
Establishment, Resource Acquisition, and Early Productivity as Determined by Biomass Allocation Patterns of Three Tropical Tree Species

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ABSTRACT. Speed of stand establishment and rate of stem biomass production after canopy closure are two important criteria in the selection of species in the expanding field of tropical reforestation. How biomass allocation patterns determine establishment and stem production was studied in 0 to 2-yr-old plantations of *Cedrela odorata*, *Cordia alliodora*, and *Hyeronima alchorneoides* on fertile soil in the humid Atlantic lowlands of Costa Rica. The species were evaluated by: (1) their allocation of biomass to leaves and fine roots; (2) the resource-capturing capacity of the stands as expressed in leaf area, cover, fine-root length, and root distribution; and (3) biomass accrual and aboveground productivity.

All species grew very fast: average stand heights at 2 yr ranged from 4 to 6 m, and some individuals were >12 m tall. Canopy closure and root-system overlap were fastest in *Cordia*, occurring within a year after planting. *Cordia's* rapid stand closure was achieved by its higher specific leaf area and specific root length, plus an architecture that distributed leaves and fine roots more widely. Maximum aboveground net primary productivities after canopy closure were 7.3, 4.9, and 3.3 g m⁻² d⁻¹ for *Hyeronima*, *Cordia*, and *Cedrela* stands, respectively. High productivity of *Hyeronima* correlated with development of a high LAI coupled with a low leaf turnover rate.

Cordia and *Cedrela*, on the other hand, had higher rates of leaf turnover, so a higher rate of leaf production was required to maintain a given leaf area; this, in turn, limited biomass allocation to production of stem biomass. *Cedrela* productivity was severely reduced by attacks of the stem-borer *Hypsityla grandella*.

Biomass allocation patterns that promoted rapid establishment of a tree stand, such as broad crowns, high specific leaf area, and high specific root length, did not lead to the highest levels of stem biomass production after canopy closure. Once stand closure is achieved, species having low rates of leaf turnover, high leaf area indices, and high density of fine roots are likely to be most productive. Fast-growing tropical tree species should be evaluated not just on initial growth but also on the stem production attained after stand closure. FOR. SCI. 41(4):689-708.

ADDITIONAL KEY WORDS. *Cedrela odorata*, *Cordia alliodora*, *Hyeronima alchorneoides*, leaves, roots.

FAST-GROWING TREE SPECIES ARE PLANTED with increasing frequency throughout the humid tropics. Efforts include reforestation with native species (e.g., Stöhr and Carvalho 1980, Butterfield 1990), secondary forest management (Finegan 1992), biomass production (Bastista and Woessner 1980, Lugo et al. 1988), and agroforestry (Somarriba and Beer 1987). Although species are being screened for many uses, ranging from soil improvement (through fixation of

diatomic nitrogen, for example) to yields of fruit and forage (Huxley 1985), the production of timber remains a priority almost everywhere. Foresters have therefore focused attention on fast-growing species that produce high-value wood. Rather than the low wood-density pioneers that often colonize deforested landscapes, these species are analogous to those that temperate-zone foresters refer to as "late secondary."

There are possibly hundreds of tropical tree species in this category of fast growth and high quality wood (Finegan 1992). Nevertheless, the species within this group represent a variety of phenologies, architectures, and morphologies. Can we generalize beyond wood quality and growth rates? What other traits might these species share and, conversely, to what extent must each species be considered *de novo*?

In selecting species, attention must be paid to two sequential phases. Early growth characteristics influence rates of sequestering nutrients and filling space, thereby achieving full site occupancy. In both natural habitats and in plantations, early dominance of sites is important for suppression of competitors. In the humid tropical lowlands, the outcome of this phase is sometimes determined within the first year or two. The second phase begins at stand closure (i.e., when crowns and root systems of adjacent trees overlap). During this phase foresters are primarily interested in stem-biomass production. Thus, defining how allocation patterns determine plant productivity during establishment and after stand closure are essential parts of the selection process.

Tree growth models have been used to determine planting densities and rotation times that lead to maximum biomass production of fast-growing tropical trees (Pereira and Landsberg 1989, Fownes and Harrington 1990). At the level of the single plant, vegetative growth is normally maximized through optimal allocation of resources (Bloom et al. 1985). McMurtrie (1985) developed such an optimization model to determine allocation of resources within a tree that leads to maximum productivity. Models such as McMurtrie's indicate that growth form has a large effect on productivity through its effects on allocation of resources within the tree, principally to carbon-gathering leaves and mineral-nutrient-gathering fine roots. The models demonstrate that there is an optimal level of allocation of carbon to leaf tissue, above and below which net productivity of stem biomass declines. The optimal allocation to leaves, in turn, is modified by the degree of nutrient limitation to growth: the lower the nutrient availability, the higher the allocation to fine roots (and symbionts) needed to meet nutrient requirements of assimilate production by leaves. With higher allocation to roots, allocation to leaves declines and productivity falls, reducing demand for nutrients. Thus, allocation of assimilate to leaves and roots is such that at maximum productivity both light interception by leaves and nutrient uptake by roots will be simultaneously limiting, irrespective of levels of resource availability. These conditions hold during the low competition phase of growth, up to canopy and root-system closure.

After canopy closure, allocation of carbon to leaf and fine-root biomass should stabilize at the amount necessary to maintain a constant leaf area and fine-root length (Cannell 1985, Waring and Schlesinger 1985). Nevertheless, the allocation pattern that maximizes stemwood biomass of a stand, the primary interest of foresters, may not maximize productivity of an individual in a competitive environment. King (1993), for example, has shown that allocation patterns that maximize competitive ability of an individual would lead it to allocate more resources

to roots than is optimal to maximize stand productivity. Because natural selection operates on the individual and not the stand, allocation patterns that maximize relative productivity of the individual tend to dominate and lead to less than maximum stand productivity.

The influence of different allocation patterns on early phases of tree growth was studied by comparisons among three fast-growing tropical hardwood species, selected to represent a broad cross section of families, architectures, and phenologies. Both monospecific and polyspecific stands were studied. The site conditions of high rainfall, warm air, and fertile soil were as nonconstraining to plant growth as might be found anywhere in nature. Under these conditions the investment each tree makes to capturing resources is likely to be a prime determinant of stand productivity. Nevertheless, the stands were grown in an environment where proximity to the native rain forest challenged them with the biotic hazards of insects, diseases, and large herbivores; these factors are an integral part of most environments where such plantations are being established throughout the tropics, and their influence cannot be ignored.

The development of resource-capturing structures and productivity were evaluated during both the establishment phase of the stands and for the first year after stand closure. The species were assessed by (1) the allocation of biomass to resource capture; (2) the development of leaf area, canopy cover, fine-root length, and root distribution; and (3) the productivity achieved by these resource-capturing structures.

SITE DESCRIPTION AND EXPERIMENTAL DESIGN

SITE AND SPECIES DESCRIPTIONS

The experiment was conducted at La Selva Biological Station in the Atlantic lowlands of Costa Rica, at an elevation of about 40 m (McDade et al. 1994). Mean annual rainfall and temperature are approximately 4 m and 24°C respectively. There is a short dry season in February–March, although mean monthly rainfall is never less than 0.1 m. The site is on an alluvial terrace with a deep, well-drained soil classified as a mixed, isohyperthermic, possibly andic, fluventic Dystropept, with pH 6.5 (Haggar and Ewel 1994).

In April 1991 the site was cleared of an abandoned cocoa plantation, merchantable overstory trees (mostly *Cordia alliodora*) were harvested, and the slash was burned. Immediately following manual clearing of charred logs, tree plantations were established. At the time of planting, the topsoil (0–10 cm) contained 5.9% (standard deviation = 1.2) organic matter, 13.7 (0.8) µg/g of available nitrogen (extractable nitrate and ammonium), 18.2 (8.7) µg/g of Olsen-extractable phosphorus, 1.6 (0.3) mg/g extractable calcium, 0.24 (0.04) mg/g extractable magnesium and 0.50 (0.24) mg/g extractable potassium (Haggar and Ewel 1994).

Three species of fast growing tropical hardwoods—*Cedrela odorata* L. (Meliaceae), *Cordia alliodora* (R. & P.) Cham. (Boraginaceae), and *Hyeronima alchorneoides* Allemao (Euphorbiaceae)—were chosen for their contrasting physiognomic characteristics, which indicated a potential for different resource capture capabilities (Table 1). All three species are native to Costa Rica. *Cedrela*, a close relative of mahogany, is a Neotropical timber tree of considerable value and

TABLE 1.

Physiognomic characteristics of 1–2-yr-old trees of the experimental species. Leaf size is the mean area of leaf (*Hyeronima* and *Cordia*) or leaflet (*Cedrela*) samples ($n \approx 100$).

Species	Family	Leaf phenology	Leaf type	Leaf size (cm ²)	Crown structure
<i>Hyeronima alchorneoides</i>	Euphorbiaceae	Evergreen	Simple	278	Sympodial, orthotropic branching
<i>Cordia alliodora</i>	Boraginaceae	Semi-deciduous	Simple	33	Monopodial; plagiotropic branching
<i>Cedrela odorata</i>	Meliaceae	Semi-deciduous	Pinnately compound	41	Monopodial, orthotropic branching

is widely planted in the humid tropics; in its native range it seldom escapes attack by larvae of a well-studied shoot-boring moth, *Hypsipyla grandella* (Whitmore 1976). *Cordia* is a locally prized timber tree, known for its ability to colonize pastures and old fields on fertile soils. A substantial amount of genetic and silvicultural work has been done on *Cordia* by foresters (Greaves and McCarter 1990). *Hyeronima*, the least studied of the three species, is a promising species for reforestation of degraded pastures (Butterfield 1990). *Hyeronima* is a massive emergent rainforest tree with dense, durable heartwood. Studies of its ecology have shown that saplings are fast-growing and light-demanding, but trees may take 100–300 yr to grow to full size in natural forest (Clark and Clark 1992).

PLANTATION ESTABLISHMENT AND EXPERIMENTAL DESIGN

Tree seedlings were produced in a nursery at La Selva from seeds of known Costa Rican provenance. Seeds of *Cedrela* and *Cordia* were purchased from the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), located in Turrialba, Costa Rica; the *Cedrela* provenance was Pococi, and the *Cordia* provenance was Talamanca. Because of *Cordia* failures in the nursery, the purchased seed lot yielded sufficient seedlings for only one (of three) blocks, so seedlings for the other two blocks had to be purchased from a private nursery which used seeds from an area of similar elevation, rainfall, and soil as the study site. *Hyeronima* seeds were gathered from the immediate vicinity of La Selva.

Cedrela and *Cordia* were planted as “pseudo-cuttings,” or “stumps,” which are seedlings whose tops and roots are severely pruned; about 15–20 cm of taproot and about 15–20 cm of stem (0.8 to 1.8 cm in basal diameter) constitute the stump, which resprouts after planting. *Hyeronima* were planted, without pruning, from bag-grown seedlings, which were about 0.8 cm in basal diameter and 40 cm tall.

In mid-1991, three 50 by 40 m plantations of each species, arranged in a randomized block design, were established. The trees were planted in rows 1.73 m apart, with 2 m between trees within rows, and the planting within each row was offset by 1 m from the rows on either side; thus, each tree was surrounded by six other trees, each 2 m away. Each tree, therefore, occupied a hexagonal area of 3.46 m², and stand density was 2887 trees per ha. The *Hyeronima* plantations were established between May 20 and 28, and the *Cedrela* plantations

were established between June 7 and 11. One block of *Cordia* was planted on June 13 and the other two on July 24 and 26. Average planting dates for each species are used herein when discussing development of the stands over time. All stands were weeded every 2–4 wk.

During the same period (May 25 to June 15) two mixed stands were established adjacent to the main experiment. These contained equal proportions of *Hyeronima*, *Cedrela*, *Cordia*, and palms of the genus *Euterpe* (*E. macrospadix* and *E. oleracea*, which were alternated at planting points designated for a palm). The planting density and spacing were the same as in the main experiment. The planting arrangement was such that an individual of one genus was surrounded by a hexagon delineated by two individuals of each of the other three genera. One of the mixed stands was not weeded for the first 4 months, and the other stand was, like the main experiment, weeded regularly.

METHODS

BIOMASS MEASUREMENTS

A sample of 40 individuals of each species was taken at the time of planting, and the biomass (total for *Cedrela* and *Cordia*; subdivided into roots, stem, and leaves for *Hyeronima*) of each individual was measured. These initial values enabled us to calculate net aboveground productivity during the first 4 mo. At 4, 8, 12, 18, and 24 mo after planting, 8 randomly selected trees were harvested from each block of each species (from within specific areas of the stands designated for this purpose). After measuring heights and basal diameters, the trees were harvested and divided into leaves, stems, branches, and coarse roots. The total fresh weight of each component was measured in the field, and a subsample (0.3 to 0.8 kg) was oven-dried at 70°C to determine water content and calculate the dry weight of the component. The area of the fresh leaf subsample was also determined (LiCor model LI-3000 area meter), and from this measurement the specific leaf area (ratio of area when fresh to oven-dry mass) was calculated.

ROOT BIOMASS AND DISTRIBUTION

The coarsest roots (>5 mm diameter) were sampled by excavation, and fine roots (<2 mm diameter) were sampled by coring. For harvests at 4, 8, and 12 mo, roots 2–5 mm in diameter were excavated together with larger roots; after 15 mo they, like fine roots, were sampled by coring. Regardless of sampling protocol, coarse roots always refer herein to those >2 mm in diameter.

To evaluate extent and rate of development of root systems, we measured spatial distribution of coarse roots with respect to distance from tree and depth in soil. Coarse root distribution was measured on the 24 trees selected for the 4 and 8 mo biomass harvests and on 9 trees from the 12 mo biomass harvest (it was not evaluated for the 18 and 24 mo biomass harvests). The entire coarse-root system of each tree was excavated by hand and divided into three distances from the tree (0–33 cm, 33–67 cm, and 67–116 cm) and several depths (0–10 cm, 10–30 cm, continuing down in increments of 20 cm until there were no more coarse roots).

Fine-root biomass, length, and distribution through the soil volume were eval-

uated in single-species stands by taking soil cores at 3, 9, 12, 19, and 25 mo after planting. In the 3 mo sample, 8 cm diameter cores were taken from around 9 randomly chosen trees in each stand, and in the 9 and 12 mo samples, 5.5 cm diameter cores were taken from around 8 trees. For these samples cores were taken from the center of a set of concentric circles around the tree: at 17 cm, 50 cm, and (after 3 mo) 83 cm from the base (i.e., near the midpoints of three equidistant intertree annuli). Once trees were more than a year old, heterogeneity in distribution of fine roots was no longer related to distance from tree. Therefore, at 19 and 25 mo, the nine 5.5 cm cores, taken from 9 randomly chosen points stratified with respect to distance from nearest tree, were combined for analysis.

The depth to which roots were sampled was increased as root systems developed. Root-biomass cores were taken to a depth of 50 cm at 3 mo, 90 cm at 9 mo, and 110 cm at 12, 19, and 25 mo. They were divided into the top 10 cm and then into 20 cm segments to the bottom of the core. Roots were separated from soil using a hydropneumatic elutriator, then separated by hand into diameter classes (>5 mm, 2–5 mm, and <2 mm). Length of fine roots was estimated using the line intersection method (Tennant 1975) before oven-drying.

To convert root sample lengths and masses to an area basis, values were summed over all depths at each distance and divided by the area of the core. The latter value was then multiplied by the area effectively sampled by each core. The sum of fine-root biomass in each area gave the average fine-root mass per tree, which was then converted to an area basis by dividing by the area occupied by the tree.

LITTERFALL

Litter was collected in eight traps per stand, each of which was 1.73 m long (i.e., equivalent to inter-row distance) and 0.5 m wide and about 20 cm off the ground. Each trap was positioned with one end at the base of a tree and pointing into the row between the columns of trees so that it sampled evenly the area of influence of a tree.

Litter was collected from traps every 3 wk for the first year and every 2 wk thereafter. Litter that could be identified as allochthonous was discarded, but litter inputs (assumed to be very small) from older *Cordia* and *Cedrela* trees around the site could not be distinguished from autochthonous litter. Litter was divided into leaf and branch material, dried, and weighed.

STAND BIOMASS AND NET PRIMARY PRODUCTIVITY

Stand inventories of mortality, tree height (to the nearest 1 cm up to a height of 3.0 m, to the nearest 10 cm thereafter), and either basal or breast height (i.e., at 1.3 m) diameter (to 1 mm) were measured approximately 3, 6, 9, 12, 18, and 24 mo after planting. Buffer strips of four rows of trees along the 50 m sides and two rows on the 40 m ends of the plots were not measured.

Using the data from harvested trees, equations were developed to estimate the biomass of each component (leaves, stems, coarse roots) of each species. Separate equations were developed for trees <1.5 m tall (using basal diameters) and

taller trees (using dbh). With each additional biomass harvest the new data were combined with the original data, and new equations were created.

The basic equation (Satoo and Madgwick 1982) to which data were fitted was

$$M = aX^b$$

where M is mass, X is a measure of tree size, and a and b are constants fitted after logarithmic transformation of the equation:

$$\log M = Y = \log a + b \log X$$

For each data set (i.e., for each plant part of each species), four measures of tree size, X , were tested: diameter (d), d^2 , $d \times$ height (h), and d^2h . The equation that best fit the data (usually the one in which $X = d^2h$), based on the amount of variance accounted for by the regression (F-value) and the r-squared value, was then chosen as the basis for converting inventory data to biomass. Because the trees of each species were relatively uniform in size and a large number of individuals was sampled, the fits of the data to the equations were generally good, with an average r-squared value of 0.81 (range 0.39–0.99). (The equations are available from the authors.)

The appropriate equation was applied to each tree in the stand, and the correction factor required to eliminate bias induced by logarithmic transformation (Sprugel 1983) was applied to derive stand-level estimates of leaves, stems, and coarse roots. Stand-level fine-root biomass was then added to the sum of these values to give standing biomass of the stand at each inventory time (except for the 6 mo inventory, when no fine-root biomass measurements were made). Only aboveground biomass per tree was estimated for mixed stands, as fine roots were not sampled there.

The change in standing biomass of aboveground parts was calculated between successive inventories. Litterfall for a particular interval was added to the change in aboveground standing biomass to yield estimates of aboveground net primary productivity.

CANOPY DEVELOPMENT

Cover was measured in the single species stands at 2, 4, 6, and 9 mo after planting using a vertical point intercept method. Two hundred random points per stand were scored for presence or absence of overtopping vegetation. At 9, 12, 16, and 24 mo after planting, canopy development was assessed using hemispherical photography. Two fixed photo points approximately 25 m apart and 50 cm above the ground were established in the central part of each stand. Photographs were analyzed using the CANOPY program (Rich 1990). Indirect site factor (ISF) was chosen as the closest approximation to cover, but the two measures do differ: ISF is percentage of sky seen in a hemispherical arc from a point, whereas canopy cover is a vertical projection of the canopy on the ground.

Stand leaf area was determined by applying specific leaf area to the stand leaf biomass estimate. Leaf area index was derived by dividing stand leaf area by stand area.

STATISTICAL ANALYSIS

Analyses over time were done using the repeated measures option within an analysis of variance (SAS Institute 1988). Repeated measures analysis was used

because the same trees were remeasured at the end of each interval, making successive estimates of stand variables (such as biomass, productivity, and canopy and root-system development) nonindependent. As there were large changes in magnitude over time for many variables, log transformations were made to normalize the data. Species differences were tested using specific contrasts within the analysis of variance. Unless otherwise stated, differences quoted as significant have a probability of a type I error of <0.05 .

In the figures, real values (i.e., not transformed) are plotted as a function of time after planting as the most informative way of presenting the data. As measurements were taken on approximately the same date for all species, but the species were planted at slightly different times, measurements are staggered with respect to time after planting. This means that statistical differences between species at any sampling time need to be interpreted with caution and also that it is more difficult to see the statistical differences among species at any one time. Where significant differences among species were found in the analysis of variance, these have been indicated by presenting least significant differences (LSDs) in the figure legends.

RESULTS

DEVELOPMENT OF RESOURCE-CAPTURING STRUCTURES

Within 9 mo after planting, leaf area index of the tree species diverged, reaching the highest values in *Hyeronima* and lowest in *Cedrela* (Figure 1). As *Hyeronima* had the lowest specific leaf area, and *Cedrela* the highest (Table 2), differences in leaf biomass among species were even greater than differences in leaf area.

Although leaf turnover rates could not be calculated from our data because leaf biomass and litterfall rates were not at steady state, ratios of litterfall to standing leaf biomass indicate that leaves of *Cordia* and *Cedrela* were substantially shorter lived than those of *Hyeronima*. The higher leaf turnover rates of *Cordia* and *Cedrela* can be seen in the higher biomass investment required to maintain a unit of leaf area for those two species compared to that for *Hyeronima*. To sustain a square meter of *Hyeronima* leaf, for example, required a leaf production of only 0.36 g/day, whereas a square meter of *Cedrela* or *Cordia* leaves required significantly higher investments: 0.84 and 0.77 g/day, respectively.

Interspecific differences in canopy cover developed by the time stands were 6 mo old. Up to 10 mo after planting, cover was highest in *Cordia* stands (Figure 2), but after 16 mo, cover became significantly higher in *Hyeronima* stands. Crown closure (identified as the time when cover approached an asymptote) occurred at 10, 14, and approximately 16 mo in the case of *Cordia*, *Hyeronima*, and *Cedrela*, respectively. At 10 mo comparison of the two methods of assessing cover (point intercept and hemispherical photography) indicated that the point intercept method gave higher values of cover in *Cordia* than the hemispherical photos, but lower cover values for *Hyeronima*. The difference between the two methods may be due to the fact that the crown of *Hyeronima* is compact and its foliage is densely packed, whereas the crown of *Cordia* is tiered, with up to a meter or more separating successive branch whorls. When assessed radially from a fixed point near the ground (i.e., as with a hemispherical photograph), a dense, compact

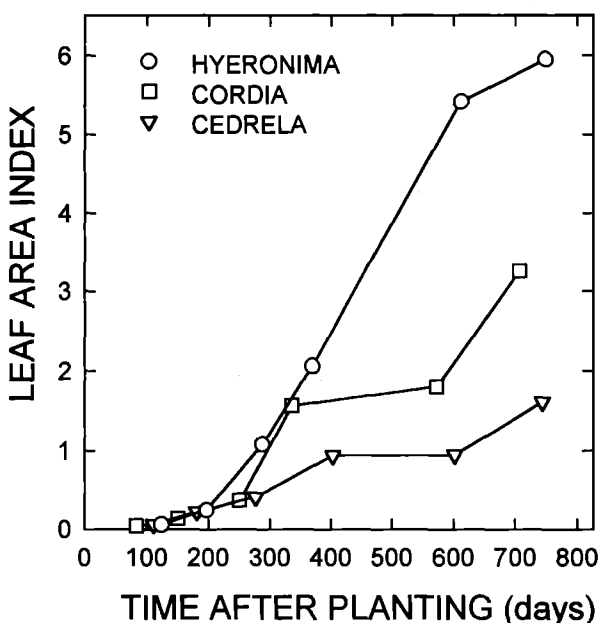


FIGURE 1. Leaf area index of stands up to 2 yr old. Least significant differences for species comparisons within the following times after planting are, 250–290 days, LSD = 0.26; 330–370 days, LSD = 0.41; 570–620 days, LSD = 0.75; and 700–750 days, LSD = 1.12.

canopy such as that of *Hyeronima* would obscure more sky than when assessed by vertical projection of the canopy.

By 12 mo after planting, *Hyeronima* stands had higher fine-root length than the other species (Figure 3A). *Cordia* had greater fine-root length than *Cedrela* throughout stand development, but the differences were significant only in stands more than 12 mo old. The smallest roots of *Hyeronima* are short and thick and thus have a low specific root length (Table 2). Therefore, *Hyeronima* fine-root biomass, relative to the other species, was even higher than fine-root length (Figure 3B). Fine roots of *Cordia*, in contrast, are long and slim, enabling *Cordia* to achieve a higher density of fine roots than *Cedrela* without investing significantly more in fine-root biomass.

Hyeronima had significantly higher densities of fine roots close to the base of the tree and in more superficial soil depths, but further away from the base and deeper in the soil, fine-root density of *Hyeronima* was not significantly different

TABLE 2.

Specific leaf area and specific root length for the three tree species.

Species	Specific leaf area cm ² /g		Specific root length m/g	
	Mean	Range	Mean	Range
<i>Hyeronima</i>	133	120–150	7.2	5.2–12.0
<i>Cordia</i>	148	136–170	20.0	10.3–35.0
<i>Cedrela</i>	157	135–190	14.1	5.2–25.6

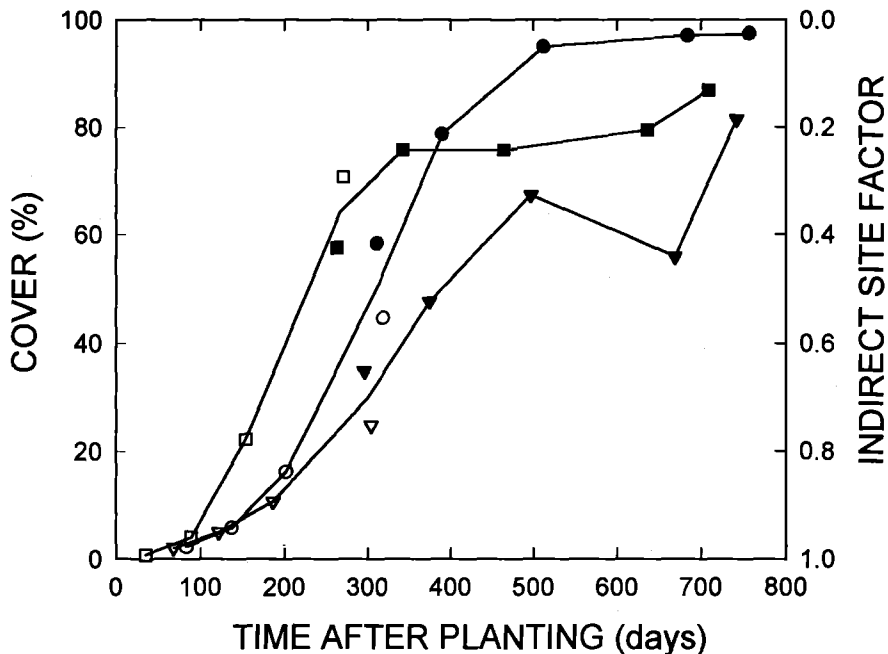


FIGURE 2. Cover and indirect site factor (ISF, an approximation of cover; see Rich 1990) of stands up to 2 yr old. Open symbols refer to cover and closed symbols refer to ISF. Least significant differences for species comparisons within the following times after planting for cover are, 150–210 days, LSD = 11.4; and 270–320 days, LSD = 25.8. LSDs for ISF are, 260–310 days, LSD = 0.10; 340–390 days, LSD = 0.14; 460–520 days, LSD = 0.15; 630–690 days, LSD = 0.11; and 710–760 days, LSD = 0.11. Symbol shapes = species (see Fig. 1).

from that of other species (Figures 4, 5). The distributions and densities of fine roots of all species did not change significantly after 19 mo. Fine roots of *Cordia* and *Cedrela* were remarkably well distributed both vertically (to 110 cm) and horizontally. In stands >4 mo old, *Cordia* and *Cedrela* demonstrated no significant decline in density with depth (except *Cordia* at 25 mo, July 1993) and distance from the tree sampled.

The distribution of coarse roots showed that *Cordia* had both the deepest and most laterally extensive root system, while *Hyeronima* had the most compact, surficial root system (Figure 6). The absolute depth to which the coarse roots penetrated did not substantially increase between 8 and 12 mo, suggesting that the phase of rapid root system expansion was completed as early as 8 mo after planting. At this time coarse roots of *Hyeronima* extended to a depth of 70 cm, those of *Cedrela* reached about 110 cm, and those of *Cordia* penetrated to about 170 cm.

EFFECTIVENESS OF STAND STRUCTURE IN CAPTURING RESOURCES

Stand biomass of *Cedrela* was significantly lower than that of the other two species in stands more than 4 mo old (Figure 7). By the time plantations were 18 mo old, stand biomass of *Hyeronima* increased significantly above that of *Cordia*.

One-year-old *Hyeronima* stands, in comparison with the other species, had a very high proportion of biomass (45% in resource-capturing structures: leaves

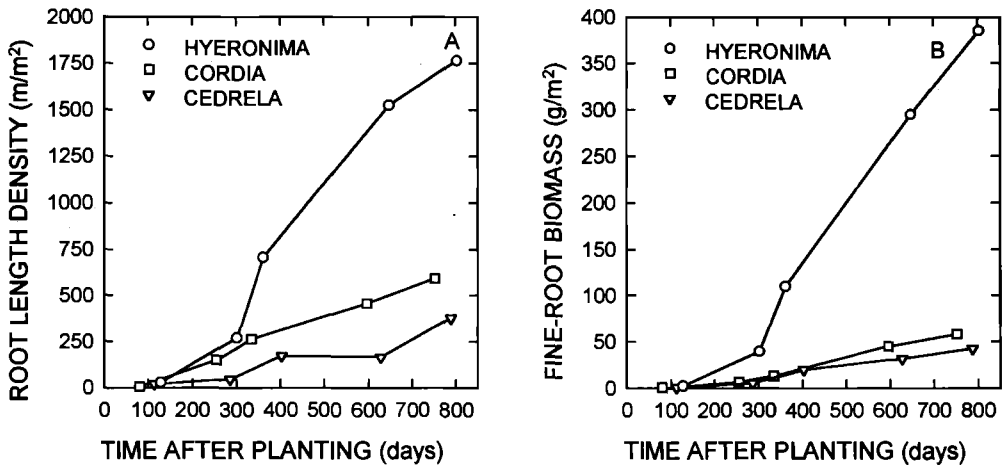


FIGURE 3. Development of fine roots (<2 mm in diameter) in stands up to 2 yr old. (A) Fine root length. (B) Fine root biomass. Least significant differences for species comparisons within the following times after planting for fine root length are, 250–310 days, LSD = 157; 330–410 days, LSD = 185; 590–650 days, LSD = 360; and 750–810 days, LSD = 276. LSDs for fine root biomass are, 250–310 days, LSD = 15.6; 330–410 days, LSD = 32.4; 590–650 days, LSD = 43.9; and 750–810 days, LSD = 29.8.

and fine roots (Figure 8). One-year-old *Cedrela* and *Cordia* stands, in contrast, had high allocations of standing biomass to structural components, *Cedrela* in large roots and *Cordia* in stems. The species differences in allocation patterns were maintained in 2-yr-old stands, although all species had higher proportions of standing biomass in stems compared to the 1-yr-old stands.

During the first year, aboveground net primary productivity was higher in *Cordia* than *Hyeronima* (Figure 9). *Cordia* productivity began to taper off to about $4.5 \text{ g m}^{-2} \text{ day}^{-1}$ after 1 yr, whereas *Hyeronima* productivity continued to rise (to $>7 \text{ g m}^{-2} \text{ day}^{-1}$). Early high productivity of *Cordia* did not lead to high standing biomass (Figure 7) due to high rates of leaf and branch litter production.

GROWTH IN MIXED STANDS

Generally, the growth of individual trees of *Hyeronima* and *Cordia* was faster in mixed than pure stands (Table 3). This may have been due to differences in crown and root-system geometry that enable the species to partition space effectively. More likely, it was due to the fact that a quarter of the planting sites in the mixed species stands were occupied by palms which had poor growth and survival; thus, the mixed stands effectively had lower tree densities.

The growth of *Cordia*, but not that of *Hyeronima* or *Cedrela*, was considerably suppressed in the unweeded plot compared to the weeded plot (Table 3). As the weeding treatment was unreplicated, we cannot be completely certain that the differences in growth between the plots is due solely to weeding. Nevertheless, the weeding treatment is the most likely explanation, for the two plots were nearly contiguous; the soil, topography, and site history are extremely uniform; and tree-growth suppression in the unweeded plot was conspicuous during the first 4 mo, when it was not weeded.

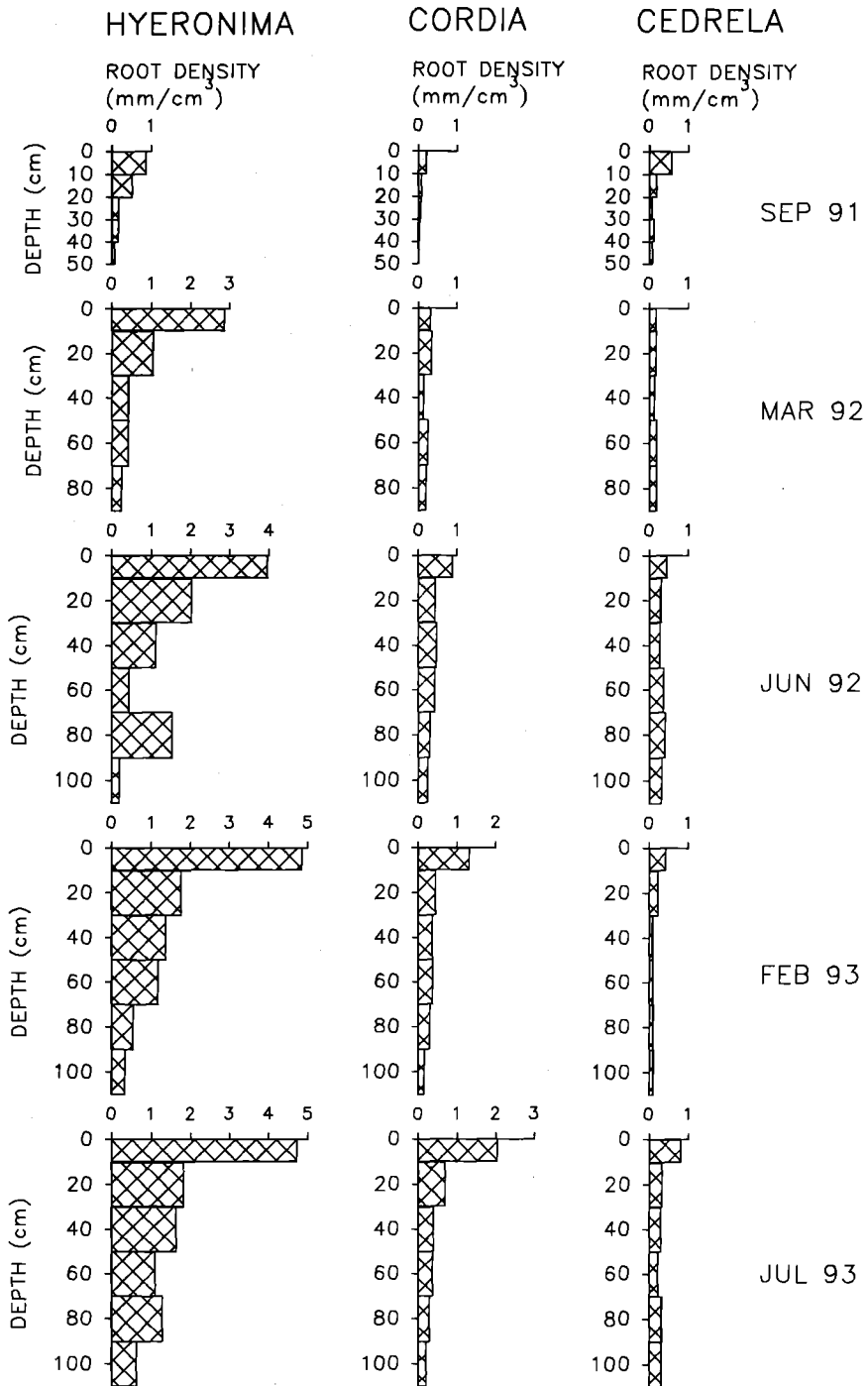


FIGURE 4. Distribution of fine roots (<2 mm diameter) with depth for stands up to 2 yr old.

In the weeded plot, 1-yr-old *Cordia* trees were taller and had higher biomass than *Hyeronima* or *Cedrela* trees, the same as in the main experiment (Table 3). In contrast with the main experiment, by the time they were 2 yr old, *Cordia* in the weeded mixed plot were still taller and had greater biomass than *Hyeronima*.

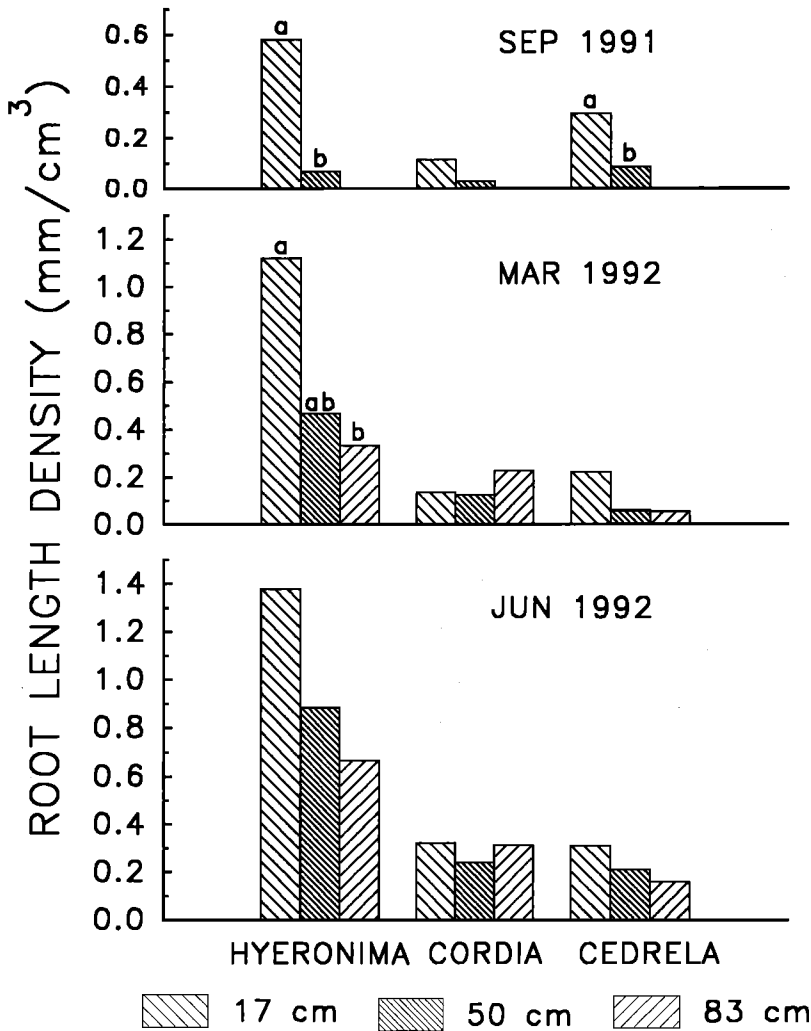


FIGURE 5. Distribution of fine roots (<2 mm diameter) as a function of distance from tree in stands up to 1 yr old. Columns with different letters indicate significant differences between distances within a species.

Even in the unweeded plot, 2-yr-old *Cordia* had similar biomass and were taller than *Hyeronima*.

DISCUSSION

In the first year, *Cordia* achieved higher aboveground productivity than *Hyeronima*. One result of this was that the crowns in the *Cordia* stands closed sooner than those of *Hyeronima*. At canopy closure, when the productivity of the two stands was similar, *Cordia* had substantially lower leaf area (Figure 10). The high productivity of *Cordia* in its early phase of growth was not due to higher investment in leaves and fine roots but to the fact that it invested less biomass in each unit of leaf area or fine root length (i.e., it had a higher specific leaf area and

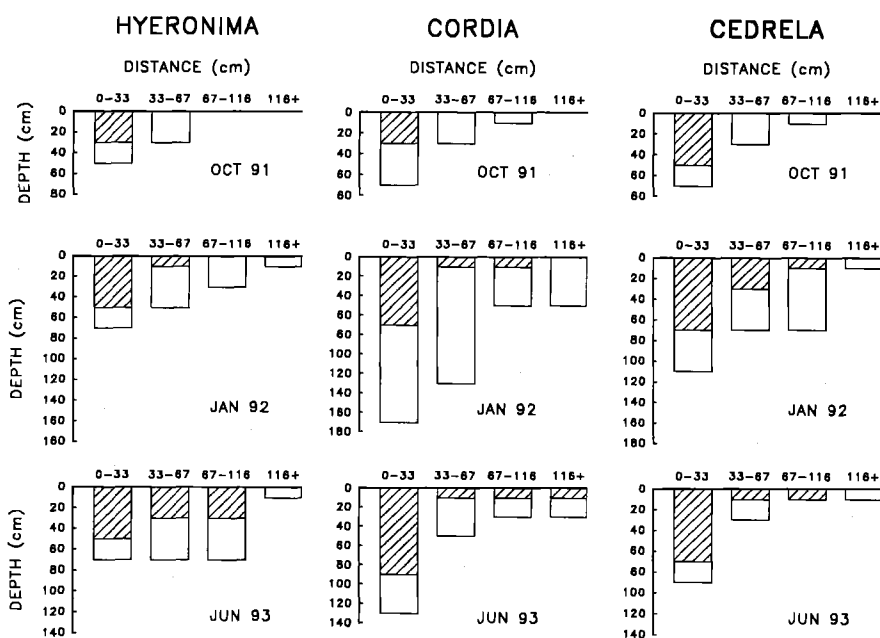


FIGURE 6. Distribution of coarse roots (>2 mm in diameter) with respect to depth and distance from the tree in stands up to 1 yr old. The diagonal-hatched area is modal depth and distance reached by roots, and the blank area is extreme of depth and distance reached.

specific root length). The low allocation to leaves and roots allowed a higher allocation to structural biomass during establishment.

The architecture of *Cordia* was important to its high initial productivity and rapid canopy and root-system closure. *Cordia alliodora* conforms to Fagerlind's model (Hallé et al. 1978); its plagiotropic branching results in a multilayered crown, with little overlapping of leaves. Fisher (1986) has shown that packing of leaves is nearly optimal in trees with a pagodal architecture consisting of tiers of five branches, such as found in *Cordia* and *Terminalia*. The dispersion of leaves and fine roots in *Cordia* reduces competition between resource-capturing units of the same individual, thus increasing resource capture by each unit of leaf area or fine-root length. In an experiment comparing stand development of secondary successional communities and a monoculture of *Cordia*, the latter achieved a fine-root biomass similar to successional communities within 18 mo after planting, demonstrating *Cordia's* rapid establishment capability (Berish and Ewel 1988).

The early productivity of *Cedrela* was almost certainly severely affected by intense attacks by the stem borer *Hypsipyla grandella*. Despite those attacks, when both species had an LAI of 1, aboveground productivity of *Cedrela* was similar to that of *Cordia*. *Cedrela* allocated substantial biomass to coarse roots, however, which inevitably limited its allocations to leaves and fine roots. Its high allocation to coarse roots probably facilitates recovery from *Hypsipyla* attacks, as indicated by Rogers et al. (1994) who found that the substantial starch reserves in thick roots were depleted as the tree respouted after excision of the terminal shoot.

The relatively lower productivity of *Hyeronima* early in stand development (Figure 9) correlates with its high biomass allocation to fine roots (Figure 3b).

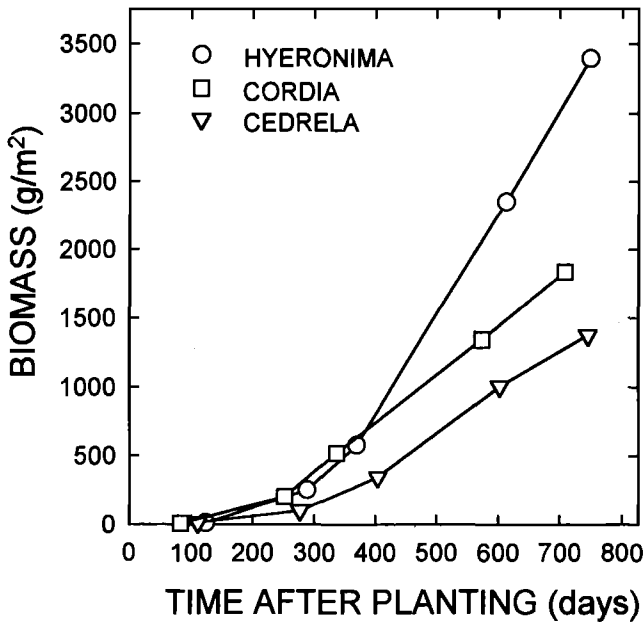


FIGURE 7. Standing biomass of the tree stands up to 2 yr old. Least significant differences for species comparisons within the following times after planting are, 150–200 days, LSD = 72; 330–400 days, LSD = 134; 570–620 days, LSD = 534; and 700–750 days, LSD = 619.

This confirms the conclusion of McMurtrie (1985), that high allocation of biomass to roots lowers aboveground production. The considerably higher fine-root density of *Hyeronima* implies that this species was less likely to experience nutrient limitation. This difference in nutritional status was likely to have been further accentuated by higher leaf turnover of *Cordia* and *Cedrela*, which would have increased their nutrient demand per unit of productivity. The lower fine-root density of *Cordia* and *Cedrela* may have resulted in nutrient limitations to leaf production and contributed to the lower leaf area indices these species supported (Figure 10). The incomplete utilization of light by *Cordia* was shown by the increased growth of invading shrubs (genus *Piper*) when root competition was eliminated by trenching; in contrast, elimination of belowground competition in *Hyeronima* stands had no effect on *Piper* growth, presumably due to heavy shading (Gerwing 1994).

Tree species typically maintain an approximately constant LAI and therefore a constant or declining net productivity, after canopy closure (King 1990). This proved to be the case for *Cordia* and *Cedrela*. In contrast, aboveground productivity continued to increase in *Hyeronima* stands after canopy closure. Due to faster leaf turnover, it was presumably more expensive for *Cordia* and *Cedrela* to maintain a given leaf area than for *Hyeronima*: only 22% of *Hyeronima*'s productivity was lost as litter as opposed to 38% and 36% for *Cordia* and *Cedrela*, respectively (shown by the difference between the two vertical axes on Figure 10).

In a competitive environment, individuals that occupy the site first and grow tallest are most likely to capture and dominate use of available resources (Firbank and Watkinson 1990). Consider the case of *Cordia*: despite the fact that in 2-yr-old

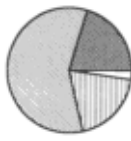
TREES 1 yr OLD

HYERONIMA



579 g/m²

CORDIA

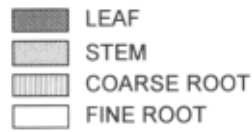


519 g/m²

CEDRELA

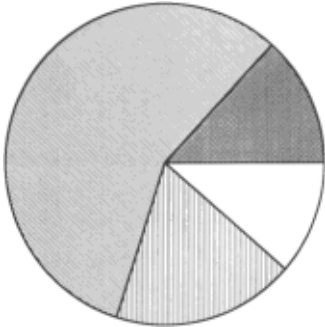


344 g/m²



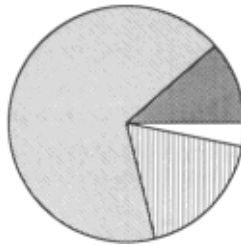
TREES 2 yrs OLD

HYERONIMA



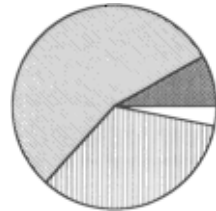
3392 g/m²

CORDIA



1835 g/m²

CEDRELA



1374 g/m²

FIGURE 8. Biomass allocation within 1- and 2-yr-old stands.

monocultures *Hyeronima* individuals on average were taller and more productive than *Cordia* grown in monoculture, the faster initial height growth of *Cordia* allowed it to outperform *Hyeronima* when the two were grown together. As pointed out by King (1990), maximizing productivity does not necessarily maximize the ability to grow tall and dominate competitively. A species' growth in mixed stands depends heavily on its speed of establishment.

It should be stressed that the fast early establishment of *Cordia* was under conditions of almost zero weed competition. When the weeded and unweeded mixed-species stands were compared, the early growth of *Cordia* was severely suppressed, but that of *Hyeronima* was hardly affected (Table 3). King (1993) demonstrated that higher allocation of biomass to roots will increase belowground competitive ability and may explain why *Hyeronima* would be less affected by herbaceous weed competition than *Cordia*.

Tilman (1988) has proposed optimal biomass allocation patterns that maximize competitive ability at different relative availabilities of aboveground and belowground resources. Before stand closure, on sites where belowground resources are abundant, light interception is likely to limit production. Optimal allocation under these conditions is for high allocation of biomass to stems, as with *Cordia*. After stand closure, belowground resource availability is also likely to become limiting, and optimal allocation should be for higher allocation to roots and a reduction in stem allocation: the standing biomass allocation pattern seen for *Hyeronima*. These optimal allocations are for standing biomass and do not take into account any differences in leaf or root turnover that may lead to very different allocations of assimilate to production.

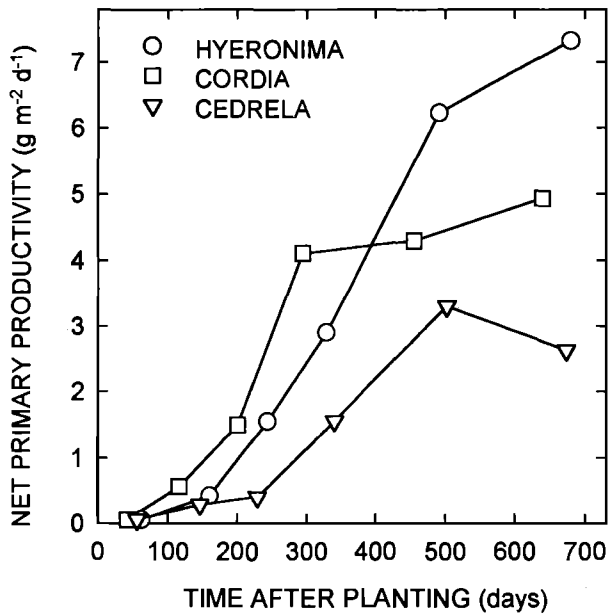


FIGURE 9. Aboveground net primary productivity in tree stands up to 2 yr old. Least significant differences for species comparisons within the following times after planting are, 110–160 days, LSD = 0.16; 200–250 days, LSD = 0.57; 290–510 days, LSD = 1.21; 455–503 days, LSD = 1.91; and 640–680 days, LSD = 1.07.

In a comparison of early and late successional tropical tree species, Shukla and Ramakrishnan (1984a,b) found that early successional species exhibited high leaf turnover rates, fast growth (both radial and height), and high allocation of biomass to stems, whereas late successional species exhibited low leaf turnover, a clumped leaf distribution, and high allocation of biomass to roots. The high initial productivity of tree species with a more pioneer-type growth habit, such as

TABLE 3.

Average tree height and biomass in 1- and 2-yr-old single-species and mixed-species stands. Parenthetical values are ranges of block means.

Species	Management	Height (m)		Biomass (kg/tree)	
		1 yr	2 yr	1 yr	2 yr
<i>Hyeronima</i>	Monoculture, weeded	2.2 (2.1–2.3)	5.7 (5.5–5.9)	1.3 (1.1–1.5)	8.2 (7.9–8.6)
	Polyculture, weeded	2.4	5.3	1.8	9.1
	Polyculture, unweeded	2.4	5.4	1.9	10.3
<i>Cordia</i>	Monoculture, weeded	2.6 (2.0–3.0)	4.9 (3.5–5.7)	1.7 (1.5–1.8)	5.8 (5.4–6.8)
	Polyculture, weeded	4.4	7.9	4.9	16.0
	Polyculture, unweeded	2.6	5.8	1.5	9.9
<i>Cedrela</i>	Monoculture, weeded	1.6 (1.6–1.7)	3.9 (3.7–4.2)	0.9 (0.8–0.9)	3.5 (3.3–3.9)
	Polyculture, weeded	1.3	3.1	0.7	2.6
	Polyculture, unweeded	1.4	3.3	0.6	2.5

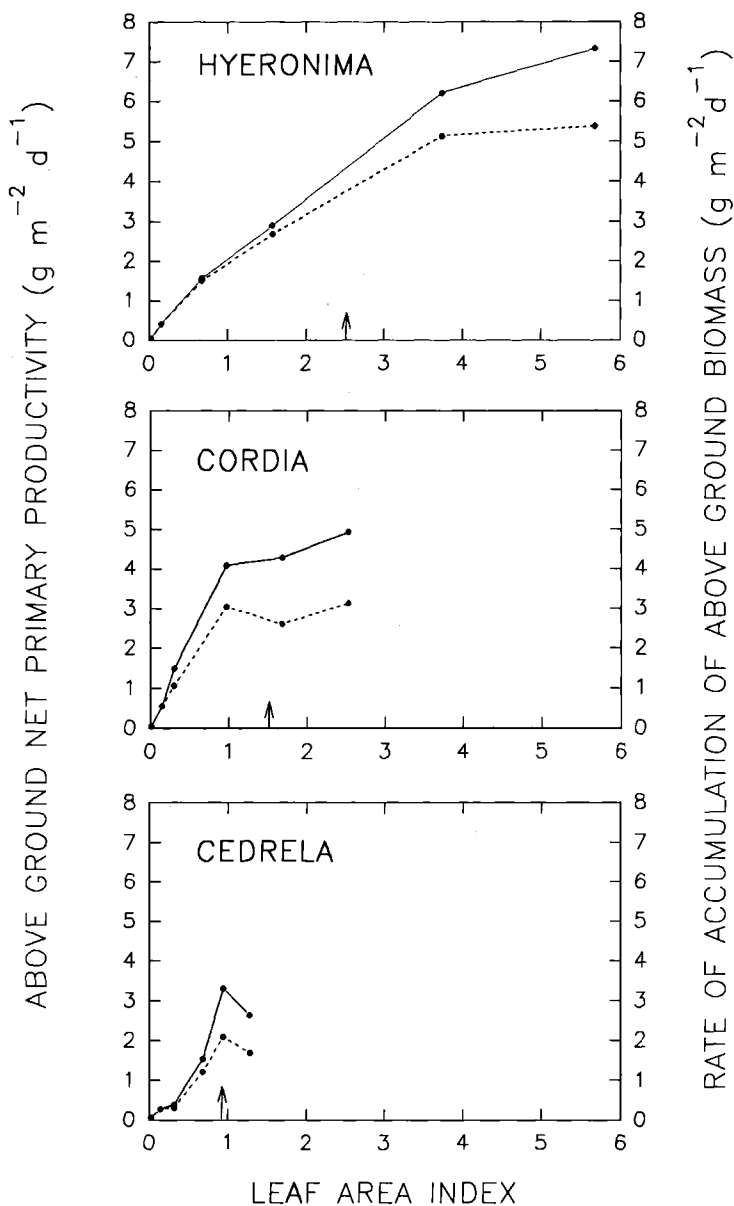


FIGURE 10. The relationship between LAI and two measures of growth. The solid line shows aboveground net primary productivity and the dashed line the rate of accumulation of aboveground biomass. Arrow indicates LAI at canopy closure.

Cordia, may allow them to capture the site quickly while conditions of low competition prevail. After canopy closure, however, fast turnover of leaves (and perhaps other plant parts) means that a high allocation of carbon is required to maintain leaf area, which limits stem biomass production. In contrast, species such as *Hyeronima* can maintain leaf area with lower rates of investment and therefore can maintain higher rates of stem biomass production.

The selection of species only on the basis of early growth of isolated individuals

is not recommended. Instead, stand productivity needs to be measured both before and after stand closure, for biomass allocation patterns that favor rapid establishment differ from those that maximize stem biomass increment in closed-canopy stands. Situations where rapid site occupancy is required would include reforestation after cutting and burning or restoration of otherwise devegetated sites with little competition. In this case species with high specific leaf area, high specific root length, and a spreading architecture may be preferable. Species with low leaf turnover rates may achieve higher stem production after stand closure and may also grow better. Where reforestation of abandoned pastures or enrichment planting in secondary growth is being carried out, the stem production of the trees under highly competitive conditions is likely to be of primary importance. In this environment species with low leaf turnover rates, high leaf area indices, and high root density should be among those that perform best.

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