests studied.

For moderate- and low-quality timber species, second-growth forests showed significantly higher basal area in the 10–30 cm dbh size class, but not for stems ≥30 cm dbh (Fig. 6b). The enhanced timber basal area of this smaller size class in second-growth forests is due largely to the high density of small trees of moderate timber value, such as *Goethalsia meiantha*, *Laetia procera*, and *Pentaclethra macroloba*.

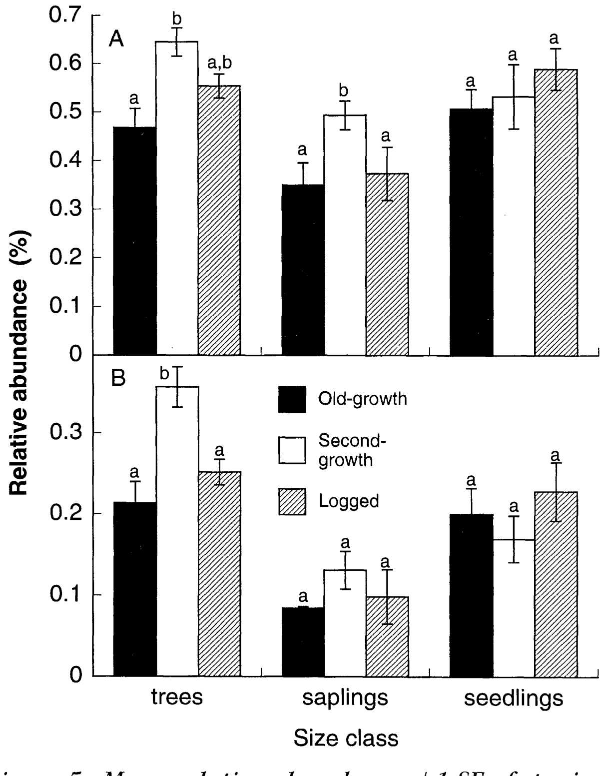

Figure 5. Mean relative abundance ±1 SE of species with (a) medicinal use and (b) timber use in old-growth, second-growth, and recovering logged stands.

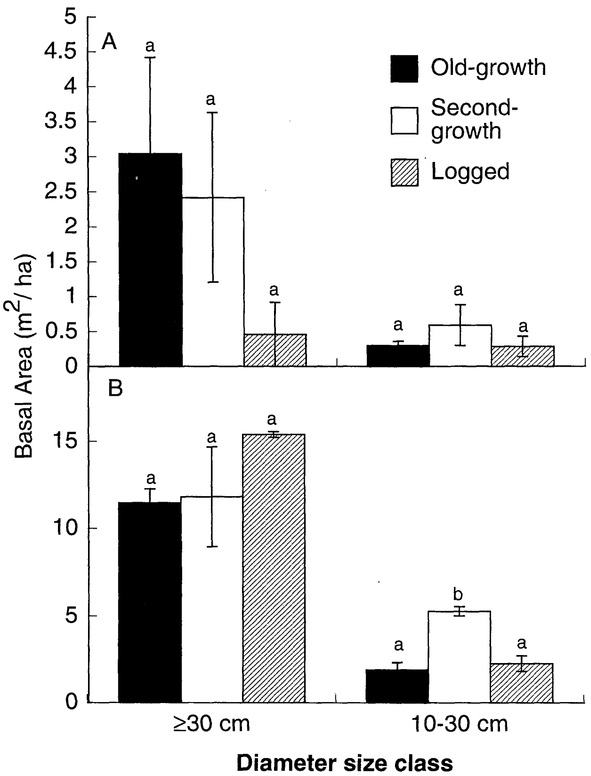

Figure 6. Mean basal area (m^2/ha) ± 1 SE of (a) high-quality commercial timber species and (b) low- to moderate-quality timber species in two diameter size classes: ≥ 30 cm dbh and 10–30 cm dbh. Letters indicate significantly different means across stand types based on Tukey's HSD post-hoc test ($p < 0.05$).

Nontimber Uses

The abundance of trees, saplings, and seedlings of species used for construction, firewood, crafts, food, boxes and crates, matchsticks, and charcoal did not differ significantly among stand types (Figs. 2–4). The density of trees used for tool handles was greater in second-growth than old-growth or selectively logged forests, whereas trees used for thatch, fence posts, and resins were significantly less dense in second-growth forests (Fig. 2). Saplings of species used for thatch were less dense in second-growth forests than in old-growth forests (Tukey's HSD post-hoc test; $p = 0.03$; Fig. 3). The low density of thatch species can be attributed to the relatively low density of mature canopy and understory palms in 15- to 25-year-old second-growth forests (Guariguata et al. 1997). Seedling density showed significant differences among stand types for only two use categories, tool handles and cordage (Fig. 4).

Discussion

Second-growth forests in the Sarapiquí region of Costa Rica are rich in useful species and contain higher densities of trees used for medicinal and timber purposes than neighboring old-growth forests (Fig. 2). In fact, these well-developed secondary forests show a significantly greater relative abundance of medicinal and timber species in the tree size class due to differences in both species composition and tree density (Fig. 5). Dominant tree species in second-growth forests of this region have notable medicinal and timber values as well as other uses. These dominant species include *Casearia arborea*, *Cordia bicolor*, *Goethalsia meiantha*, *Laetia procera*, and *Pentaclethra macroloba* (Finegan 1996; Guariguata et al. 1997), which all have low or moderate traditional medicinal uses. With the exception of *Pentaclethra macroloba*, these species have greater total abundance in the second-growth than in the old-growth stands in our study (Guariguata et al. 1997). *Goethalsia meiantha*, *Laetia procera*, and *Vochysia ferruginea* reach high densities in the second-growth canopy and have moderate to high timber value on the commercial market (Guariguata et al. 1997). Although the commercial use of timber species in old-growth forests of Costa Rica is generally restricted to boles above 70 cm dbh, exploitation of trees with diameters as small as 10 cm is increasing in second-growth forests and plantations.

These findings suggest that rapid regeneration of secondary forest and recovery of selectively logged stands can restore, and in the case of medicinal and timber uses, even augment the utilitarian value of these forests. The high abundance of useful tree species in the second-growth forests is particularly notable given their lower overall tree species richness (Guariguata et al. 1997). It is essential to note, however, that these young stands represent a best-case scenario for successful secondary forest regeneration (Uhl et al. 1988; Corlett 1991; Nepstad et al. 1991; Lugo et al. 1993; Guariguata et al. 1997). Several large areas of old-growth forest remain in the region and serve as important seed sources. Remnant trees of commercial timber species are found within many of these second-growth stands (Guariguata et al. 1997). Moreover, these stands have been protected from harvesting and exploitation since the second-growth vegetation developed. These factors contribute to the rapid recovery of tree basal area, recovery of woody seedling abundance and species richness (Chazdon et al. 1998; Nicotra et al. 1999), and the high abundance of useful species currently found within these 15- to 25-year-old stands.

Our emphasis on woody species results in an underestimation of useful species richness and abundance in these forests. Of the 153 species of alkaloid-containing medicinal species used by the Garífuna, about one-half are herbaceous and only 28% are trees (Coe & Anderson 1996*b*). In a regional survey of 1380 species in the humid Mexican tropics, herbaceous species (including herbs, vines, and epiphytes) constituted the largest fraction of useful species (Toledo et al. 1995). Wood and food resources tended to be concentrated in primary forests, whereas medicinal and other nontimber products were associated with secondary forest (Toledo et al. 1992).

Our results support the findings of Toledo et al. (1995) in the humid tropics of Mexico, Boom (1989) in Bolivia, Balick and Mendelsohn (1992) in Belize, and Grenand (1992) in French Guiana and Brazil. A quantitative survey of five 1-ha plots in tropical wet forests of Mexico by Toledo et al. (1995) showed that 72% of the individuals >3.3 cm dbh had at least one ethobotanical use. Moreover, their regional floristic and ethnobotanical database revealed that second-growth forests produce twice as many forest products as old-growth forests. In the Atlantic rain forest of eastern Brazil, plots in second-growth forest yield 2.7 times the number of medicinal species identified in primary forest plots (Voeks 1996). In eastern lowland Ecuador, medicinal species from secondary forest and gardens are used more frequently than those from primary forest (Kohn 1992).

Species from second-growth habitats are more familiar and accessible and may be more pharmacologically rich than species found in old-growth forests (Kohn 1992; Voeks 1996). Voeks (1996) suggests the notion of a "disturbance pharmacopoeia": secondary forest species, weeds, and even garden cultivars may represent a more likely and accessible source of bioactive compounds than primary forest taxa. Furthermore, ecological studies show that the amounts and type of secondary compounds associated with leaf defense against herbivory are correlated with ecological conditions, leaf lifetime, and tree growth rates (Coley et al. 1985). Concentrations of immobile leaf defenses, such as phenolics, are lower in fast-growing tree species with short leaf lifetimes than in slow-growing mature forest tree species with long leaf lifetimes (Coley 1983). In contrast, mobile leaf defenses, such as alkaloids, phenolic glycosides, and cyanogenic glycosides are expected to be higher in species with short leaf lifetimes in resource-rich environments because of the high metabolic cost of turnover (Coley et al. 1985).

Increased knowledge of the uses of species found in regenerating and logged tropical forest stands will increase public awareness of the need for the conservation and sustainable management of these lands. Old-growth stands in all tropical regions continue to be exploited for timber and other forest products. Yet these old-growth forests should become increasingly protected as their value in conserving biodiversity becomes critical (Whitmore 1997; Bawa & Siedler 1998). If timber and nontimber forest products can be obtained sustainably from managed second-growth forests, protection of existing old-growth forests may be a more attainable conservation goal (Budowski 1988). In many tropical countries, second-growth and logged forests will of necessity become the focus of increasing exploitation for timber as well as nontimber forest products. In Costa Rica, the area of second-growth forest suitable for timber harvesting now exceeds the area of productive old-growth forests (Müller & Solís 1997). Tropical second-growth forests may be more amenable to sustainable management than old-growth forests due to their high total and relative abundance of useful species, greater accessibility to human settlements, and more even age structure (Finegan 1992; Weaver 1995; Sips 1997; Guariguata 1999).

The rapid pace of secondary forest regeneration observed in many abandoned pastures of Costa Rica and Amazonia depends on many factors, including a surrounding landscape matrix with intact areas of old-growth forest, viable populations of seed dispersing animals, and protection from fire and overexploitation (Uhl et al. 1989; Holdsworth & Uhl 1997; Turner & Corlett 1996). Just as regeneration of second-growth depends critically on the proximity of old-growth areas, the protection of old-growth forests depends upon the sustainable extraction of forest products from managed second-growth, logged forests, or plantations. Our findings suggest that a diverse landscape matrix of managed and protected forests offers a promising vision of sustainable extraction of useful products while protecting biological diversity in tropical wet forests.

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