Competition from below for light and nutrients shifts productivity among tropical species

John J. Ewel[a,1] **and María Julia Mazzarino**[b]

[a]Department of Biology, University of Florida, Gainesville, FL 32611; and [b]Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina, Universidad Nacional del Comahue, 8400 Bariloche, Argentina

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Chance events such as seed dispersal determine the potential composition of plant communities, but the eventual assemblage is determined in large part by subsequent interactions among species. Postcolonization sorting also affects the ultimate composition of communities assembled by people for restoration, horticulture, or conservation. Thus, knowledge of the mechanisms controlling interspecific interactions in plant communities is important for explaining patterns observed in nature and predicting success or failure of utilitarian combinations. Relationships among species, especially those from studies of biological diversity and ecosystem functioning, are largely based on studies of short-lived, temperate-zone plants. Extrapolation to perennial plants in the humid tropics is risky because functional relationships among large-stature species change with time. Shifts in competitive relationships among 3 life forms—trees, palms, and perennial herbs—occurred during 13 yr in experimental tropical ecosystems. In 2 cases the novel competitive mechanism responsible for the shift was reduction in crown volume, and therefore light-capturing capability, of overtopping deciduous trees by intrusive growth from below a palm. In a third case, complementary resource use developed between 2 evergreen life forms (overstory tree and palm), probably because of differential nutrient acquisition. Species-level traits and adequate time for shifts in interspecific relationships to emerge are crucial for predicting community trajectories.

complementarity | diversity | ecosystem functioning | fertile soil | plant competition

Design of sustainable ecosystems, whether for biodiversity conservation, economic gain, or restoration of ecosystem services, involves the assembly of plant communities comprising species of high ecological combining ability (1, 2). That combining ability is determined by interspecific interactions and refers to the ways and degree to which common resources, particularly light, water, and mineral nutrients, are shared. Does the nature of plant interactions remain relatively constant over time? If not, prediction of combining ability will require either case-specific long-term observation or thorough understanding of the mechanisms involved.

To examine the stability of plant interactions, and to reveal mechanisms driving any changes observed, we constrained the number of perennial life-form groups in simple experimental communities while varying the specific identity of 1 of them. The study site, a young alluvial terrace at La Selva Biological Station in the humid tropical lowlands of Costa Rica, was chosen because of its exceptionally fertile soil and warm, wet climate. By conducting experiments in an environment where plants experienced few abiotic constraints on growth we achieved results quickly and avoided the delays intrinsic to environments where plant growth is slow or where the ecological clock is reset annually.

The life forms selected are among those most common in mature forest at La Selva (3) and characteristic of forests in warm, wet climates on all continents. They are structurally and functionally very different from one another and included 3 native, fast-growing tree species capable of reaching the forest canopy: *Hyeronima alchorneoides*, *Cedrela odorata*, and *Cordia alliodora*; 1 alien palm, *Euterpe oleracea*, which has a native congener; and 1 native, giant perennial herb, *Heliconia imbricata* (all species are referred to hereafter by genus). The intent was to encompass some of the variability within the broad category of canopy-tree life form while holding the identity of the monocots (palm and herb) constant. Among other differences, *Hyeronima* (like the 2 monocots) is never leafless whereas the other 2 tree species are deciduous after attaining age 5–7 yr, *Cedrela* in the dry season and *Cordia* in the wet season. Tree seedlings were planted at high density (2,887 plants per hectare) in replicated 0.24-ha plantations (3 per tree species). Trees were lightly thinned periodically during the early years of the study to avoid stand stagnation while sustaining complete use of resources. Half of each plantation was retained as a single-species community (monoculture), and *Euterpe* and *Heliconia* were added to the other half, creating polycultures. Both monocots have very long leaves (*Euterpe*, ≈3 m; *Heliconia*, ≈2 m) and display their lamina almost vertically, giving them very high leaf area.

Results

To assess the performance of individual plant species as well as entire communities, we used aboveground net primary productivity (ANPP), which integrates net growth and biomass produced but lost during the growth-measurement interval (e.g., as mortality or litterfall). ANPP increased in all monocultures for the first 3–4 yr, then declined moderately (*Hyeronima*, from ≈30 to 18 Mg $\text{ha}^{-1}\,\text{yr}^{-1}$; *Cedrela*, from ≈18 to 11 Mg $\text{ha}^{-1}\,\text{yr}^{-1}$) or oscillated around relatively high levels (*Cordia*, 15; range 10–21 Mg $\text{ha}^{-1}\,\text{yr}^{-1}$) for the next decade (Fig. 1). These values are at the middle to high end of the range typically reported for fast-growing trees in the tropics (4).

The time course of tree ANPP in polycultures was very different from that of monocultures in the case of the deciduous trees *Cedrela* and *Cordia*, whose ANPP in polyculture plummeted dramatically after 3 yr, even becoming negative (because of mortality) after 10 yr (*Cedrela*) or dropping to ≈1 Mg $\text{ha}^{-1}\,\text{yr}^{-1}$ (*Cordia*). The start of the decline in tree ANPP in polyculture was synchronous with (in the case of *Cedrela*) or briefly preceded (in the case of *Cordia*) the peak of *Heliconia* ANPP, at which time *Heliconia* contributed 30–40% of ecosystem-level ANPP. By stand age 5 yr *Heliconia*, which has a basal meristem and whose maximum height is therefore biomechanically constrained, had been overtopped by the dense-canopied, evergreen *Euterpe* and no longer contributed to ANPP. Then, *Euterpe* ANPP soared as deciduous-tree ANPP plummeted,

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[1]To whom correspondence should be addressed at: Department of Biology, University of Florida, P.O. Box 118526, Gainesville, FL 32611. E-mail: jackewel@ufl.edu.

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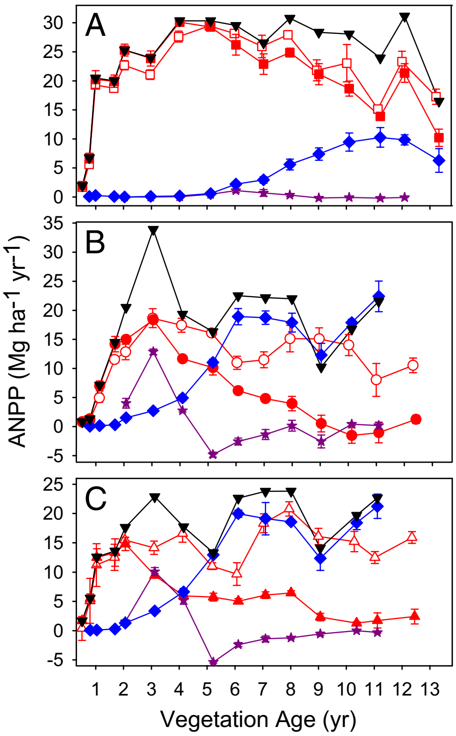

Fig. 1. ANPP in monocultures and 3-species polycultures dominated by different tree species. (*A*) *Hyeronima*. (*B*) *Cedrela*. (*C*) *Cordia*. Open red symbols, tree in monoculture; filled red symbols, tree in polyculture; star, *Heliconia*; diamond, *Euterpe*; inverted triangle, polyculture total. Values are means ± SE from 3 blocks.

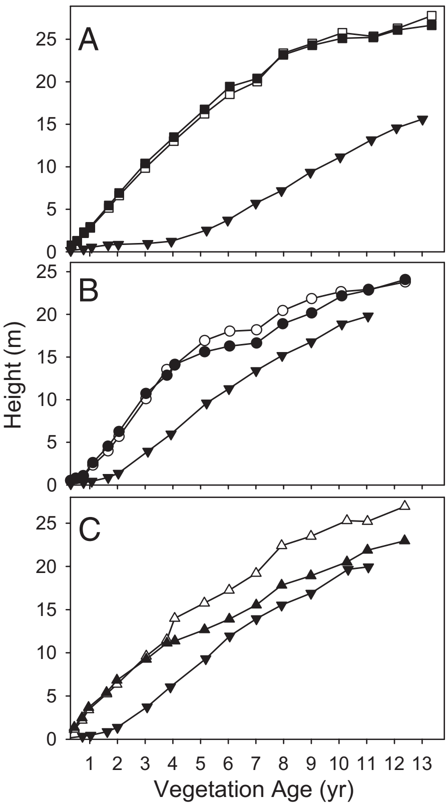

Fig. 2. Height relationships between tree species and palm (*Euterpe*, inverted triangle). (*A*) *Hyeronima* (squares). (*B*) *Cedrela* (circles). (*C*) *Cordia* (triangles up). Open symbols are trees in monoculture; filled symbols are trees in polycultures. Values are means of all individuals greater than or equal to the third quartile in each of 3 blocks. SEs are too small to show at this scale.

making *Euterpe* the dominant component of *Cedrela* and *Cordia* polycultures.

In the case of the evergreen *Hyeronima*, the time course of tree ANPP in polycultures was similar to that of monocultures, but the monocots responded very differently than when they were grown with the deciduous tree species. *Heliconia* never contributed measurably to total ANPP, and *Euterpe* growth was negligible for the first 6 yr beneath the *Hyeronima* canopy. Thereafter *Euterpe* began to grow more rapidly, eventually boosting ecosystem-level ANPP above levels in the *Hyeronima* monoculture—an example of complementary resource use.

Even through the later years of the experiment, when growth of the deciduous trees in polycultures was stunted and many individuals died, the trees retained their canopy position as the tallest components in each of their respective polycultures (Fig. 2). Despite occupying the tallest stratum in these 3-life-form systems, the leaf area of the deciduous trees dropped well below their values in monocultures while the evergreen *Hyeronima* sustained high values in both monoculture and polyculture (Fig. 3). What resource or process limited *Cedrela* and *Cordia* productivity while the overtopped *Euterpe* thrived? There are 4 potential explanations: growth-limiting (*i*) light, (*ii*) nutrients, or (*iii*) water or (*iv*) differential herbivory or disease. Water and pests were assessed but not implicated [supporting information (SI) *Text* and Fig. S1].

Given the marked growth decline of the tallest components in the *Cedrela* and *Cordia* polycultures, it was logical to seek an explanation in competition for nutrients. After the expected rise in soil nutrients from the burning of cut vegetation that accompanied site preparation, most measures of soil fertility declined over time under all species (Fig. S2). Nevertheless, concentrations of extractable soil nutrients did not drop to critically low levels (5, 6). Furthermore, despite the major physiognomic and floristic differences between monocultures and polycultures, differences among species in concentrations of foliar nitrogen (N) and phosphorus (P) were consistent throughout the 13-yr study, regardless of the community in which they were located: tree species alone or in polyculture, and *Euterpe* and *Heliconia* grown with any of the 3 tree species (Fig. S3). Foliar N and P concentrations of all species were high in comparison with data from many tropical forests (7). Thus, there is no compelling evidence indicating that competition for N or P led to *Euterpe* dominance in the *Cedrela* and *Cordia* polycultures.

Reduced light capture proved to be the primary mechanism causing ANPP of the overtopping *Cedrela* and *Cordia* trees to decline: *Euterpe* reduced the leaf area of both of these tree species by invading their crowns from below. The result was a reduction in crown volume, and therefore leaf area, of both *Cedrela* and *Cordia* (Fig. 4). These 2 species are deciduous for part of each year, which provides the understory *Euterpe* (an evergreen, like all palms) with full access to sunlight during the time of tree leaflessness and facilitates its growth.

Although light was the resource that limited tree growth in polycultures containing *Cedrela* and *Cordia*, the evergreen *Hyeronima* did not suffer commensurate losses of leaf area in polycultures (Fig. 3). Nevertheless, the nutritional status of *Hyeronima* did change and may foreshadow its eventual fate. Foliar concentrations of N (but not P) in *Hyeronima* leaves declined significantly ($P < 0.001$ for all regressions) and at the same rate in monoculture and polyculture (Fig. 5). That decline might be explained partially by a dilution effect, because LAI (leaf surface area, 1-sided, per unit area of ground) increased in both monoculture and polyculture by a little more than 11%, while N concentrations declined by a little

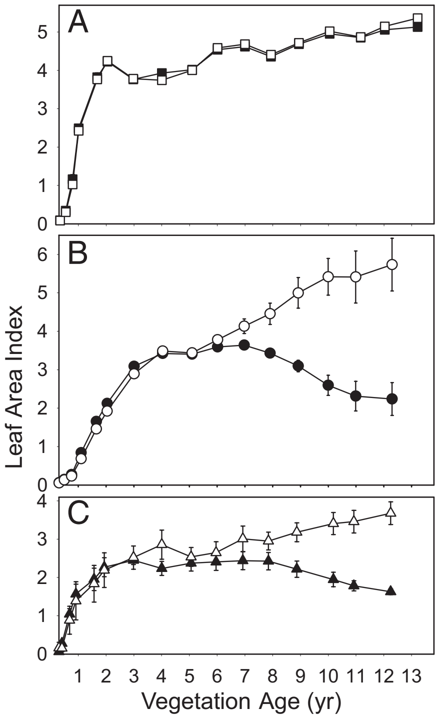

Fig. 3. Leaf area index of tree species grown in monoculture (open symbols) and polyculture (filled symbols). (*A*) *Hyeronima*. (*B*) *Cedrela*. (*C*) *Cordia*. Leaf area index is leaf surface area, 1-sided, per unit area of ground. Values are means ± SE from 3 blocks.

more than 20%. The remaining decline in foliar N (≈45% of the total) is almost certainly a consequence of lower rates of N mineralization under *Hyeronima*, whether in monoculture or polyculture, than under the other 2 tree species (8). The more-rapid decline in foliar N than of P led to a decline of N:P from ≈40 (molar basis) to values in the range of ≈20–27 (Fig. 5*C*); a ratio <31 is indicative of N limitation to growth (provided that N or P is limiting) (9, 10). Thus, competition between *Hyeronima* and *Euterpe* for ever-smaller supplies of N could lead to slower growth of *Hyeronima* and eventually to the same crown invasion from below that led to the demise of *Cedrela* and *Cordia* in their respective polycultures.

A second possible outcome for the *Hyeronima* polyculture is coexistence of *Hyeronima* and *Euterpe* in a 2-tiered community. *Hyeronima* trees attain heights of 50 m (3) whereas *Euterpe* is biomechanically constrained to ≈25 m. *Hyeronima* may maintain its considerable height advantage over *Euterpe*, precluding crown invasion from below by the palm. Coexistence might also be fostered by spatial partitioning of soil by root systems. The burst of growth by *Euterpe* in *Hyeronima* polycultures that only began ≈6 yr into the study (Fig. 1*A*) led us to investigate that possibility through root excavations. *Hyeronima* roots dominated the sur-

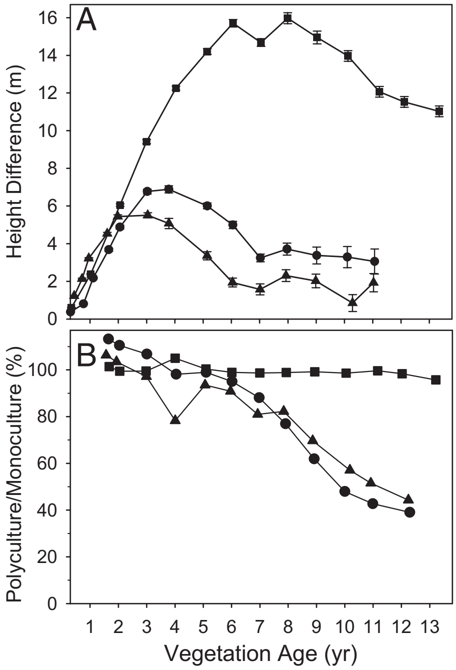

Fig. 4. Bottom-up tree crown compression by understory palm. (*A*) Difference between height of tree in polyculture and coplanted palm. (*B*) Ratio of mean leaf area index of trees in monoculture to their leaf area index in polyculture. Squares, *Hyeronima*; circles, *Cedrela*; triangles, *Cordia*.

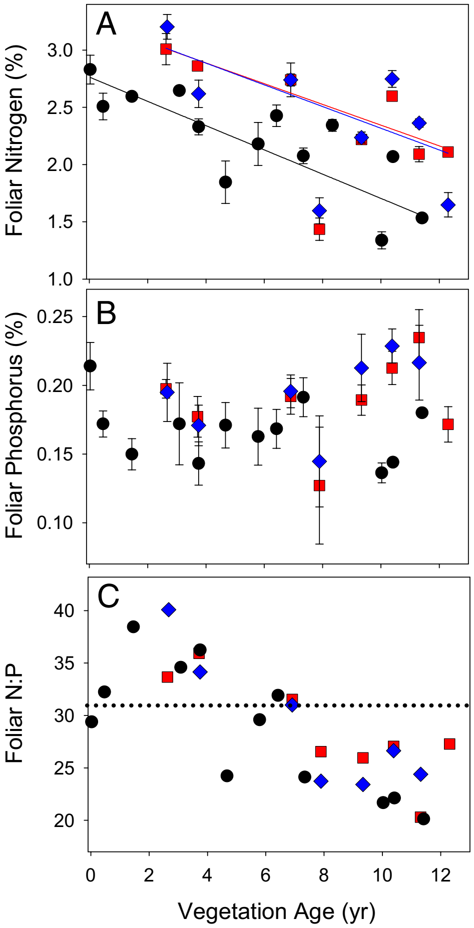

Fig. 5. Foliar nutrients in *Hyeronima*. Shown are nitrogen (*A*) and phosphorus (*B*) (both on mass basis), where filled circles are analyses of bulk leaf samples ($n = 3$) from monocultures and other symbols are disks punched from lamina free of large veins. Values are means ± SE. Squares are samples from monoculture; diamonds are from polyculture. Nitrogen regressions for disks are not different between monoculture and polycultures; bulk samples differ in intercept from the disk samples, as expected ($P = 0.007$), but not slope ($b_{\text{mono}} = -0.091$ disks and -0.106 bulk samples; $b_{\text{poly}} = -0.097$; difference test $P = 0.776$). N values from disks for age 8 yr were not included in calculation of regressions because of uncertainty of their validity. (*C*) Ratio of nitrogen to phosphorus, molar basis, where dotted line indicates level below which N may be limiting (9, 10).

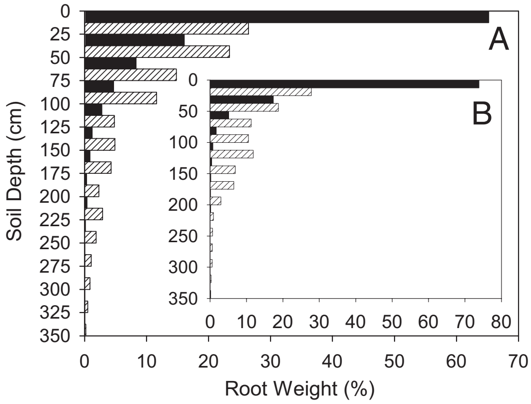

Fig. 6. Vertical distribution of tree (*Hyeronima*; filled bar) and palm (*Euterpe*; hatched bar) roots in 12-yr-old polyculture. Each pit had a surface area of 1.0×2.0 m. Pits were excavated in 2 blocks (*A* and *B*). Total root biomass was 7,357 g (*Hyeronima*) and 870 g (*Euterpe*) in pit A and 6,954 g (*Hyeronima*) and 1,077 g (*Euterpe*) in pit B.

ficial horizons, whereas *Euterpe* roots dominated lower horizons and extended deeper into the soil (Fig. 6). Furthermore, *Hyeronima* (after age $\approx$7 yr) appeared to be N limited (Fig. 5*C*) whereas *Euterpe* appeared to be P limited (Fig. S3). Continued height growth by *Hyeronima*, spatial partitioning of soil, and different N-P stoichiometries could sustain a dual-life-form ecosystem.

Discussion

The important role of species traits became readily apparent in our experiments. The evergreen *Hyeronima* shaded the understory palm throughout the year, whereas the other 2 tree species, both deciduous, underwent several weeks of leaflessness annually, exposing the evergreen palm to full sunlight. Thus, the major trait that influenced our findings was phenology: an evergreen dominant gave a result that differed markedly from that yielded by 2 deciduous tree species. Despite their common trait of deciduousness, *Cedrela* and *Cordia* differ strongly in many other traits. For example, their leaf losses are not synchronous—one (*Cedrela*) is dry-season deciduous, and the other (*Cordia*) loses its leaves in the rainy season. Furthermore, they differ in leaf-level N use efficiency (11), their root systems and crowns develop very differently (12), and they are vulnerable to different herbivores against which they defend themselves using dissimilar mechanisms. The implication is that there is not a unique outcome for each and every combination of species, but that a particular key trait (leaf phenology in this case) can dominate the trajectory of ecosystem development and the eventual outcome of interspecific competition. Identification of those key traits, rather than endless trial and error, is the challenge.

To what extent might this newly revealed mechanism of plant competition—reduction of the light-capturing capacity of a tree crown by invasion from below—be a general phenomenon? Among life forms, palms are exceptionally well-suited to penetrate tree crowns. The single apical bud of a palm is extremely well-protected (13), and although the fibrous, sturdy fronds may fray they do not manifest the shyness that characterizes the bud-tipped edges of abrading dicotyledonous tree crowns (14). Furthermore, their evergreen habit and relatively low requirement for P (at least among the handful of species studied, e.g., refs. 15 and 16 and Fig. S3) make palms well-suited for opportunistic growth in the understory. Nevertheless, although invasion from below may be a behavior for which many palms are exceptionally well-adapted, there is no reason to think that it is a unique phenomenon. For example, an evergreen dicotyledonous tree having sturdy branches and well-protected buds might well exhibit the same competitive mechanism.

In wet forests like La Selva, where deciduous tree species are relatively uncommon (perhaps 1 individual per hectare), the temporal gaps created by periods of overstory leaflessness may not provide major opportunities for competition from below, but in drier environments it may be a major process structuring the canopy. In 3 Panamanian forests receiving 71%, 64%, and 52% of La Selva's mean annual rainfall, the fraction of the canopy that is deciduous is 4%, 10%, or 19%, respectively (17), affording substantial opportunity for growth from below. In an extreme case of deciduousness, arborescent cacti reach the canopy of dry forest in Mexico by sustaining growth during periods when the overtopping canopy is leafless (18).

Interactions among species having access to a common pool of resources can change dramatically with time (19, 20), a phenomenon that has important implications for restoration and management. Even under the unconstrained conditions for plant growth at our study site, it was several years into the 13-yr study before important shifts in interspecific relationships emerged. Complementary resource use by co-occurring species does promote enhanced ecosystem productivity, but resource sharing and partitioning are not inevitably sustained as plants grow. Furthermore, a complementary relationship can become competitive through unanticipated mechanisms: 2 of our tree species were starved for light not by being overtopped but by having their canopy space reduced 2- to 5-fold by invasion from below. As demonstrated by our findings, traits of individual species, or of narrowly defined functional groups, can lead to shifts in ecosystem functioning over decadal time scales. Those attempting to build ecosystems for conservation, restoration, or production must consider not only static measures of potential combining ability, such as phenology, growth rates, stature, architecture, and resource requirements, but also dynamic components including changes in relationships among species as they grow at different rates and use resources in different ways.

Materials and Methods

The research was conducted at La Selva Biological Station of the Organization for Tropical Studies, Inc.: 10° 26′ N; 83° 59′ W; 41 m above sea level; mean annual rainfall and temperature 3.9 m and 25°C, respectively (www.ots.ac.cr). The 8-ha site was on a recent alluvial terrace derived primarily from volcanic material (21). The soil (eutric Hapludand) (22) was deep ($\gg$4 m) and very well-drained and had high base cation saturation and high capacity to stabilize organic matter and retain P and water (30–34% by volume of residual water content).

The study involved 3 life forms, or functional groups: dicotyledonous canopy trees (3 species) and 2 perennial monocotyledons, a palm and a large-stature herb. The tree species differed in phenology, physiology, and architecture. *H. alchorneoides* Allemão (Euphorbiaceae) is an evergreen species whose leaf size declines $>$4-fold from youth (when leaves average $\approx$280 cm^2) to adulthood (23); it forms a dense canopy that captures most incident radiation. *C. odorata* L. (Meliaceae) has long (0.5–1.0 m) compound leaves containing 20–40 leaflets, each $\approx$40 cm^2. *Cedrela* is rarely leafless before age $\approx$5 yr, after which it becomes dry-season deciduous. *C. alliodora* (R. & P.) Cham. (Boraginaceae) has simple leaves ($\approx$30 cm^2) and a tiered, open crown that permits substantial light to penetrate to the understory; it is evergreen in youth but wet-season deciduous after age 5–7 yr. The ranges of both deciduous tree species, *Cedrela* and *Cordia*, extend well into much drier climates, indicating that their leaf loss in the wet climate of La Selva may be a trait carried over from selection in dry forests. The 3 tree species differ in leaf-level nutrient use efficiency (NUE) of N (*Cedrela* $>$ *Hyeronima* $=$ *Cordia*) but not P (11), and in whole-tree NUE of P (*Hyeronima* $>$ *Cedrela* $=$ *Cordia*) but not N (24). Subcanopy palms are an important life form at La Selva, where they constitute 3 of the 4 most common species on rolling terrain (3). The palm we used (*E. oleracea* Mart; Arecaceae) was the only alien species in the experiment; it is native to floodplains of lower Amazonia, but it has a native congener (*Euterpe precatoria*) in the local forest. One large *Euterpe* typically has $\approx$20 ramets, each of which supports numerous pinnate leaves ≈3 m long; the 40–80 leaf segments, each ≈1 m long, droop vertically, and their combined number, size, and orientation result in extremely high leaf area (LAI of *Euterpe* reaches 10). The other monocot [*H. imbricata* (Kuntze) Baker; Heliconiaceae] is a giant perennial herb that produces multiple monocarpic shoots. Its leaf blades are ≈0.3 m wide and 2 m long. Like *Euterpe*, the vertical orientation of its foliage results in extremely high leaf area (LAI of up to 8). Because of its basal meristem and the mass of its leaf blades, the height of *Heliconia* is biomechanically constrained to ≈6 m. All 5 species used in the experiments occur naturally and grow rapidly on fertile, well-drained alluvium.

Before the start of the experiment existing vegetation (an abandoned cacao plantation) was felled, commercial logs were removed, and slash was burned. The experimental design was a split plot of 3 blocks. Data were analyzed (SAS version 9.1, Mixed Procedure) with blocks as a random factor, tree species as the whole-plot factor, and treatment as the subplot factor. Because of the multiple measurements over time at each block–tree species–treatment combination, repeated-measures analyses were performed allowing for serial correlation in the covariance structure. Each block contained 6 plots, each 30 × 40 m, plus exterior rows of the same species to act as a buffer between treatments and surrounding vegetation, which was maintained at the same stature as the experimental vegetation. Each plot was surrounded by a root-barrier cloth, buried vertically in the soil to a depth of 1 m. Two contiguous plots (60 × 40 m) in each block were planted to the same tree species with individuals 2.0 m apart. One plot of each pair was left as a monoculture. The other plot was enriched to become a polyculture, created by additive planting (25) of the 2 monocots, the palm (*Euterpe*) at one-fourth the tree density and, a year later, the large, perennial herb (*Heliconia*) at one-half the tree density. Natural colonists were removed as they appeared, a process that was unnecessary after about age 2 yr in any plantation containing *Hyeronima* or in any polyculture.

Heights and diameters of all plants in the core 30 × 30 m of each plot were measured annually (each trimester in the first 2 yr). Heights were measured to the crown apex (trees) or top of the tallest unfurled leaf bud (monocots). Diameters were measured at the base of trees, just above the root collar swelling, until they attained a height >1.5 m, after which diameter was measured at the standard height of 1.3 m. Counts of all shoots from the same ramet and their sizes were recorded for the monocots. The final growth measurements of *Euterpe* in *Cedrela* and *Cordia* polycultures were made at age 11 yr, when the trajectory of tree growth in those stands became obvious and irreversible (near-zero ANPP).

At least annually 6–18 individuals of each species were harvested for biomass assessments. Harvesting was done from 5-m border zones designated for that purpose along the edges of each plot and outside of data-gathering zones. Plants were separated into leaves, branches, bole, petiole or petiolule, rachis (*Cedrela* and *Euterpe*), and reproductive structures. Parts <1 kg were taken in their entirety as a sample; components of larger mass were pooled, mixed, and subsampled (≈1 kg) for analysis. Specific leaf area (SLA, cm^2/g) was determined by measuring the area (to 0.01 cm^2; LiCor 3100 area meter) of fresh leaf samples (≥30 leaves or leaflets per subsample) and determining their mass after oven-drying for ≥24 h at 70°C. Plant dimensions were converted to biomass by using allometric equations involving 258–379 individuals of each tree species and *Euterpe* (26) and unpublished equations in the case of *Heliconia*. The mass of each plant was estimated, and then these values were summed over the entire plot and divided by plot area to obtain biomass/area. Total leaf area was estimated by converting stand-level leaf biomass (by species, from allometry) to leaf area based on measurements of SLA.

Litterfall was collected biweekly from 4 screen-bottomed, 50 × 173-cm traps in each plot. Traps were elevated 10 cm above the soil to reduce losses to decay between collections. Litter was separated by species and component (leaves, rachises, twigs, reproductive parts). Early in the study the trees were lightly thinned at 2- to 3-yr intervals to ensure full use of resources while avoiding stand stagnation. Trees (primarily *Cedrela*) whose main stems divided below the height of diameter measurement were pruned when young to a height of 1.5 m. ANPP was calculated as the difference between successive stand-level biomass determinations plus litterfall, increment of trees that died in the interval between measurements (whether from natural causes or thinning), and pruned tissues.

Soil was sampled annually at depths of 0–10, 10–25, 25–70, and 70–120 cm (70–155 cm in the 6 plots of 1 of the 3 blocks). At each depth, 1 composite sample ($n = 3$ cores) was taken from each of the 3 plots per treatment. Samples were air-dried and ground to pass a 2-mm sieve. Soil pH was measured in water and KCl by using a soil-to-solution ratio of 1:2.5. Organic carbon (C) was determined by wet digestion (Walkley-Black). Calcium (Ca), magnesium (Mg), and exchangeable acidity [aluminum (Al) + hydrogen (H)] were extracted with unbuffered 1 M KCl and determined by atomic absorption spectrometry (Ca and Mg) or titration (Al+H) (27). Potassium (K) and P were extracted by using an Olsen solution (sodium bicarbonate at pH 8.5) modified by addition of EDTA and superfloc (28) and determined by atomic absorption spectrometry and the ascorbic acid-molybdate method, respectively. Effective cation exchange capacity (effective CEC) was calculated as the sum of extractable cations plus exchangeable acidity. CEC was also determined by saturation with NH_4OAc at pH 7 (29). Total N was measured 4 times over the study period by using elemental analyzers.

Foliar nutrients were determined annually in subsamples of material taken for biomass assessments and in 8 of 13 yr in disks (each 0.25 cm^2; samples of $n \geq 600$) punched from intervein lamina. Samples were oven-dried at 70°C for ≥24 h, finely ground in a Wiley mill, and digested following a Kjeldahl protocol; N and P in the digests were analyzed by automated colorimetry.

We excavated roots from 2 large (1.0 × 2.0 m) soil pits in 12-yr-old *Hyeronima* polycultures. Each pit was positioned midway between 2 rows of trees such that it intersected root systems of vigorous *Hyeronima* and *Euterpe*. The pits were excavated by 0.25-m layers to the deepest extent of roots (3.5 or 3.75 m). Soil from each layer was sieved (0.1-cm mesh screens) to extract roots, which were then sorted into 3 diameter classes (0–0.2, >0.2–0.5, and >0.5 cm), separated by species, oven-dried at 70°C, and weighed.

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