

Canopy development in tropical tree plantations: a comparison of species mixtures and monocultures

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Abstract

In this study, the early development of monocultures and mixtures of *Cedrela odorata*, *Cordia alliodora*, and *Hyeronima alchorneoides* was measured to determine what interspecific differences in structural characteristics lead to good ecological combining ability in fast-growing tropical tree species. Plantations were established at high density (2887 trees/ha) on fertile alluvial soil in the humid Atlantic lowlands of Costa Rica. The three species are native to the region and were selected to represent a range of crown structure, leaf morphology, and phenology. Height growth was rapid for all three species, with dominant heights (mean height of tallest 20% of trees) of monocultures reaching 7–8 m at age 2.0 yr, and 14–15 m at age 4.0 yr. At age 2.0 yr, monocultures had nearly reached their maximum leaf area index (LAI), with *Hyeronima* forming a denser canopy (LAI of 4.5) than the other two species (LAI's of 2.5). In mixtures, a partially stratified canopy developed with the tallest *Cordia* forming an upper canopy stratum above *Cedrela* and *Hyeronima*. Mixtures reached an LAI of 3.9 by age 3.0 yr, approaching the level of the *Hyeronima* monoculture. Compared to their growth in monoculture, *Cordia* was taller and *Hyeronima* was shorter in mixture, but both species developed larger mean crown size and breast-height diameters in mixture. In contrast, *Cedrela* was smaller in all dimensions in mixture than in monoculture. The poor growth of *Cedrela* in mixture likely resulted from the early onset of interspecific competition coupled with damage from attacks of the shootborer *Hypsipyla grandella*. *Cedrela* seedlings recovered their rapid growth in monoculture after early insect attacks, but were suppressed in mixtures by the competition from surrounding trees of *Cordia* and *Hyeronima* which are not susceptible to the shootborer. The compatibility of *Cordia* and *Hyeronima* was related to the formation of a stratified canopy in mixture. *Cordia* has more rapid seedling height growth than *Hyeronima*, but forms a more open canopy with low LAI and semi-deciduous foliage. This results in the interception of sufficient solar radiation in the upper canopy to allow high productivity of *Cordia*, and yet adequate transmission of radiation to the dense, evergreen crowns of *Hyeronima* for rapid growth of that species in the lower canopy. This combination of characteristics is likely to lead to compatibility in other sets of tree species. © 1998 Elsevier Science B.V.

Keywords: Leaf area index; Ecological combining ability; *Cordia*; *Cedrela*; *Hyeronima*

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1. Introduction

1.1. *Stand development in mixtures*

The establishment of plantation monocultures has dominated much of the intensive forest management practiced in the humid tropics of America. Moreover, although many neotropical tree species produce wood with high timber value, most forestry research and practice has concentrated on a small number of non-indigenous species. Growing interest exists in modifying these practices both by creating mixed-species plantations and by making greater use of native tree species.

The idea of mixing two or more plant species in a single plantation is a fundamental part of agroforestry practice, but it has not been as widely applied to the design of timber plantations. The potential advantages of species mixtures over monocultures have been reviewed recently for a variety of tropical regions (FAO, 1992; Ball et al., 1995; Keenan et al., 1995; Montagnini et al., 1995). Some of these advantages can be achieved with plantations in which each species is grown in monospecific groups (a ‘coarse-grained’ mixture). Such mixtures may improve wildlife habitat and landscape aesthetics and, by diversifying forest product outputs, reduce the landowner’s market risk. However, other advantages of mixtures require a plantation structure in which species are intimately intermixed (a ‘fine-grained’ mixture). These include the potential for increasing total wood production per unit land area, for providing for compensatory growth of one species if disease or pests affect another, and for achieving better site protection from nutrient leaching, erosion, or invasion of weeds.

Because individuals of different species do not directly interact in coarse-grained mixtures except along edges of groups, criteria for choosing tree species to plant in such stands do not differ markedly from those used in establishing large monocultures. In contrast, the selection of species to combine in fine-grained mixtures demands more attention to the compatibility of growth characteristics. The concept of competitive exclusion suggests that if two species are identical in their growth characteristics (i.e., there is complete overlap in their ecological niches) one

will be more successful in a given habitat and exclude the other. Thus, it is necessary to combine species that differ in such characteristics as height growth, shade tolerance, crown structure, phenology, or rooting depth. If the species differ sufficiently, they will capture growing space and use resources differently when grown together in mixture. Such species will be able to coexist and are said to have complementary characteristics, or good ‘ecological combining ability’ (Harper, 1977). In these mixtures, the intensity of interspecific competition is likely to be less than that of intraspecific competition. This has been found in some cases to lead to greater overall productivity in mixtures than in monocultures of the component species—an outcome referred to as the competitive production effect or competitive reduction (Vandermeer, 1989; Kelty, 1992).

Evidence from monoculture planting trials can provide some indication of whether sets of species possess complementary characteristics. However, interactions between individuals within a stand alter the size, allometry, growth rate, and survival of trees, and these effects differ between intraspecific competition and interspecific competition (Cannell et al., 1984; Sørensen-Cothorn et al., 1993). Therefore, it is necessary to compare the effects of competition in mixtures with that in monocultures of the component species, and a variety of experimental approaches have been developed for this purpose (e.g., Harper, 1977; Vandermeer, 1989; Firbank and Watkinson, 1990; Snaydon, 1991; Kelty and Cameron, 1995).

One model for use in designing mixed-species tropical plantations can be drawn from studies conducted in temperate forests. Although slower tree growth rates in temperate climates make it more time-consuming to measure the growth of experimental plantings, the presence of annual growth rings in temperate tree species has made it possible to reconstruct the development of mature stands. For many combinations of species, naturally regenerated even-aged mixed stands have been found to develop canopies in which the crowns of different species are partially or completely segregated into separate canopy strata (Smith, 1986; Oliver and Larson, 1996). This ‘even-aged stratified-canopy’ model of mixed stand development is most commonly found in regions with ample precipitation where tree species diversity is high.

The relationship between juvenile height growth rates and shade tolerance among species plays an important role in determining development patterns in this model. Shade-intolerant species dominate early successional stands through high allocation of production to stem and branch growth, thereby capturing above-ground growing space quickly (Firbank and Watkinson, 1990; King, 1990). Species of greater shade tolerance have comparatively higher allocation to root and leaf production, with lower total production rates as seedlings. This results in relatively slow height growth for some shade-tolerant species throughout their life. However, slower productivity and height growth is confined to the seedling stage in many species of intermediate shade tolerance, so if they are not overtopped by other vegetation in early development, they begin to grow as rapidly in height as early successional, shade-intolerant species after reaching the large seedling or sapling stage. Thus, species with different growth-allocation patterns and shade-tolerance levels may develop approximately the same canopy height in monocultures, after initial differences in the seedling stage. In contrast, differences in seedling height growth rates have lasting effects on the development of mixtures. Fast-growing species reach greater heights early in development and partially or completely overtop the species with slower initial height growth, whose subsequent survival depends upon their degree of shade tolerance. The tallest individuals of the upper canopy species are expected to reach the same height in mixture as they would in monoculture, but the lower canopy species are limited in height growth by shading or physical abrasion of terminal shoots against branches of the overstory trees.

Canopy leaf area is strongly affected by differences in moisture and nutrient availability among sites, but on a given site it is largely controlled by the shade tolerance characteristics of the species. Shade-tolerant species generally have greater leaf area than intolerant species in monocultures because their efficiency at low light levels allows more foliage to survive in deeper canopy layers (Assmann, 1970; Monsi et al., 1973). The canopy of a mixture is predicted to develop the same leaf area as a monoculture of the most shade-tolerant component species, because the canopy depth in both cases is controlled by the shade-tolerance of the foliage at the

bottom of the canopy, which is that of the most shade-tolerant species (Kelty, 1992).

1.2. Objectives

The purpose of this study was to compare the development of monocultures and mixtures plantations composed of three fast-growing tropical tree species and test development patterns against the predictions of the even-aged stratified-canopy model formulated for natural stands in temperate regions. The goal is to develop a better understanding of the characteristics that contribute to ecological combining ability in tree species. The specific objectives were: 1) to compare the height, diameter at breast height (DBH), and crown structure (size and shape) of each species established in monocultures and fine-grained mixtures composed of all three species, and 2) to assess leaf area index (LAI) and light interception of the canopies of those plantations.

The three species used in the study are *Cedrela odorata* L. (Meliaceae), *Cordia alliodora* (Ruiz and Pav.) Oken (Boraginaceae), and *Hyeronima alchorneoides* Allemão (Euphorbiaceae), growing in a humid tropical region of Costa Rica. All three are native to the region, and were selected because their differences in growth and structural characteristics indicated potential for complementary interactions. *Cedrela* and *Cordia* are commercially important timber species and have been relatively well-studied for use in agroforestry and reforestation. Less is known about *Hyeronima*, which grows as an emergent in natural stands of the region (Clark and Clark, 1992), but recent work (Butterfield and Fisher, 1994) has shown that its wood quality and growth rates in full sun make it suitable for use in forest plantations. Haggard and Ewel (1995) assessed the biomass allocation strategies, leaf area development, canopy dynamics, and productivity during the first two yr of development of these plantations. This study examined growth from age 1.5 to 4 yr, a period that included the formation of fully closed canopies of 15 m and greater in height.

In order to make predictions about development patterns for these three species based on the even-aged stratified-canopy model, their relative shade-tolerance levels must be known. Although these

species have not been studied in detail at the physiological level, some inferences about relative shade tolerance levels can be drawn from observations of their growth habits. *Cordia* appears to be intolerant of shade and weed competition throughout its life; it is a frequent colonizer of pastures and abandoned fields, and has been classified as a pioneer species (Liegel and Stead, 1990). *Cedrela* is tolerant of shade and weed competition as a seedling, but is intolerant in the sapling stage and beyond; like *Cordia*, it invades pastures and burned sites (Cintron, 1990; Gerhardt, 1993). Thus, *Cedrela* is capable of becoming established either in full sun or shade, but in the latter situation, it requires a large gap or stand-replacing disturbance to grow to mature size. *Hyeronima* has been described as an 'exemplary gap species' (Clark and Clark, 1992). It becomes established in small gaps in mature forests (but rarely beneath closed canopies) and can survive and grow slowly with moderate levels of overtopping foliage as a seedling, sapling, or pole tree; it may require repeated minor canopy disturbances to allow it to advance into the main canopy (Clark and Clark, 1992). *Hyeronima* has not been reported as becoming established in clearings with pioneer species, but it is capable of rapid growth when planted in full sun (Haggard and Ewel, 1995, Butterfield and Fisher, 1994). Thus, a tentative ranking of these species in increasing shade tolerance is *Cordia* < *Cedrela* < *Hyeronima*, with *Cedrela* being more similar to *Cordia* than to *Hyeronima*, and with none of the three showing the high level of shade tolerance of other native species capable of establishment and growth beneath intact overstory canopies. This tentative ranking of shade tolerance is consistent with the greater allocation of growth to stems and branches in *Cordia* and *Cedrela* seedlings compared to *Hyeronima*, when all are growing in full sun (Haggard and Ewel, 1995). This leads to the following predictions about the relative growth rates of these species in mixture and monoculture: (1) in monoculture, all three species will grow in height at approximately equal rates, except in initial stages when *Hyeronima* will lag behind the other two species, and (2) in mixture, *Cedrela* and *Cordia* will form an upper canopy stratum above *Hyeronima*, with *Cordia* and *Cedrela* dominants reaching the same height as they would in monoculture, and (3) the mixture and the

Hyeronima monoculture will have similar LAI, which will be greater than the LAI of *Cedrela* and *Cordia* monocultures.

2. Materials and methods

2.1. Study site and species description

The study was conducted at La Selva Biological Station (10°26' N, 84°00' W) in the Atlantic lowlands of Costa Rica. The Station is located within the Tropical Wet Forest life-zone (sensu Holdridge, 1967), at 40 m elevation above sea-level. It has a mean annual temperature of 26°C, and receives approximately 4000 mm precipitation annually; a dry season extends from January to April, but no month has less than 100 mm precipitation (Sanford et al., 1994). The 7.5-ha study site was situated on an abandoned cacao plantation located on a fertile alluvial terrace with deep, well-drained soil, with pH 6.5 (Haggard and Ewel, 1994).

The three tree species used in the study have markedly different phenologies, leaf sizes, and branching patterns. *Cedrela odorata* is dry-season deciduous and has long, pinnately compound leaves with leaflets of 40 cm² in area. It forms narrow crowns because it does not branch during early growth unless the terminal shoot is damaged by insect attack or other injury. However, when established in plantations, *Cedrela* seedlings seldom escape attack by the mahogany shootborer (*Hypsipyla grandella* Zeller); on fertile soils, most trees survive but the death of the terminal shoot results in the formation of one or more orthotropic branches (Cintron, 1990). *Cordia alliodora* produces plagiotropic branches that grow in whorls of five, forming a crown with distinct horizontal layers of foliage, with leaves of about 30 cm² in area. *Cordia* is evergreen as a seedling, semi-deciduous (in the dry season) as a sapling, and deciduous (in the wet season) as a mature tree. *Hyeronima alchorneoides* is evergreen, has large leaves (about 300 cm² in area on juveniles), and produces whorls of orthotropic branches that form dense compact crowns.

2.2. Plantation establishment

The site was prepared for planting by cutting and burning all vegetation in May 1991. All seedlings were planted between May 20 and June 26, 1991. Further details of plantation establishment techniques and seedling origins are available in Haggard and Ewel (1995). For this study, the planting design consisted of two blocks, with four plantations in each block—one monoculture of each of the three species and one mixture combining all three species. Each monoculture plantation was 0.12 ha in area, and each mixed-species plantation was 0.16 ha. The experiment followed the substitutive (or replacement series) design, in which the mixture is planted at the same density as the monocultures (Vandermeer, 1989; Snaydon, 1991). Each plantation was established with an initial density of 2887 trees/ha in a hexagonal pattern in which each tree is 2 m from each of six neighbors. All plantations were weeded regularly throughout the 4 yr of this study, except that the mixture in one block was not weeded during the first four months after planting; it was subsequently weeded on the same schedule as the other stands.

The mixture was composed of 25% each of *Cordia*, *Cedrela*, *Hyeronima*, and a palm species of the genus *Euterpe* (either *E. macrospadix* Ørst or *E. oleracea* Mart., which were alternated at the planting points designated for *Euterpe*). Within the mixture, each individual of one genus was surrounded by a hexagon comprised of two individuals of each of the other three genera. *Euterpe macrospadix* had poor survival and *E. oleracea* did not grow rapidly in height, so they had little competitive effect on the other three species during early development. For the present study, the mixtures are considered to be composed of one-third each of *Cedrela*, *Cordia*, and *Hyeronima* planted at 75% of the initial density of the monocultures. A mortality rate of about 20% occurred in the *Cedrela* monocultures during the first 2 yr after establishment, largely as a result of shootborer damage. This density reduction was approximately matched by a thinning carried out in the *Cordia* and *Hyeronima* monocultures at age 2.3 yr, which removed approximately 25% of the trees. The mixture was not thinned, as it had begun with an initial tree density (excluding *Euterpe*) that was 25%

lower than that of the monocultures. This reduced the confounding effect of the different tree planting densities on comparisons between monocultures and mixtures.

2.3. Field measurements

Inventories of tree height (to the nearest 0.01 m up to a height of 3.0 m, to the nearest 0.1 m thereafter) were made in each plantation at age 2.0 and 4.0 yr. Buffer strips along all sides of the plantations were not measured.

When stands were 1.5 yr old, permanent plots containing an average of 34 trees each were established for detailed measurements of tree size and crown structure. Two plots were established in each treatment in each block, for a total of 16 plots. Numbers of individual trees measured of each species at the time of plot establishment ranged from 109 to 119 in monoculture and 27 to 45 in mixed stands. Crown measurements were made at age 1.5, 2.5, and 3.5 yr for every tree within each plot; measurements included total height, height to the first leaf, and diameter at breast height (DBH). Measurements of crown radius and height of the widest point of the crown were taken in eight compass directions from the base of each tree. Height was measured to the nearest 0.01 m with a telescoping rod, DBH was measured to the nearest 0.1 cm by a diameter tape, and crown radius to the nearest 0.05 m with a tape. Volume of each crown was calculated by dividing it into 8 sections. Each section was delimited by the top and bottom of the crown at the main stem (crown length), and two adjacent radii of the 8 crown radii measured for each tree. The volume of each section was calculated, and the eight values were added to obtain total crown volume.

Assessment of canopy development was made using two methods. Leaf area index was assessed using a Plant Canopy Analyzer (PCA, LI-COR, Lincoln, NE, USA, model LAI 2000), an instrument that uses a hemispherical optical sensor to measure the proportion of the sky obscured by foliage. One LAI measurement was obtained in each of the four corners of each plot using a 45° view cap. To improve the spatial average of measurements, four to six below-canopy readings were made along a diagonal transect between tree rows (LI-COR, 1989). Hemi-

spherical canopy photographs were used to estimate canopy light interception within each plot. Photographs were taken in the center of each plot from 50 cm above the ground with a 8-mm hemispherical lens (Nikon). Hemispherical photos and PCA measurements were taken every 6 months.

2.4. Data analysis

Differences between monocultures and mixtures in stem height, DBH, crown height, crown projection area, and crown volume at the time of the first measurement (at age 1.5 yr) were assessed using analysis of variance (ANOVA). Because measurements were then repeated on the same individuals at age 2.5 and 3.5 yr, differences in growth over the two-year period were analyzed by repeated-measures ANOVA, using a three-factor model (treatment, block, and age) with a repeated measure on the last

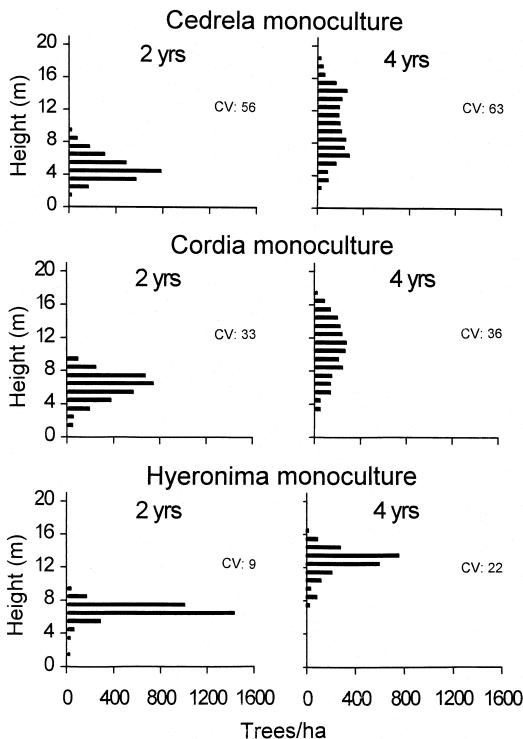


Fig. 1. Height distributions of monoculture plantations of *C. odorata*, *C. alliodora*, and *H. alchorneoides* at ages 2 and 4 yr at La Selva Biological Station, Costa Rica. CV, coefficient of variation (%).

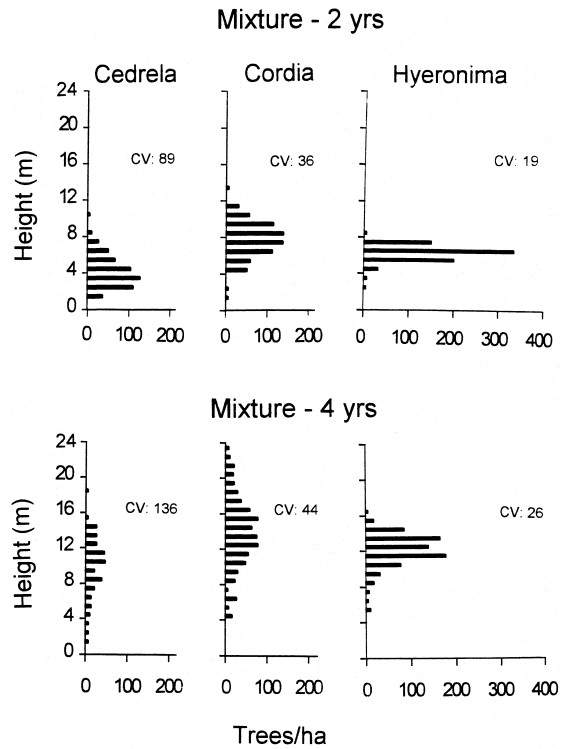


Fig. 2. Height distributions of mixed-species plantations of *C. odorata*, *C. alliodora*, and *H. alchorneoides* at ages 2 and 4 yr at La Selva Biological Station, Costa Rica. CV, coefficient of variation (%).

factor. Treatments (monoculture or mixture) and blocks were considered as fixed effects, and repetitions within blocks as random effects (Bennington and Thayne, 1994); type III sums of squares were used in the analysis because data sets were not balanced. To reduce potential problems of failing to meet the assumptions of normality and equality in the variance–covariance matrices, the degrees of freedom of the repeated-measures *F*-test was adjusted with the Geisser–Greenhouse correction (Crowder and Hand, 1990). The repeated-measures ANOVA tested for differences over the entire two-year measurement period; a profile analysis was also carried out to analyze differences in growth rates for each of the two yr separately. A statistically significant difference indicates that trees growing in different treatments and/or blocks have different growth rates over the time period measured, rather than

Table 1

Dominant height^a (m) of monocultures and mixtures of *C. odorata*, *C. alliodora*, and *H. alchorneoides* at ages 2.0 and 4.0 yr, growing at La Selva Biological Station, Costa Rica

	<i>Cedrela</i>	<i>Cordia</i>	<i>Hyeronima</i>
<i>Age: 2.0 yr</i>			
Monoculture	7.0 (0.3)	8.2 (0.1)	7.8 (0.3)
Mixture	6.8 (0.1)	10.0 (1.0)	7.5 (0.1)
<i>Age: 4.0 yr</i>			
Monoculture	15.1 (0.3)	14.5 (0.2)	14.3 (0.7)
Mixture	13.9 (0.6)	18.6 (1.7)	14.3 (0.3)

^aDominant height is defined as the mean height of the tallest 20% of trees of each species in each plantation. Standard errors in parentheses.

different sizes at a given time, as in ANOVA. To reduce redundancy in data analysis, the repeated-measures ANOVA and profile analysis were conducted for stem height, DBH, and crown volume, but

not for crown length and crown projection area because the latter two variables are highly correlated with crown volume. All analyses were conducted using PC Statistical Analysis Systems (SAS Institute, 1988).

Negatives from hemispherical photography were digitized to allow calculation of the fraction of solar radiation transmitted through the canopy for both direct beam radiation (DSF: direct site factor) and reflected skylight (ISF: indirect site factor) using the CANOPY software (Rich, 1989). The fraction of total solar radiation (GSF: global site factor) at La Selva was defined as 0.45 DSF + 0.55 ISF (Rich et al., 1993). These indices of light transmission are strongly correlated with photosynthetic photon flux density (Rich et al., 1993). Data are reported as 1-GSF, which represents the fraction of solar radiation intercepted by a canopy. Plots were only 12 m by 10 m on average, so only one photo point could

Table 2

Mean tree height, DBH, crown length, crown projection area, and crown volume for *C. odorata*, *C. alliodora*, and *H. alchorneoides* growing in monocultures and mixtures at La Selva Biological Station, Costa Rica

Age (yr)	<i>Cedrela</i>		<i>Cordia</i>		<i>Hyeronima</i>	
	Monoculture	Mixture	Monoculture	Mixture	Monoculture	Mixture
<i>Tree height (m)</i>						
1.5	3.40 (0.10)*	2.51 (0.20)	4.32 (0.11)*	5.24 (0.18)	4.11 (0.06)*	3.85 (0.12)
2.5	6.73 (0.22)	4.62 (0.43)	7.36 (0.19)	9.06 (0.28)	8.41 (0.11)	7.17 (0.14)
3.5	9.35 (0.33)	7.19 (0.61)	9.45 (0.29)	11.33 (0.40)	11.40 (0.14)	9.98 (0.21)
<i>DBH (cm)</i>						
1.5	4.0 (0.1)*	3.2 (0.3)	4.4 (0.1)*	7.0 (0.3)	5.7 (0.1)ns	5.7 (0.3)
2.5	6.6 (0.2)	4.4 (0.5)	7.1 (0.2)	9.0 (0.4)	9.6 (0.2)	10.5 (0.3)
3.5	8.0 (0.3)	5.3 (0.6)	8.0 (0.3)	10.2 (0.6)	11.1 (0.3)	12.5 (0.3)
<i>Crown length (m)</i>						
1.5	1.39 (0.06)ns	1.27 (0.12)	3.36 (0.10)*	4.18 (0.20)	3.23 (0.05)*	2.92 (0.12)
2.5	2.40 (0.12)	1.37 (0.19)	2.56 (0.12)	3.27 (0.18)	3.53 (0.09)	5.31 (0.13)
3.5	3.27 (0.20)	0.98 (0.4)	2.61 (0.13)	2.97 (0.22)	3.27 (0.10)	6.17 (0.22)
<i>Crown projection area (m²)</i>						
1.5	2.19 (0.12)ns	1.76 (0.20)	4.02 (0.16)*	6.22 (0.37)	4.81 (0.18)*	6.01 (0.51)
2.5	4.14 (0.27)	1.91 (0.37)	5.03 (0.31)	7.10 (0.55)	7.80 (0.33)	13.18 (0.53)
3.5	4.15 (0.34)	1.53 (0.29)	5.53 (0.45)	8.10 (0.86)	7.40 (0.45)	14.00 (0.54)
<i>Crown volume (m³)</i>						
1.5	1.57 (0.13)ns	1.14 (0.18)	6.32 (0.37)*	11.73 (1.08)	6.10 (0.33)*	8.16 (0.92)
2.5	5.42 (0.58)	1.37 (0.38)	6.36 (0.58)	11.18 (1.28)	12.09 (0.67)	30.52 (1.79)
3.5	6.70 (0.79)	0.92 (0.20)	8.06 (0.98)	12.45 (1.80)	11.27 (0.90)	37.80 (2.33)

Tests of differences between monoculture and mixture within each species were conducted for the initial measurement only, at age 1.5 yr (*, significant at $p < 0.05$; ns, not significant). Repeated-measures ANOVA and profile analysis were used to assess growth differences over the subsequent two yr (see Tables 3 and 4).

fit in each without overlap with an adjacent photo; thus, results must be interpreted cautiously and are used here to corroborate PCA measurements of LAI.

3. Results

3.1. Plantation height structure

Height distribution patterns diverged among the monocultures, with *Cedrela* and *Cordia* developing greater variability in height than *Hyeronima*. This difference was already present at age 2.0 yr (Fig. 1), and was maintained during the next two yr. At age 4.0 yr, *Cedrela* and *Cordia* had broad distributions in tree height, ranging from 3 to 17 m in both species; in contrast, *Hyeronima* maintained a more uniform distribution, with most trees 12 to 14 m tall. The height distribution of each species in the mixtures followed a pattern similar to that in the monocultures, with *Cedrela* and *Cordia* more variable than *Hyeronima* (Fig. 2).

The height of the trees forming the upper canopy in each stand was compared using the concept of 'dominant height' (defined here as the mean height of the tallest 20% of trees in each stand). Although height distributions of all trees varied among the species in monoculture, the dominant heights were similar for all three, reaching approximately 7–8 m at age 2.0 yr and 14–15 m at age 4.0 yr (Table 1). *Cordia* dominant height in mixture was greater than that of *Hyeronima* or *Cedrela*; some *Cordia* rose above the other two species, forming an upper stratum. The tallest *Cordia* trees reached greater heights in the mixtures than in monocultures—the dominant height of the *Cordia* component of the mixture was greater by 4.1 m (28% greater) than that of *Cordia* in monoculture at age 4.0 yr.

3.2. Growth of individual trees

Cedrela was significantly smaller in mean height and DBH in mixture compared to monoculture in the initial measurement at age 1.5 yr (Table 2), and grew significantly more slowly in height from age 1.5–2.5 and in DBH from age 2.5–3.5 yr (Table 3, Fig. 3). Crown volume growth was less in mixture in both years of measurement (Tables 3 and 4). Mean crown

Table 3

Results of profile analysis for comparison of monocultures and mixtures growing at La Selva Biological Station, Costa Rica

	Tree height	DBH	Crown volume
<i>C. odorata</i>			
Measurement period: 1.5–2.5 yr			
Treatment	0.0002 *	0.0563	0.0101 *
Block	0.0005 *	0.5703	0.1154
Treatment × block	0.0151 *	0.3274	0.7719
Measurement period: 2.5–3.5 yr			
Treatment	0.5563	0.0047 *	0.0066 *
Block	0.8510	0.0877	0.1331
Treatment × block	0.4803	0.1419	0.6244
<i>C. alliodora</i>			
Measurement period: 1.5–2.5 yr			
Treatment	0.0147 *	0.3738	0.7579
Block	0.8012	0.2406	0.0308
Treatment × block	0.9590	0.5305	0.0135 *
Measurement period: 2.5–3.5 yr			
Treatment	0.2361	0.4102	0.3702
Block	0.5736	0.5326	0.9521
Treatment × block	0.0058 *	0.1426	0.1509
<i>H. alchorneoides</i>			
Measurement period: 1.5–2.5 yr			
Treatment	0.0002 *	0.0074 *	0.0006 *
Block	0.0005 *	0.0496	0.2010
Treatment × block	0.0151 *	0.9649	0.4317
Measurement period: 2.5–3.5 yr			
Treatment	0.5563	0.0371	0.0032 *
Block	0.8510	0.1623	0.7531
Treatment × block	0.4803	0.2630	0.5698

Values are probabilities to test for differences in growth rates between treatments (monoculture vs. mixture), blocks, and treatment × block interactions for each species (* denotes *p* values < 0.025, which maintains an experiment-wise rejection rate of 0.05). Growth was analyzed separately for each year of the two-year study period (ages 1.5–2.5 yr and 2.5–3.5 yr).

volume of *Cedrela* in mixture decreased in the second year, while increasing at a moderate rate in monoculture. At age 3.5 yr, crown volume in mixture was less than 15% of that in monoculture, as a result of both smaller crown length and crown area. Crown differences were greater than differences in height and DBH.

Cordia, in contrast, developed greater size in all dimensions in mixtures than in monocultures (Table 2). The height difference was more than 1 m at the time of first measurement (age 1.5 yr), and height growth was significantly greater from age 1.5 to 2.5 yr, but not later (Table 3); the first-year difference

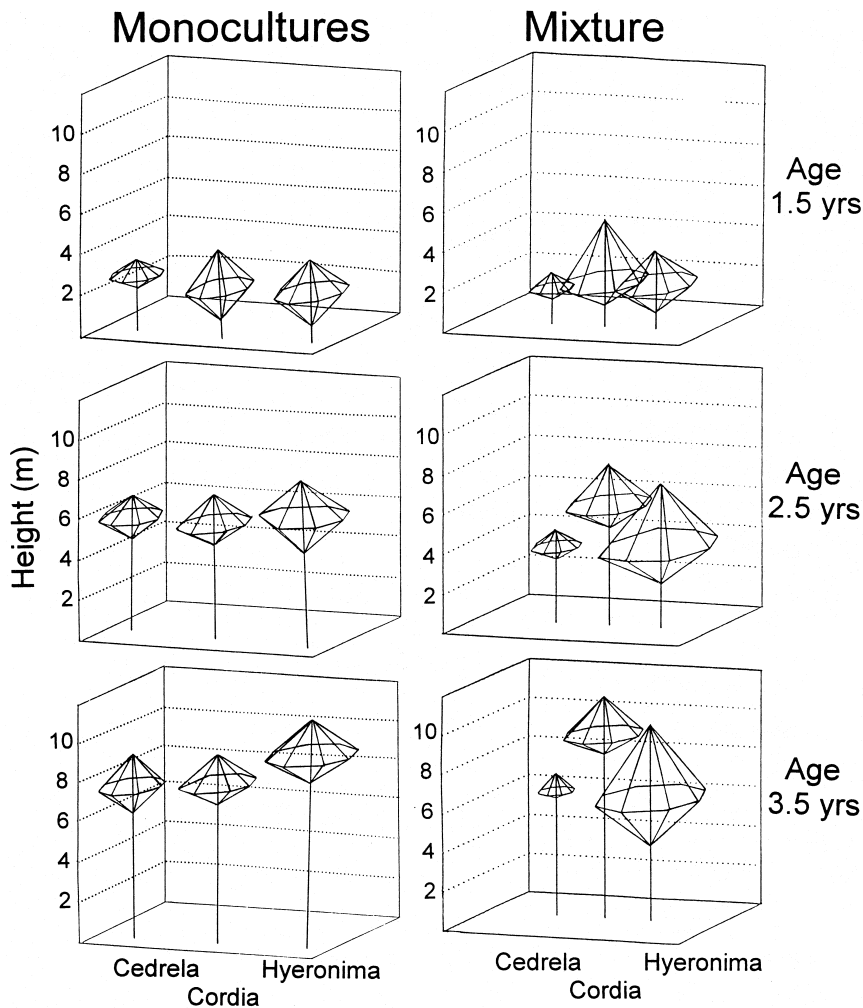


Fig. 3. Schematic representation of mean stem height and crown dimensions of *Cedrela*, *Cordia*, and *Hyeronima* trees growing in monocultures and mixtures at ages 1.5, 2.5, and 3.5 yr at La Selva Biological Station, Costa Rica. Crown dimensions are drawn to the same scale as tree height.

was great enough to produce a significant difference for the two-year period as a whole (Table 4). Crown volume and DBH growth were not significantly different between monocultures and mixtures after age 1.5 (Table 4), so the initial difference that had developed in the first 1.5 yr was maintained. At age 3.5 yr, mean crown volume was 50% greater in mixture, which was due mainly to greater crown area rather than crown length.

Hyeronima was shorter but had greater crown volume in mixture than monoculture at age 1.5; these differences were not large, but were statistically

significant because *Hyeronima* trees were quite uniform within each stand. During the subsequent two yr, large differences developed. Height growth was significantly less in mixture from age 1.5–2.5, but crown volume growth was significantly greater during both years (Tables 3 and 4). From age 1.5 to 2.5 yr, crown volume doubled in monoculture, while in mixtures it increased nearly four-fold as a result of greater growth in both crown length and crown area (Table 2). Crown volume remained unchanged in monocultures during the second year, but continued to increase at a moderate rate in mixture. By age 3.5

Table 4

Results of repeated-measures ANOVA for comparison of monocultures and mixtures growing at La Selva Biological Station, Costa Rica

	Tree height	DBH	Crown volume
<i>C. odorata</i>			
Treatment	0.0077 *	0.2229	0.0003 *
Block	0.0310 *	0.6298	0.1146
Treatment × block	0.1457	0.3874	0.7698
<i>C. alliodora</i>			
Treatment	0.0265 *	0.4633	0.5699
Block	0.3062	0.5506	0.1689
Treatment × block	0.0935	0.2234	0.0329 *
<i>H. alchorneoides</i>			
Treatment	0.0077 *	0.0016 *	0.0001 *
Block	0.0310 *	0.0244 *	0.2031
Treatment × Block	0.1457	0.5352	0.3930

Values are probabilities for tests of differences in growth rates for main effects of treatments (monoculture vs. mixture) and blocks, and for the treatment × block interaction (* denotes p values < 0.05; values are adjusted Greenhouse–Geisser probabilities). Species were analyzed separately for the two-year study period from age 1.5 to 3.5 yr.

yr, mean crown length and projection area in mixture were double that in monoculture. DBH growth did not differ between stands as much as height and

crown growth. Mean DBH was equal at age 1.5 yr but growth was significantly higher in mixture during the next year (age 1.5–2.5 yr). At age 3.5 yr, mean DBH was 1.4 cm greater (about 10%) in mixture than monoculture.

3.3. Canopy development

Monocultures developed large differences in LAI during the first stages of stand development. At age 1.5 yr all three monocultures had nearly reached their maximum LAI values (Fig. 4). *Hyeronima* attained a LAI greater than 5, *Cordia* LAI was approximately 2, and *Cedrela* LAI was less than 1 at age 1.5 yr. *Hyeronima* leaf area remained relatively constant after that age, but *Cedrela* and *Cordia* showed seasonal variations, with lower LAI values associated with partial loss of leaves during the dry season (measurements obtained in January 1993, 1994, and 1995; ages 1.5, 2.5, and 3.5 yr, respectively). The wet-season LAI of the *Cedrela* monoculture increased from age 2.0 to 3.0, possibly due to recovery from early shootborer damage. The decrease of 1.0 LAI unit in *Hyeronima* and 0.5 LAI units in *Cordia* after age 2.0 yr may have resulted from the thinning conducted in those two monocul-

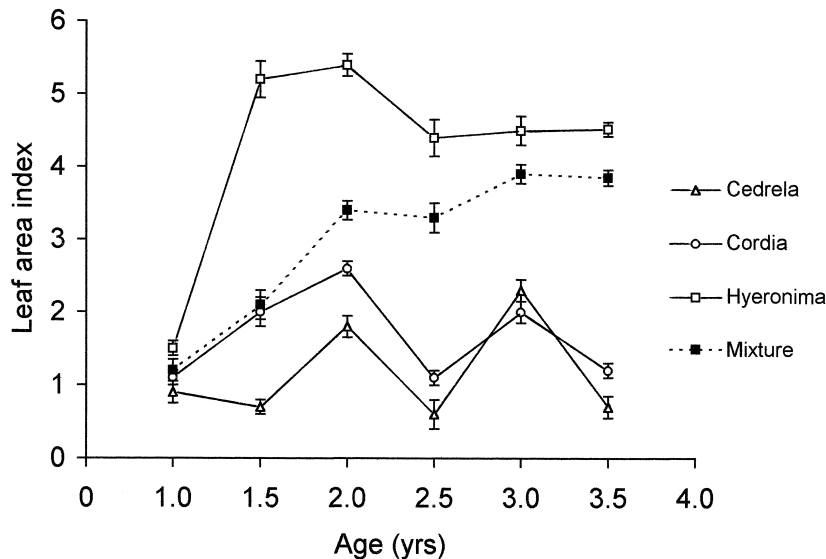


Fig. 4. Leaf area index in monocultures and mixtures of *Cedrela*, *Cordia*, and *Hyeronima* from age 1.0 to 3.5 yr at La Selva Biological Station, Costa Rica. Bars indicate standard error of means.

tures at age 2.3 yr. However, because LAI would be expected to recover quickly after a light thinning performed during this period of rapid stand growth, the decrease may be associated with crown interference among neighboring trees. LAI reaches a maximum soon after canopy closure, then as the stand continues to increase in height, swaying from wind action causes adjacent crowns to abrade one another, reducing crown overlap and decreasing total LAI (Kira and Shidaie, 1967; Oliver and Larson, 1996). At age 1.5 yr, the LAI of the species mixtures was 2.1, similar to that of the *Cordia* monoculture, but only 40% of that of *Hyeronima*. The mixtures increased in leaf area over the next two yr to an LAI of 3.9, which was 89% of the LAI of the *Hyeronima* monocultures.

Estimates of canopy light interception corroborate LAI measurements. After age 1.5, the *Hyeronima* monocultures intercepted 90% of solar radiation, whereas *Cordia* and *Cedrela* varied between 65–75% interception in the wet seasons to 45–60% in the dry seasons. The species mixture increased from 60% interception at age 1.5 to 85% at age 3.0–3.5 yr, when it nearly equaled the interception level in the *Hyeronima* monocultures.

4. Discussion

4.1. Crown and canopy development in monocultures and mixtures

The favorable soils and climate of the study site produced rapid growth of all three species, with canopy closure and crown differentiation occurring during the first four yr after planting. *Hyeronima* developed only limited size differentiation, as is common in dense, uniformly spaced, monoculture tree plantations, but *Cordia* and *Cedrela* had more variable sizes in monoculture. Mixed stands composed of all three species developed partially stratified canopies with the tallest *Cordia* in an upper canopy stratum above the other two species.

The size and allometry of trees in monocultures are strongly affected by the intensity of intraspecific competition, as controlled by stand density. This principle is well known in silviculture, and forms the

basis for thinning practice. By regulating the timing and intensity of thinning, it is possible to alter the relationships among tree height, stem diameter, and crown size, and even control stem taper (Assmann, 1970). The relationship between stand density and allometry has been verified more recently in theoretical studies of annual plant species (Ellison, 1987, Geber, 1989; Weiner and Fishman, 1994). In the current study, size and allometry of each of the three species varied greatly between monoculture and mixed-species plantations of approximately equal total tree density. *Cordia* was taller with wider crowns and greater stem diameters in mixture, and *Hyeronima* was shorter with much longer, wider crowns and slightly larger stem diameters. The simplest explanation for this growth pattern is that the vertical separation of crowns of the two species reduced the intensity of interspecific competition in mixture compared to the intensity of intraspecific competition in monocultures. *Cedrela* did not follow that same pattern, but rather was smaller in all dimensions in mixture than monoculture, and declined in absolute crown size in mixtures after age 2.5 yr. The poor development of *Cedrela* in mixture contributed to the reduction in crown competition intensity for *Hyeronima* and *Cordia*.

Three predictions about the development of these plantations were presented in Section 1.2 based on the even-aged, stratified-canopy model of development. The first prediction dealt with the relative height growth of the three species in monocultures, and was supported by results of this study. The mean height of *Hyeronima* lagged behind that of *Cordia* at age 1.0 yr (Haggard and Ewel, 1995), but the two species were similar by age 1.5 yr, and *Hyeronima* had greater mean height at age 2.0 yr and older (this study). *Cedrela* had the lowest mean height at age 1.0, but this was largely a result of insect damage to terminal shoots in the seedling and sapling stage. It had reached a mean height equal to that of *Cordia* by age 2.5 yr. The greater mean height of *Hyeronima* compared to the other species at age 2.0 yr and older was influenced by differences in size hierarchies among species. *Cordia* and *Cedrela* had greater proportions of short trees, which reduced mean heights, but the height of the main canopy (assessed by dominant height comparisons) was equal for all three species at ages 2.0 and 4.0 yr.

The second prediction dealt with the relative sizes and canopy positions of each species in the mixture, and was partly supported by the results of the study. The tallest *Cordia* formed a partially closed overstory layer above *Hyeronima*, as predicted. However, other growth patterns in the mixture departed from the prediction in two important ways: *Cedrela* occurred in the lower rather than upper canopy stratum, and the dominant *Cordia* reached greater heights in mixture than in monoculture. Both of these exceptions will be discussed below.

The height growth of *Cedrela* was limited in both mixture and monoculture by repeated attacks of the mahogany shootborer during the first year after planting (Rodgers et al., 1995). Because these insects usually fly no higher than 5 m (Grijpma and Gara, 1970), the frequency of attack declined with increasing height of trees, and the trees subsequently began to recover their rapid height growth rate. In monoculture, the recovery was so complete that dominant *Cedrela* were equal in height to the other two species at age 4.0 yr. However, in the mixture at age 4.0, *Cedrela* and *Hyeronima* both occupied the lower canopy beneath the dominant *Cordia*. *Cedrela* had smaller mean crown volume and DBH in mixture than in monoculture, and decreased in mean crown size after age 2.5 yr. The reduced growth of *Cedrela* in mixture was likely the result of an interaction between shootborer damage and early onset of competition with neighboring *Cordia* and *Hyeronima* trees, which are unaffected by shootborers. By the time *Cedrela* trees grew tall enough to escape the insect attacks, a partially closed canopy of *Cordia* and *Hyeronima* had already formed above and adjacent to them. The poor growth of *Cedrelas* in the lower canopy compared to that of *Hyeronima* supports earlier observations that *Cedrela* has lower tolerance of shade beyond the seedling stage.

The greater height growth of *Cordia* in mixture than in monoculture was an unexpected result that is more difficult to explain. The height of dominant trees is not expected to increase in mixtures as a result of reduced crown competition between trees of different canopy strata. Height growth is of great adaptive significance for competitive success in trees, and has a high priority in carbohydrate allocation (King, 1990; Oliver and Larson, 1996). Although crown size and stem diameter growth are strongly

affected by variations in stem density in monocultures, height growth of dominant trees generally does not vary with stem density except at extremely wide or narrow spacing (Lanner, 1985).

One explanation for the growth pattern observed in this study is that competition was more severe in the monocultures than in mixtures, and that *Cordia* is more sensitive than many tree species to increased competition. This competition might have taken either (or both) of two forms: intraspecific or interspecific. The resource most likely to be limiting is nitrogen, for which *Cordia* exerts a high demand, having foliar concentrations as high as 4% at our site. The roots of *Cordia* extend far from the trunk, branching only sparsely, as might be predicted for a plant adapted to capture a highly mobile anion such as nitrate. In monoculture, the resulting intraspecific competition could impede height growth, even though the densities at which this takes place are much higher for most tree species (Lanner, 1985). Furthermore, the open-crowned *Cordia* trees permit ample light to penetrate the understory, and other plants would flourish there if not controlled. At our site this control was effected by cutting (at approximately 3-week intervals) with machetes, a process that selected for weeds that grew close to the ground and had either a basal meristem or the ability to resprout from cut segments (e.g., members of the Poaceae, Cyperaceae, and Commelinaceae). The resulting carpet of shallow-rooted monocots may have been potent interspecific competitors with *Cordia* for nitrate–nitrogen located in the surficial soils, again leading to reduction of the tree's height growth. The sensitivity of *Cordia* to monocot competition has been demonstrated in plantations adjacent to those used in this study, in which productivity of overstory *Cordia* trees was decreased by the presence of planted understories of the large, perennial monocots *Heliconia imbricata* (Kuntze) Baker and *Euterpe oleracea* (Haggar and Ewel, 1997).

At the same time, height growth of *Cordia* in the mixtures may have been enhanced by the suppression of the understory monocots due to heavy shade cast by *Hyeronima*. If the demand for nitrogen by *Hyeronima* is lower than the demand that would have been exerted by the monocots it shaded out, or if the deeper-rooted *Hyeronima* obtains its nitrogen from different soil depths than the *Cordia*, then more

nitrogen would have been available to the *Cordia* in the mixtures. Furthermore, despite the high nitrogen content of its foliage, *Cordia* leaves are slow to decompose (Babbar and Ewel, 1989), so within-system turnover of nitrogen is slow. It is possible that in mixed stands *Hyeronima* and *Cedrela* increase the rate of nutrient cycling compared to that in *Cordia* monocultures by producing more rapidly decomposed litter, a phenomenon that has been reported in other species mixtures (Kelty, 1992). These proposed alternative explanations describe ‘facilitative’ interactions (sensu Vandermeer, 1989) in which the presence of one species directly favors the growth of another in mixture rather than simply reducing the level of competition through complementarity of resource use.

The third prediction involved the relative stand-level leaf area development of the monocultures and mixtures. As predicted based on its greater shade tolerance, *Hyeronima* developed the greatest leaf area of the three monocultures. *Hyeronima* showed no seasonal changes in leaf area, but partial leaf fall in *Cordia* and nearly complete leaf fall in *Cedrela* occurred in the dry periods from January to April. Nevertheless, even in wet seasons, *Cordia* and *Cedrela* LAI were less than half of that of *Hyeronima* after canopy closure.

As a closed canopy began to form in the mixture at age 1.5 yr, it consisted of non-overlapping crowns of adjacent trees (plus gaps where palms had been planted). The canopy reached an LAI of 2.0 at that age, which was approximately equal to the mean LAI of the three monoculture plus a zero value of LAI for the palms. As stratification developed, with *Hyeronima* filling in the lower canopy stratum with wide, deep crowns, the mixture LAI increased until it reached nearly 90% of the level of *Hyeronima* in monoculture at age 3.5 yr. This too was in agreement with the predicted pattern. This result contrasts with an alternative LAI development pattern found in conifer stands in the western U.S. (Smith and Long, 1992) in which the mixture maintains, even as mature stands, an LAI that is a weighted average of the monoculture leaf areas of the component species. The latter pattern is hypothesized to occur with species which either form a single-layered canopy (unstratified) in mixture, or which have an inherently narrow crown architecture with limited plasticity such

that a continuous canopy of shade-tolerant foliage does not develop in the lower stratum.

4.2. Ecological combining ability: applying theory to silvicultural practice

The concept of ecological combining ability was first used to describe pairs of plant or animal species that had, through the process of coevolution, developed niche differences that were sufficient to allow them to coexist (Harper, 1977). The idea of selecting species to combine in mixed stands for forestry, agriculture, or agroforestry practice is based on the premise that many characteristics which control plant productivity are the result of diffuse rather than specialized coevolution, as well as of direct evolutionary response to environmental factors. As a result, a pattern of broad differences in growth characteristics has developed among species (e.g., shade tolerant vs. shade intolerant, evergreen vs. deciduous, rapid vs. slow juvenile height growth, deep vs. shallow rooting). It should be possible to select combinations of species that are desirable for fiber or food production, and that also have good ecological combining ability, even though they may not have grown together in natural plant communities.

In this study, the crown characteristics that appeared to be of primary importance for combining ability were those that led to the formation of a stratified canopy. The two early successional species allocate a high proportion of biomass in the seedling stage to stem growth (in *Cedrela*) or to stem and branch growth (in *Cordia*). This results in a limited amount of foliage being displayed at the upper levels of the newly developing canopy, with little overlap of leaves within each crown. Thus, these species capture growing space quickly but also allow substantial solar radiation to be transmitted through the crowns to lower canopy trees. *Hyeronima*, the species of greater shade tolerance, develops dense, compact crowns that intercept most of the light transmitted to the lower canopy. These complementary characteristics would be expected of many potential mixtures that combine species of different successional status. However, actual combining ability may be decreased by other factors. For example, *Cedrela* and *Cordia* both appear to have crown characteristics that are compatible with those of *Hyeronima*, but insect

damage to *Cedrela* seedlings caused that species to be incompatible at least in the planting pattern and density used here.

Compatibility was enhanced in mixtures by the semi-deciduous nature of *Cordia* foliage, which allows greater light transmission in some seasons. Dry-season leaf loss in *Cordia* may have little effect on growth compatibility if *Hyeronima* photosynthesis is limited by moisture stress at that time. However, the dry season in this region can be considered dry only in relation to the rest of the year; there is still moderately high precipitation in the dry season, and the loss of *Cordia* leaves would increase the moisture available to other species through reduction of its evapotranspiration. In any case, *Cordia* shifts phenology from dry-season to wet-season leaf fall as it matures, so the lack of moisture availability would not be a factor in older stands. If *Cedrela* were to occupy the overstory canopy stratum, its semi-deciduous phenology would similarly increase its compatibility with an evergreen, lower-canopy species, although it maintains a pattern of dry-season leaf loss throughout its life.

In the plantations studied here, *Cordia* and *Hyeronima* showed compatible characteristics in height growth, crown structure, and shade tolerance in mixture, but *Cedrela* did not. To make it possible to study species interactions in a short period of time, these stands were planted at a higher density than is commonly used in silvicultural practice. If the plantations had been grown at a wider spacing, *Cedrela* may have recovered from early shootborer damage without direct competition from the other two species, and become part of the overstory with *Cordia*; this would be one logical modification for management practice. It would also be possible to maintain *Cordia* and *Hyeronima* in a high density, fine-grained spatial pattern, but with *Cedrela* planted in small monospecific patches that would isolate it from early interspecific competition; the goal might be to produce one overstory *Cedrela* from each patch. Other alternatives that may achieve the same result would be to use very large *Cedrela* planting stock, or to plant *Cedrela* seedlings at least one year before the other species.

This study demonstrates the importance of directly assessing interactions between tree species when planning mixed-species plantations. The large

investments of time and land necessary for complete replacement-series experiments are often unavailable, but even experiments with limited variables such as this (one spacing and one species proportion in mixture) provide considerably greater knowledge about potential mixture designs than is gained from single-species planting trials alone. Further refinement of that knowledge may often be gained from small commercial-scale plantations.

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