

PRIMARY PRODUCTIVITY AND RESOURCE PARTITIONING IN MODEL TROPICAL ECOSYSTEMS

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Abstract. The diversity of plant life forms in tropical forests affords the opportunity for assembly of plant combinations, both natural and managed, that make full use of resources and sustain high productivity. The influence of combining life forms on productivity and resource use was evaluated using three fast-growing tree species (*Hyeronima alchorneoides*, *Cedrela odorata*, and *Cordia alliodora*); each species was grown alone and with two perennial, large-stature, self-supporting monocots (*Euterpe oleracea* and *Heliconia imbricata*).

Aboveground net primary productivity was extremely high in all stands. The monocots did not contribute significantly to the productivity of the *Hyeronima* polycultures, which was 4.5–8.4 g·m⁻²·d⁻¹ between 18 and 36 mo. In contrast, the monocots accounted for 57% of the productivity (9.7 g·m⁻²·d⁻¹) of *Cedrela* polycultures and 67% of the productivity (6.8 g·m⁻²·d⁻¹) of the *Cordia* polycultures, by age 3 yr. The leaf area and density of fine roots in the *Cedrela* and *Cordia* polycultures were also significantly increased by the presence of the monocots, reaching or surpassing the levels found in the *Hyeronima* stands.

The high productivity of *Hyeronima*, coupled with poor growth of its interplanted monocots, indicated that *Hyeronima* was able to achieve nearly complete use of resources. Ecosystem productivity and resource capture were increased when the monocots were grown with the other two tree species, and this occurred because of the inability of the tree species to completely utilize available resources, which provided an opportunity for the monocots to flourish in the understory. Monocot productivity in the *Cedrela* stands was additive to that of the trees, indicating complementary resource use between the monocots and this tree species. In the case of *Cordia*, tree productivity was slowed by the monocots, but this decline was more than compensated for by the high productivity of the associated monocots.

Whether in natural forests or human-constructed agroforestry systems, the presence of dominant species that do not fully exploit all available resources allows the coexistence of other species and creates the potential for complementary resource use. The resource use characteristics of such species should be a key consideration in forest restoration efforts and in the design of sustainable land use systems.

Key words: *Cedrela odorata*; complementary resource use; *Cordia alliodora*; ecosystem design; *Euterpe oleracea*; *Heliconia imbricata*; *Hyeronima alchorneoides*; leaf area; life-form diversity; monocots; productivity; root density.

INTRODUCTION

The diversity of life forms in tropical forests presumably contributes to a high efficacy of resource exploitation by these systems. The combination of a diversity of life forms has been suggested as a model for the design of sustainable land use systems (Ewel 1986), and such combinations are typical of many traditional agroforestry systems in the tropics (Nair 1989). If the combination of different plant life forms in tropical forests, or in tropical agroforestry systems, does in-

crease productivity and resource exploitation, this may be due to complementary resource use. The assessment of complementary resource use is important to evaluating the role of biodiversity in sustaining ecosystem processes (Ewel and Bigelow 1995).

The observation that mixtures of two plant species often have a higher productivity than either species grown alone (de Wit 1960) has led to the idea that some species may have the capacity to exploit resources unavailable to others (Harper 1977). Pursuing this implication, agronomists have focused on practices such as intercropping of annuals (Trenbath 1974, Willey 1985). Complementarity has also been invoked as the means by which combinations of crops and trees may increase production (Raintree 1983) and conserve soil fertility (Conner 1983). Some agroforestry systems have higher primary productivity than the crop alone (e.g., Yamoah et al. 1986, Hagggar et al. 1993), and mixing tree species in forestry plantations sometimes

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increases stand productivity (e.g., Assmann 1970, Binkley 1983, Binkley et al. 1992).

Ecologists followed up de Wit's (1960) competition experiments with studies of how species may exploit resources in noncompetitive ways (e.g., Trenbath and Harper 1973) and considered the implications for the coexistence of species. For example, the spatial and temporal partitioning of resources have been identified as the basis for coexistence in herbaceous plant communities (McKane et al. 1990, Campbell et al. 1991). Even in communities dominated by one life form, the interstices among individuals can provide opportunity for the noncompetitive coexistence of a second, non-dominant life form (Grubb 1986).

Three possible mechanisms of complementary resource use have been suggested (Trenbath 1976): (1) partitioning of resource use in space, (2) partitioning of resource use in time, or (3) use of different resources. There are theoretical arguments (Vandermeer 1989) and empirical evidence for complementary resource use in space, both by leaves (Trenbath 1986) and by roots (Huck 1983). Complementary use of resources in time occurs when plants have different temporal growth patterns or life spans, so that the periods of maximum demand for resources of the species are temporally separated (Rao 1986). For example, millet is frequently intercropped with *Acacia albida*, the millet thriving during the wet season when the overstory tree is deciduous (Felker 1978). Resource complementarity may also arise when species use different forms of a resource, e.g., nitrate by nonlegumes or diatomic nitrogen by legumes (Roskoski 1982, Binkley 1992; see review in Vandermeer 1989), or use resources in different ratios (Trenbath 1976).

Studies of the significance of diversity in natural tropical systems have yielded indefinite results. A previous study of successional communities and tree monocultures has shown only small differences in leaf area and density of fine roots between the systems, indicating no significant increase in the ability to capture resources by the more diverse system (Ewel et al. 1982, Berish and Ewel 1988). Nevertheless, there was some evidence that more species-rich communities better conserved soil nutrients (Ewel et al. 1991). The complexity and dynamics of species-rich successional communities, however, make it difficult to identify the mechanisms that might be involved. The current study therefore examines the possible benefits of species richness on ecosystem functioning in simpler, more controlled systems.

Our aim was to assess productivity, as influenced by complementary and competitive resource use, of combinations of two contrasting groups of large-stature, perennial plants predominant in tropical forests. To do this, we grew dense stands of trees (the most successful life form of the humid tropics) and planted perennial monocots (the second most prevalent life form) in the interstices. Because of their distinct architectures and

habits, we hypothesized that the two life forms would have a high probability of exhibiting different resource-use characteristics. The study was conducted in a humid climate on a rich alluvial soil, decreasing the likelihood that any one resource would be severely limiting. Total resource use by the combination of two life forms was assessed by measuring productivity, and the mechanisms involved were inferred from density, spatial arrangement, and temporal distribution of resource-capturing organs (leaf area and fine roots).

MATERIALS AND METHODS

Site description

The experiment was carried out at La Selva Biological Station in the Atlantic lowlands of Costa Rica, at an elevation of ≈ 40 m. 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 < 0.1 m. The site is on an alluvial terrace with a deep, well-drained, fertile soil classified as a mixed, isohyperthermic, possibly andic, fluventic Dystropept (Hagggar and Ewel 1994). The topsoil (0–10 cm), pH 6.5, contained 3.4% organic carbon, 13.7 mg/kg of extractable nitrate- and ammonium-nitrogen, and 18.2, 496, 1570, and 245 mg/kg of extractable phosphorus, potassium, calcium, and magnesium, respectively.

In early 1991 the site was cleared of an abandoned cocoa plantation, merchantable overstory trees (mostly *Cordia alliodora*) were harvested, and the slash was burned. The experimental plots were established immediately after the manual clearing of charred logs.

Species

Hyeronima alchorneoides Allemao (Euphorbiaceae), *Cedrela odorata* L. (Meliaceae), and *Cordia alliodora* (R.&P.) Cham. (Boraginaceae), which are native, commercially valuable, fast-growing tropical hardwoods, were chosen for study because of their contrasting phenologies and physiognomic characteristics, indicating a potential for different resource capture capabilities. *Hyeronima* is evergreen and, as a juvenile (for at least 5 yr), has large (up to 300 cm²), simple leaves; its branching is sympodial and orthotropic, leading to development of a compact, rounded, dense crown. *Cedrela* is semideciduous as a juvenile (up to 3 yr), later becoming completely deciduous for ≈ 2 mo during the dry season. Its long leaves (up to 1 m) are pinnately compound and contain 10–20 pairs of leaflets, each ≈ 40 cm². The monopodial, orthotropic branching of *Cedrela* is made more complex by resprouting following attacks by a shoot-boring moth, *Hypsipyla grandella*. *Cordia* is semideciduous, and its simple leaves average ≈ 33 cm²; it has monopodial, plagiotropic branching with five branches per node, giving it a tiered, open crown. More detailed species descriptions, provenances used, and methods of propagation are given in Hagggar and Ewel (1995).

Two species of monocotyledonous perennials were also planted. The first, *Euterpe oleracea* Mart (Arecaceae), is a multistemmed, tall (up to 20 m), pinnately leaved palm that grows in forests on alluvial soils. It is native to the lower Brazilian Amazon where its fruits and bud are harvested. The second monocot, *Heliconia imbricata* (Kuntze) Baker (Heliconiaceae), is a native perennial herb that is common in the secondary forest around the site. It produces numerous basal shoots, each producing leaves that extend to 5 m or more in height.

Experimental design

Between 20 May and 26 July 1991, three stands (80 × 40 m) of each tree species were established in a randomized block design. The trees were planted in a triangular pattern, with 2.0 m between trees. Thus, each tree had available to it an area of 3.46 m², and the stand density was 2887 trees/ha, which is about three times greater than would normally be used for forestry plantations of these species.

Each 80 × 40 m stand was subdivided into two parts; one part (50 × 40 m) remained as a monoculture, and the other (30 × 40 m) was interplanted with the two monocots. The *Euterpe* were planted at the same time as the trees, and were located between every other tree in every other row of trees, i.e., on a grid of 3.46 × 4 m, so the density was a quarter of that of the trees. Just over a year later (August 1992), *Heliconia* was planted to intensify the monocot–dicot interaction. The *Heliconia* were under-planted (using pieces of freshly dug rhizome) between all the trees in the rows where *Euterpe* had not been planted, i.e., on a grid of 3.46 × 2 m, and so had half the density of the trees. The stands were weeded every 2–3 wk.

Additive designs, such as used in this study, are well suited for examining the whole-system consequences of adding a second, lower stature life form to a system dominated by trees. Additive designs were also recommended (in preference to replacement designs) for testing complementarity because the density of the individual species is the same in the monocultures and polycultures (Snaydon 1991). Nevertheless, in additive designs the polyculture does have higher total plant density than the monocultures. Therefore, to conclude that higher productivity in the polyculture is due to complementarity and not to higher density, the investigator must be confident that the productivity of the monospecific stands would not be greater at higher plant densities; that is why the trees were planted at such a high density.

Stand biomass and productivity

Plant size and survival were measured ≈4, 8, 12, 18, 24, and 36 mo after planting. Tree height and either basal or breast height (1.3 m) diameter were measured, as were monocot height, basal diameter, and number of fronds (*Euterpe*) or number of shoots (*Heliconia*).

Growth measurements were confined to the cores of each plot: 30 × 30 m in the polycultures and 30 × 40 m in the monocultures.

On each occasion that size and survival were measured, several plants (both trees and monocots) were harvested for biomass determinations. These were selected from the outer 5 m of each plot (outside of the 30 × 30 m core area), which was designated expressly for that purpose. A total of 126 trees of each species (18 to 24 at each of six times) was harvested, and the biomass (separated into leaves, rachises, branches, trunks, and coarse roots, i.e., those >5 mm in diameter) was determined, as described in Haggard and Ewel (1995). Biomass of the monocots was measured using the following sampling scheme. At 12 mo after planting, 18 *Euterpe* plants were harvested from the outermost 5 m of the *Hyeronima* stands, where extra plants had been established explicitly for destructive sampling. At 18 and 36 mo after planting, two individuals each of *Euterpe* and *Heliconia* were harvested from each of the nine polyculture plots, and at 24 mo, three individuals each of *Euterpe* and *Heliconia* were harvested from each polyculture plot. The monocots were separated into leaves, rachises (*Euterpe* only), stems, and coarse roots.

Data from the biomass harvests were used to develop allometric equations for each species, relating plant dimensions (tree heights and diameters; monocot heights, diameters, shoot counts, and leaf counts) to the biomass of leaves, stems, rachises, branches, and coarse roots (Haggard and Ewel 1995). These equations were then used to estimate the biomass (leaf, stem, branch, rachis, and coarse root) of each plant in the stand.

The method of sampling fine roots (to determine their length, horizontal and vertical distribution in the soil, and biomass) changed as the plants grew and root systems merged. At 25 mo after planting, a stratified random sample of cores was taken: 9 in each monoculture and 12 in each polyculture. Stratification was done by assigning one of three distances from the nearest plant to provide a spatially unbiased sample; samples were taken 28 cm from the nearest tree (=145 cm from the nearest monocot), 86 cm from both tree and monocot, and 145 cm from the tree (=28 cm from the monocot). At 36 mo after planting (well past the date of complete closure of all root systems), cores were taken at eight randomly selected locations in each plot. All cores were 110 cm deep, and each was divided into a surface 10-cm segment plus five 20-cm segments (10 10-cm segments in the case of the sampling at age 36 mo). The same cores were used to sample both tree and monocot roots, which were readily distinguishable. Roots were separated from soil using a hydropneumatic elutriator, then separated manually into diameter classes of <2 and 2–5 mm. Fine-root length was estimated using a line intercept method (Tennant 1975) before drying.

Stand biomass was calculated by summing the stand biomass of each plant part as estimated from the allometric equations and adding the estimated fine root biomass. Aboveground net primary productivity was calculated by adding litterfall (sampled biweekly using 50×173 cm screen-bottomed, raised litter traps, three in each replication of each treatment; Hagggar and Ewel 1995) to the change in standing biomass of aboveground parts between successive inventories.

Leaf area and light interception

Stand leaf area was determined by multiplying the specific leaf area (determined on subsamples of fresh leaves from each tree or monocot harvested as part of the biomass sampling) by the stand leaf biomass estimate. Leaf area index (LAI) was then derived by dividing stand leaf area by stand area.

Efficacy of light interception by the canopy was estimated as the probability of diffuse radiation penetrating through the canopy; this has been referred to as the indirect site factor (Rich 1990), or diffuse noninterceptance (Norman and Welles 1983). Two systems, both employing images perceived through a hemispherical lens, were used to measure canopy interception of diffuse radiation. Hemispherical photographs, analyzed by the CANOPY program (Rich 1990), yielded an Indirect Site Factor, and an LAI-2000 Plant Canopy Analyzer was used to measure Diffuse Non-interceptance (LI-COR 1992; LI-COR, Lincoln, Nebraska, USA).

Hemispherical canopy photographs were taken at $\approx 10, 13, 16, 22,$ and 25 mo after planting. Two photo points ≈ 25 m apart and 50 cm above the ground were established in the central part of each monoculture plot, and one photo point was located in the center of each polyculture plot. LAI-2000 canopy measurements were taken at 32 and 37 mo after planting. Paired above- and below-canopy readings were taken using two synchronized sensors at 26 – 30 randomly chosen points in each monoculture and 15 – 17 points in each polyculture; the exact number of points was determined by the heterogeneity of readings within the stand.

Statistical analysis

The experiment had a split-plot randomized block design, with tree species as the major treatment and presence or absence of monocots as the subtreatment. Comparisons of polyculture and monoculture treatments within tree species were analyzed using specific contrasts within a split-plot analysis of variance (SAS Institute 1988). Homogeneity of variance was established at major and subtreatment levels for all analyses. For most variables two kinds of contrasts between the monocultures and polycultures were made. First, stand characteristics of the two treatments were compared where the polyculture value was the combined value for trees and monocots. Second, the influence of the monocots on the trees in the polyculture was analyzed

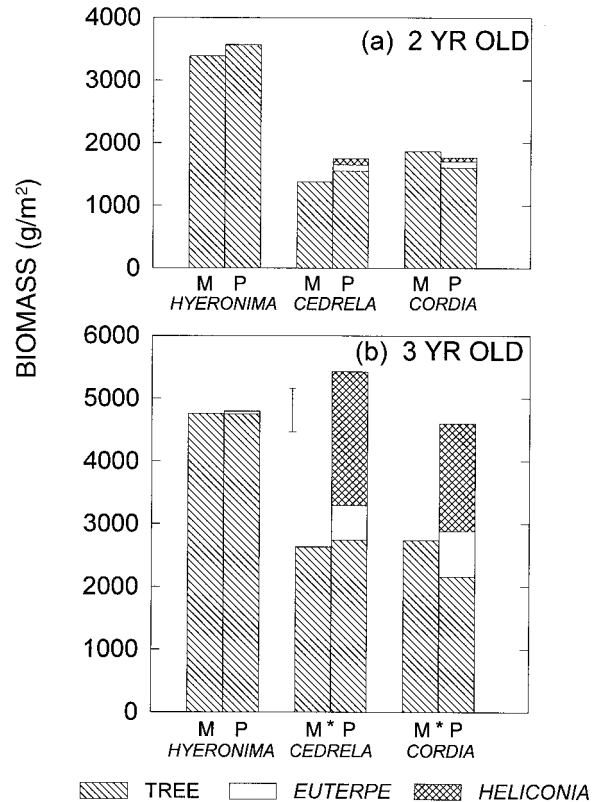


FIG. 1. Standing biomass of (a) 2-yr-old and (b) 3-yr-old stands of monoculture (M) and polyculture (P). Biomass of the polycultures is divided into its component species. Asterisks (*) indicate that there is a significant difference in total stand biomass between monoculture and polyculture for that tree species. Vertical bar shows Least Significant Difference. (LSD = 696 for 3-yr-old stands.)

by contrasting values for the trees only under the two treatments.

Specific contrasts of treatment effects were analyzed within an analysis of variance. Significant differences are shown by the use of an asterisk in the figure and/or are presented in the text, and the variance associated with such differences is indicated by least significant differences (LSD). Differences cited as significant have a probability of a Type I error of <0.05 .

RESULTS

Biomass

All species grew very rapidly. When the stands were 3 yr old, for example, mean (± 1 SD) tree heights were 8.9 ± 1.1 m for *Hyeronima*, 7.0 ± 2.7 m for *Cordia*, and 7.6 ± 2.3 m for *Cedrela*. The accumulation of biomass by *Hyeronima* was exceptional: ≈ 3470 g/m² at age 2 yr and 4760 g/m² at age 3 yr. Neither of the other two tree species (nor the two monocots) approached those amounts (Fig. 1).

During the first 2 yr there were no significant differences in total stand biomass between polycultures

and monocultures of any species (Fig. 1a). During the 3rd yr, however, pronounced differences developed between the monocultures and polycultures of both *Cordia* and *Cedrela* (but not *Hyeronima*), primarily due to substantial increases in the biomass of the monocots: *Euterpe* added 430–610 g/m² during that 3rd yr, and *Heliconia* accounted for 1660–2030 g/m² (Fig. 1b). The combined biomass of the monocots with these two tree species approached or surpassed that of the *Hyeronima* stands. Only in the case of *Cordia* was tree biomass significantly depressed by the presence of monocots in the polyculture.

Aboveground net primary productivity

Stands of all three tree species were very productive, and the addition of a second life form resulted in three kinds of responses. *Hyeronima* suppressed growth of the monocots, but they did thrive in stands of both *Cedrela*, where their production was additive to that of the trees, and *Cordia*, where tree productivity suffered as a result of monocot presence.

Monoculture stands of *Hyeronima* achieved very high levels of productivity, reaching a maximum of ≈ 8 g·m⁻²·d⁻¹ during the 2nd yr of growth, when the productivity of *Hyeronima* was about double that of the other two tree species, then dropping to ≈ 4.3 g·m⁻²·d⁻¹ during the 3rd yr, which is similar to the other species. This drop in productivity during year 3 reflects a decline in the growth rate of stems and a decrease in leaf biomass. The productivity of polycultures of *Hyeronima* was always slightly greater than that of monocultures. This increase, which was statistically significant only during the interval between ages 18 and 24 mo, was entirely due to the trees themselves, as interplanted monocots did not prosper; survival of the palms exceeded 90%, but growth was negligible.

The productivity of *Cedrela* was reduced by repeated stem-borer (*Hypsipyla grandella*) attacks in the 1st yr (Rodgers et al. 1995), but productivity increased substantially in the 2nd yr as the trees recovered and the frequency of attack diminished. Monocots contributed significantly to the productivity of *Cedrela* polycultures (Fig. 2). The productivity of the *Cedrela* trees themselves was not affected by the monocots, but the monocots contributed 5.6 g·m⁻²·d⁻¹ to the productivity of the polycultures in the 3rd yr of growth, almost doubling stand productivity compared to the monocultures.

Productivity in polycultures of *Cordia* was significantly greater than that of monocultures only after 24 mo (Fig. 2). Unlike *Hyeronima* and *Cedrela*, the productivity of *Cordia* itself was significantly lower in polycultures than in monocultures. Although the monocots contributed 4.6 g·m⁻²·d⁻¹ to the productivity of the polyculture stands in the 3rd yr of growth, total polyculture productivity during that interval was only 3.1 g·m⁻²·d⁻¹ higher than in the monoculture stands because of the suppression of tree growth.

Resource capture

Productivity is determined, in part, by stand-level capacity to acquire resources. The potential to capture aboveground resources was gauged by estimating leaf area and interception of diffuse light by the canopy, and the potential to capture water and nutrients was appraised by estimating the density and distribution of fine roots.

Aboveground

The monocots added little to the leaf area index (LAI) of *Hyeronima* stands, which, at age 2 yr, had higher LAI than either monocultures or polycultures of the other two tree species (Fig. 3). The situation was different in the *Cedrela* and *Cordia* polycultures where, even by the end of the 2nd yr of growth, the monocots accounted for a significant proportion of the leaf area. For example, at age 3 yr, the huge vertical or arching leaf blades of *Heliconia* contributed 73% of the leaf area of *Cedrela* polycultures and 62% of the leaf area of *Cordia* polycultures (Fig. 3). As reflected by its lower productivity, *Cordia* had significantly lower LAI in the polycultures than in the monocultures.

Interception of diffuse light was greatest in the *Hyeronima* stands and did not differ between monocultures and polycultures. Polycultures of *Cedrela* and *Cordia*, >22 mo old, had significantly greater diffuse light interception than monocultures of those trees (Fig. 4). The reductions in light interception of *Cedrela* stands, 22 and 32 mo after planting, and of *Cordia*, 32 mo after planting, were due to leaf loss by these tree species in the dry season. Only at age 37 mo did interception of diffuse light by *Cedrela* and *Cordia* polycultures reach values attained 20 mo earlier by *Hyeronima* stands.

Belowground

There was no evidence of vertical partitioning of soil resources by fine roots of different species: the fine roots of both trees and monocots were most concentrated in the surficial 10–20 cm of soil and quite uniformly distributed throughout the other sampled depths (Fig. 5). The fine root density of all species, and species combinations, declined by 15–45% between 24 and 36 mo.

One of the most distinguishing features of *Hyeronima* was its high density of fine roots, which was more than three times greater than that of the other two tree species (Fig. 5). The addition of the monocots led to a twofold increase in fine-root density in *Cedrela* stands. Root density in *Cordia* polycultures was high, similar to that in *Hyeronima* stands (Figs. 5 and 6), but much of this consisted of monocot roots: the increase in total density of fine roots in the *Cordia* polycultures at both 24 and 36 mo was accompanied by a decline of $\approx 30\%$ in density of fine roots of *Cordia* itself.

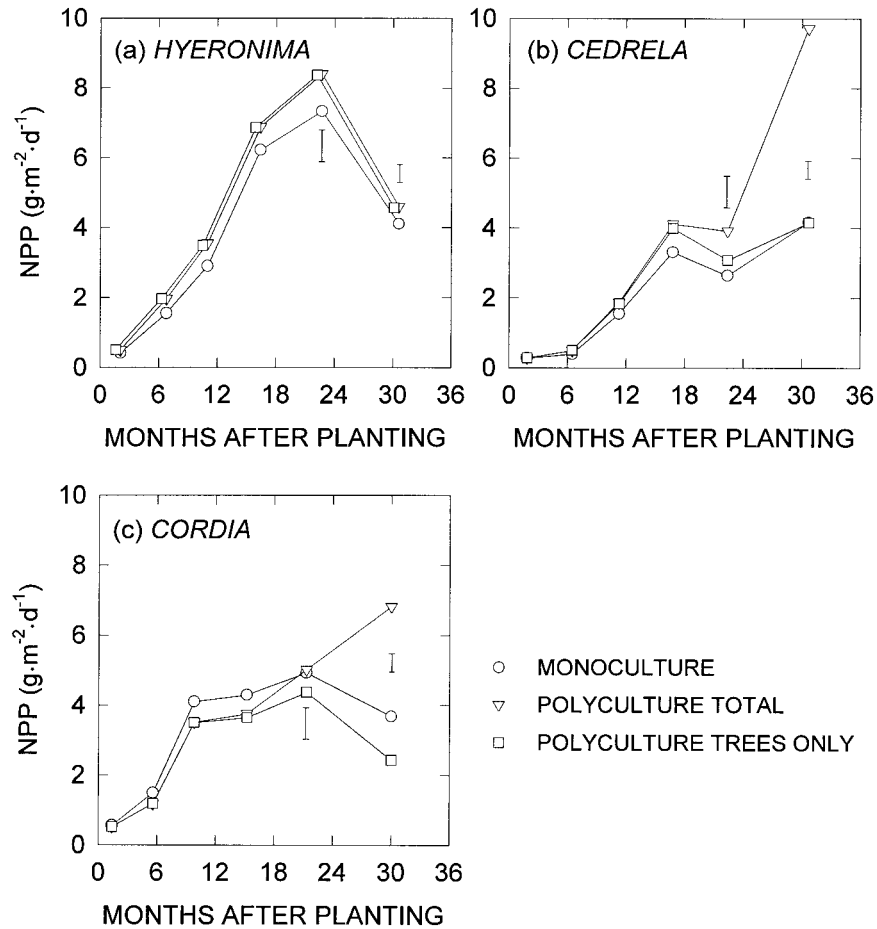


FIG. 2. Aboveground net primary productivity (NPP) of (a) *Hyeronima*, (b) *Cedrela*, and (c) *Cordia* in monoculture and polyculture stands, during six periods over 3 yr. Values are plotted at the midpoint of each period, and vertical bars show Least Significant Differences. Differences in total productivity between monocultures and polycultures were significant for *Hyeronima* and *Cedrela* at 18–24 mo (LSD = 0.86), and for *Cedrela* and *Cordia* at 24–36 mo (LSD = 0.55).

DISCUSSION

Ecosystem productivity and resource use

The very high growth rates of the species used allow us to evaluate how the interaction between large-stature perennial plants influences ecosystem productivity and resource exploitation after only 3 yr growth. The interaction of the trees and monocots yielded three outcomes. *Hyeronima* so completely used available resources that little was left to support the growth of the monocots, resulting in the almost total suppression of the latter. Productivity of the monocots in the *Cedrela* stands was substantial and *Cedrela* was unaffected by the presence of the monocots, leading to a significantly higher productivity in the polyculture than the monoculture. *Cordia* productivity was significantly reduced by competition from the monocots, but the additional productivity from the monocots more than compensated for this reduction such that polyculture productivity was still significantly greater than that of the monoculture.

The greater ecosystem productivity of some of the polycultures may be due to the greater density of plants in the polycultures or to differences in resource exploitation between the life forms. What evidence do we have that the trees in monoculture were exploiting resources to the fullest capability of the species (and thus a higher density of trees would not have had a higher productivity)? All three species were exceptionally fast growing; 12–18 mo after planting they achieved closure of both canopy and root systems (Haggar and Ewel 1995), the point at which resource acquisition and productivity should be independent of density (de Wit 1960, Assmann 1970, Watkinson 1985). This is supported by the observation that aboveground net primary productivity of *Cordia* and *Cedrela* monocultures did not increase significantly after the first 12–18 mo (Fig. 2). LAI and interception of diffuse light did increase moderately after canopy closure, approaching an asymptote between 24 and 36 mo (Figs. 3 and 4), while fine root density actually declined between 24 and 36 mo. It is for this period of stable

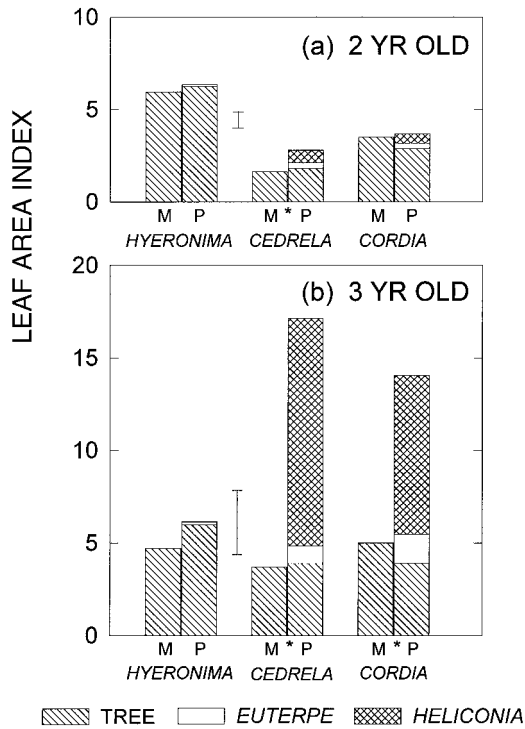


FIG. 3. Leaf area index (LAI) of (a) 2-yr-old and (b) 3-yr-old monoculture (M) and polyculture (P) stands. LAI of the polycultures is divided into the contribution from its component species. Asterisks (*) indicate that there is a significant difference in total stand LAI between the monoculture and polyculture for that tree species. Vertical bars show Least Significant Differences. (LSD = 0.9 at 2 yr and 3.4 at 3 yr.)

primary productivity by the trees in monoculture, 18–36 mo after planting, that the monocots begin to significantly contribute to the productivity of the polycultures. Even if the small increases in LAI and productivity do indicate some increase in resource capture by the trees over this time, this effect is small compared to the substantial impact of the monocots upon the productivity and resource use in the polycultures.

What evidence is there that complementary resource use plays a role in the greater productivity of the polycultures? Although our design does not include the three-way comparison between two monocultures and a polyculture normally used when evaluating relative yield totals, we can still use this concept to partially evaluate complementarity between our species. Resource complementarity occurs when the relative yield total (RYT; de Wit 1960) is >1.0 (Snaydon and Satorre 1989), where

$$RYT = y_{ij}/y_{ii} + y_{ji}/y_{jj}$$

y_{ii} and y_{jj} = yield of components i and j in monocultures, and y_{ij} and y_{ji} = yields of the components when grown together. When at least one of the two components, i , is grown such that resource use is independent of its density, then complementarity is demonstrated if y_{ij}/y_{ii}

> 1.0 and if $y_{jj} > 0$, i.e., if species i does not suffer from competition with j , and if j makes some contribution to the productivity of the total. In the case where i does suffer from competition with j , no definitive conclusions can be made with our design.

In the case of both *Cedrela* and *Hyeronima*, the productivity of the trees was unaffected by the presence of the monocots, i.e., $y_{ij}/y_{ii} > 1.0$, and in both cases at least one of the monocots survived, i.e., $y_{jj} > 0$, indicating complementary resource use between the monocots and this tree. The complementarity between the monocots and *Hyeronima* allowed the coexistence at least of the palms, but their presence did not make a significant contribution to ecosystem productivity. In contrast, the complementarity of the monocots with *Cedrela* not only allowed coexistence but greatly increased ecosystem productivity.

Relative plant sizes, whether the result of differential

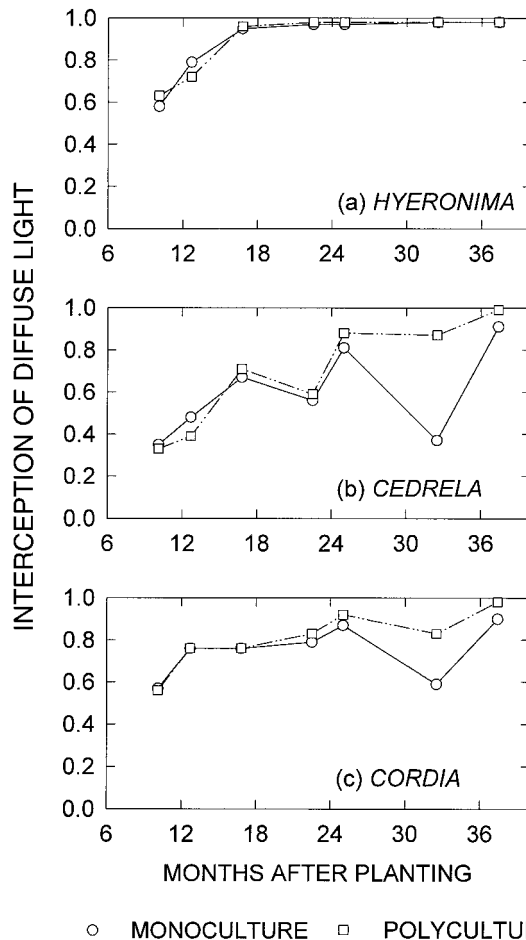


FIG. 4. Canopy interception of diffuse light in 10–37 mo old monocultures and polycultures of (a) *Hyeronima*, (b) *Cedrela*, and (c) *Cordia* as indicated by Indirect Site Factor (10–25 mo) and 1 – Diffuse Noninterceptance (32 and 37 mo). Differences between monocultures and polycultures of *Cedrela* and *Cordia* were significant at 32 mo (LSD = 0.101) and 37 mo (LSD = 0.026).

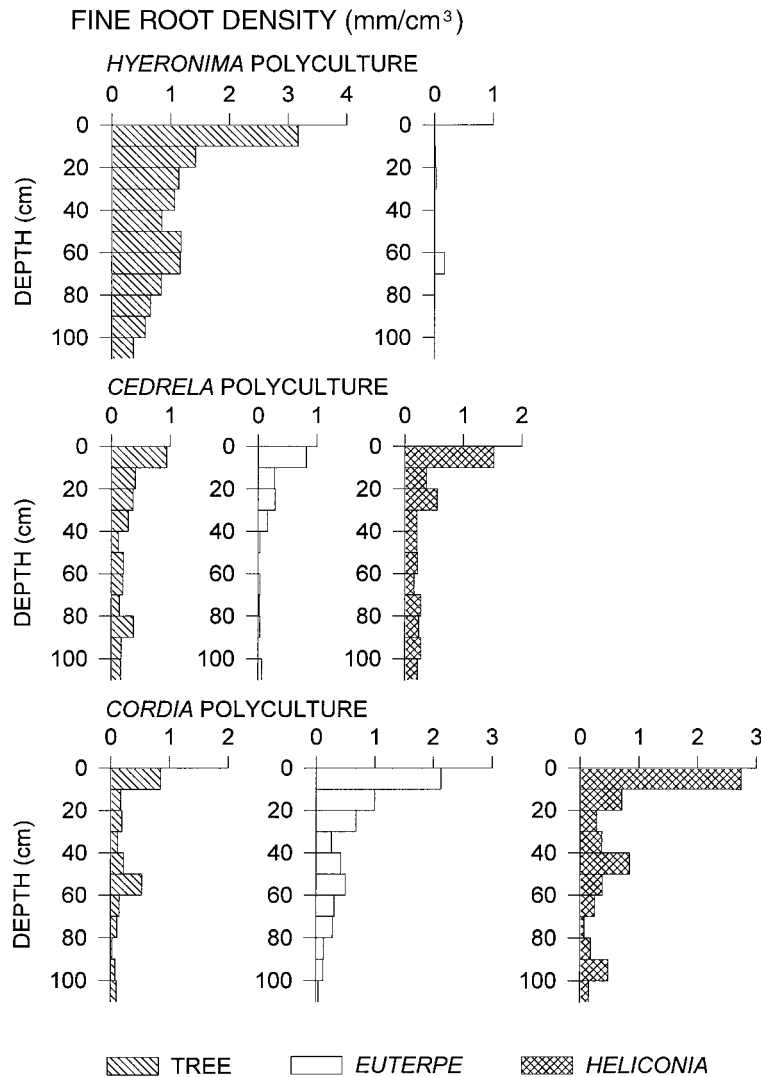


FIG. 5. Distribution of tree, *Euterpe*, and *Heliconia* fine-root density with depth in 3-yr-old polyculture stands.

growth rates between species planted synchronously or timing of establishment, can markedly affect competitive interactions. In some cases the magnitude of our results may be partially the consequence of timing in the establishment of the species. For example, the *Hyeronima* canopy intercepted almost all available light soon after establishment, providing little opportunity for the *Heliconia* to establish. Nevertheless, early growth and timing of planting were probably of little importance in the relationships between either *Cordia* or *Cedrela* and the monocots; the period of greatest productivity of the monocots was after canopy closure of these tree species, and by the time the trees were 3 yr old, the monocots and the trees had comparable biomass (Fig. 7). In neither circumstance, however, would the existence of complementarity be affected unless it led to the local extirpation of one of the two life forms.

Mechanisms

At least two of the three processes of resource partitioning reviewed by Trenbath (1976) may play a role in promoting the greater productivity in some of the polycultures. First, some temporal partitioning of resource use undoubtedly occurred. Partial leaf loss by *Cedrela* and *Cordia* did increase light availability to the understory during the 2-mo drier season (Fig. 4), and it is likely that deciduousness was accompanied by reduced root activity. Nevertheless, the brief period when the trees are leafless is also the most stressful time for large-leaved monocots, i.e., when high levels of insolation coincide with low availability of water (Sloten and Weert 1973).

A mechanism of greater importance at our site was spatial separation in the use of resources, which may have occurred above- or belowground. Even when they

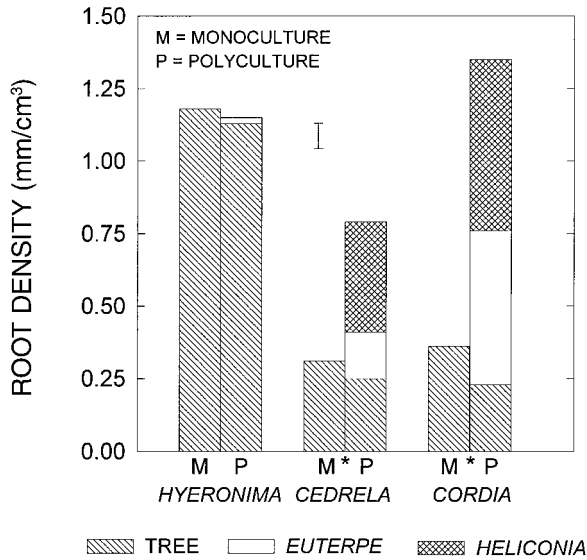


FIG. 6. Contributions of trees and monocots to stand fine-root density in 3-yr-old monocultures (M) and polycultures (P). Asterisks (*) indicate a significant difference in total stand root density between monoculture and polyculture for that tree species. Vertical bar shows Least Significant Difference (LSD = 0.09).

were in full leaf, *Cordia* and *Cedrela* developed only 80–85% canopy cover, thus allowing light penetration to the understory (Fig. 4). Trenbath (1981) demonstrated that stratification in the canopy of intercrops contributed to higher light use efficiency than in monocultures, and Binkley et al. (1992) concluded that greater light capture in mixed plantations of *Eucalyptus* and *Albizia* compared to monocultures was the principal cause of the greater productivity of the mixture (although the two species had very different nutrient demands as well). There was no discernible difference in root distribution between the trees and monocots at our site (Fig. 5), indicating no large-scale spatial separation in the exploitation of soil resources. Nevertheless, the monocots did greatly increase the density of fine roots, and this would have increased the volume of soil effectively exploited. It must also be assumed that the reduction of *Cordia* growth in the presence of the monocots was due to belowground competition mediated by the high density of monocot fine roots.

In the polycultures, the combination of two life forms was capable of sustaining higher leaf area and fine-root density than one life form alone. The greater investment in resource capture by the polycultures may have resulted from the combination of life forms with different biomass-allocation patterns (Fig. 7). *Cordia*, *Cedrela*, and monocots had similar biomass, but the allocation of that biomass to resource-capturing structures (leaves and fine roots) was higher for the monocots than the trees, whereas *Cordia* and *Cedrela* invested more biomass in support structures, particularly coarse roots. The third tree species, *Hyeronima*, main-

tained high leaf area and density of fine roots, traits that had manifested themselves early in the life of the plantations (Hagggar and Ewel 1995). This enabled it to achieve high productivity, thoroughly exploit resources, and suppress the monocots.

Analysis of the economics of growth has led to the hypothesis that plants invest in the capture of different resources such that the supply of all resources is simultaneously limiting (Bloom et al. 1985). Tilman (1988) predicted that in environments where all resources are abundant, the competitively superior pattern would be for high allocation to stem, even to the extent of reducing leaf area and productivity. This pattern of high allocation to stem tissue, and low allocation to leaf biomass, is typified by *Cordia* and *Cedrela* (Hagggar and Ewel 1995). The consequence of this model of investment is that growth is limited by the allocation of biomass to the capture of resources and not by the absolute availability of the resources per se. Such allocation patterns leave resources unused, and any other species that can accumulate leaf area (for light capture) or fine roots (for water and nutrient uptake) can exploit them. This appears to be what the monocots growing in the understory of the tree stands achieved, particularly *Heliconia* with its high alloca-

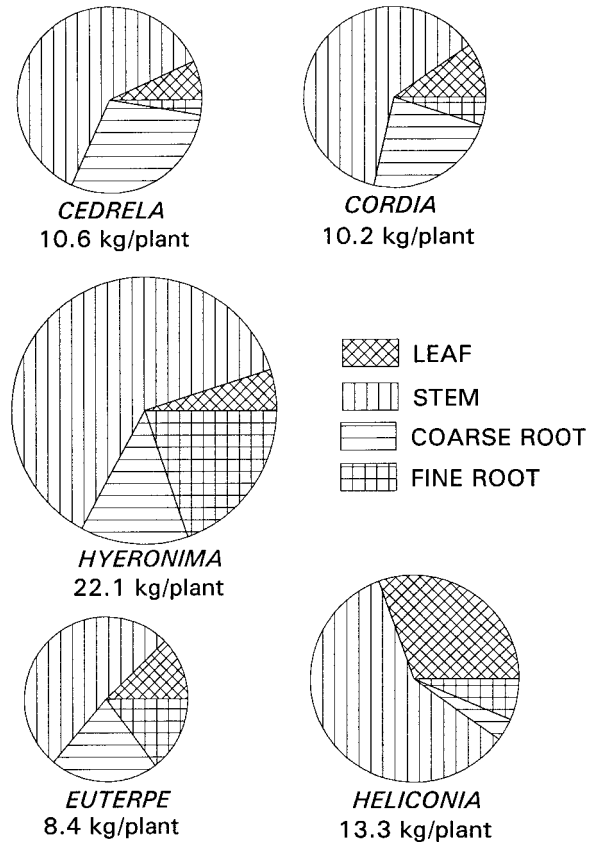


FIG. 7. Biomass allocation to leaves, stems, coarse roots, and fine roots by species, plus average biomass per plant, at age 3 yr.

tion to leaves and low allocation to belowground support structures (Fig. 7).

Thus, the greater productivity of the polycultures appears to be due to the combination of trees that have high allocation to support structures with monocots that have high allocation to resource capture. The trees maintain themselves through their greater stature, capturing a substantial portion of the light before it can reach the leaves of understory monocots, which may be more efficient at light capture. Nevertheless, the highly effective capture of belowground resources by understory vegetation can in some cases competitively reduce the growth of the overstory tree (cf. *Cordia* polyculture).

Ecological significance

There are two solutions to the problem of how to achieve full use of resources on a site having high potential productivity. Monocultures of species such as *Hyeronima* are capable of effective resource use and high productivity. This may be the case in some tropical swamps and upland forests dominated by one or a few species (Hart 1990), and perhaps in some forestry and perennial-crop plantations. Nonetheless, this solution is fraught with risk, for lack of diversity may make simple systems more vulnerable to herbivory and diseases (Altieri and Liebman 1986).

The other solution is achieved through combinations of productive species (although not, perhaps, the most productive ones that might occupy a site), such that the use of resources by one complements that of the other. If species capable of near-complete use of resources in resource-rich environments do exist (and they do, cf. *Hyeronima*), are species that only partially exploit available resources able to survive in their presence? Yes. In mixed stands containing *Cordia* and *Hyeronima* (substitutive plantings established on the same site as the plots used in this work), the growth pattern of *Cordia* enabled it to over-top *Hyeronima* in the 1st yr and maintain that dominance after stand closure (Hagggar and Ewel 1995). Thus, as predicted by Tilman (1988), the competitively superior morph (*Cordia*, in this case) was not the one that effected the most complete utilization of resources (*Hyeronima*). Species such as *Cordia*, which incompletely exploit resources but are capable of dominating species that invest heavily in resource acquisition, are common in resource-rich environments, where they provide opportunities for other life forms to coexist.

In tropical forests it may be expected that life forms will differ in their efficacy of resource exploitation, which in turn would facilitate the partitioning of resources among a number of species. The complementarity between overstory and understory species exemplifies the "ecological combining ability" of species (sensu Harper 1977), as recognized in late-successional temperate forests (Parrish and Bazzaz 1982). An example of incomplete resource use by a dominant spe-

cies from the temperate zone is seen in the additive productivity between an overstory of fast-growing, deciduous hardwoods and an understory of a slower growing, evergreen conifer (Kelty 1989). Such patterns of ecological combining ability may also be seen in perennial-crop agroforestry systems, such as shaded tea, coffee, or cocoa (Willey 1975).

Tropical ecosystems, both natural and managed, that include a combination of plant life forms have the potential to be more biologically productive and more thorough in use of resources than most monocultures. Plant breeders and tree geneticists have been effective in identifying and reproducing the handful of economically valuable super-morphs that maximally exploit the environment. Nevertheless, land uses based on combinations of plant life forms can be just as productive as the restricted set of monocultures that currently dominate tropical forestry and agriculture. The use of ecologically designed mixtures could open the way to the use of a greater array of species, while achieving high productivity.

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