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## EXPERIMENTS ON THE ECOLOGICAL BASIS OF SUSTAINABILITY: EARLY FINDINGS ON NITROGEN, PHOSPHORUS, AND ROOT SYSTEMS

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### SUMMARY

Experiments were established on fertile soil in the humid lowlands of Costa Rica to examine the effects of complementary use of resources between species and stand turnover time on sustainability. The experimental plantations are dominated by perennial plants of the two most successful life forms in this biome, dicotyledonous trees and self-supporting monocots, and are harvested and replanted at intervals of 1, 4, and 16 years. Three main categories of responses are under study, including soil fertility, plant-pest interactions, and productivity. Nitrogen is abundant in the study-site soil; nitrogen mineralization rates are about 0.85 kg ha<sup>-1</sup>day<sup>-1</sup> and nitrification rates are about 1.0 kg ha<sup>-1</sup>day<sup>-1</sup>. Phosphorus is also abundant (30 to 70 mg/g, Olsen extractable), and preliminary data indicate that much of the organically bound phosphorus is under microbial control. Root systems of the three main tree species under study differ greatly, ranging from a dense, compact mass of roots (in *Hieronima alchorneoides*) that thoroughly exploit a modest soil volume, to sparse roots that extend very far from the base of the tree (in *Cordia alliodora*), to massive starch-rich roots that enable the tree to respond to herbivore attack (in *Cedrela odorata*). KEY WORDS / Tropical agroforestry / Sustainability / Nitrogen / Phosphorus / Root systems

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In an effort to better understand the fundamental ecological underpinnings of sustainability, we established simple and mixed-species plantations on nutrient-rich soil at a high rainfall, low elevation site at La Selva Biological Station in Costa Rica. This site was selected because it represents an environmental extreme, one where there are few abiotic constraints to growth, but where there are ample biotic interactions (weeds, pathogens, large and small herbivores) from both contiguous forest and nearby farms. The experiments are designed to elucidate the roles of life-form diversity and stand turnover time in determining the rate and sustainability of production through their effects on nutrient retention and plant-pest interactions.

The rationale for combining plants of different life forms was to maximize resource use and to spread risk: some plants are deeper rooted than others, some photosynthesize better at low light, and still others influence the interactions between cohabiting plants and their pests. If plants of different species do in fact use resources in different ways, then those differences should be most evident among plants having distinct anatomy, physiology, and morphology. Thus, we combined plants from among the two most dominant, successful life forms of the lowland humid tropics: dicotyledonous trees (which tend to have many meristems; relatively small, often horizontally displayed leaves; and spreading crowns) and perennial monocots (characterized by a single meristem; limited capacity for secondary growth; and large, arching or vertically displayed leaves).

The inclusion of community turnover time (as governed by plant life span) as a key variable is a unique feature of the research. Little attention has been paid to this important attribute of agricultural and forestry systems, even though it is intimately related to ecological and economic sustainability. For example, rotation time is related to trade-off between yield and soil protection: long-lived plants provide excellent soil protection but relatively low yields, whereas high-yielding, short-lived crops are ecologically dangerous because the soil is unprotected after each harvest. On the other hand, short-lived plants escape pest buildups by spending much of their lives as seeds, whereas long-lived plants are semi-permanent, stationary targets that must invest in chemical and physical defenses.

## Study Site

La Selva Biological Station receives about 4 in of rain per annum, and temperatures are relatively uniform and high (average of about 24° C). Prior to establishment of our experiments, the study-site soil was occupied by a 30-year-old, cocoa plantation that had been abandoned for six years. This vegetation was felled, wood was harvested manually from the over story trees, and the slash was burned immediately prior to establishment of our plantations in mid-1991.

The soils at the site, classified independently by two soil scientists (see Acknowledgments), are mixed, isohyperthermic, possibly andic, fluventic Dystropepts. The site is located on a flat, alluvial floodplain at the confluence of two rivers, and the soil is well-drained to somewhat excessively drained. Although this terrace has not been flooded in recent times (including record-breaking high water in 1970), soil profiles to a depth of 2 in reveal the presence of at least three sequences, including one horizon containing considerable amounts of charcoal at a depth of 140/155 to 155/165 cm. At an average depth of about 90-125 cm there is a coarse-textured C horizon (80-87% sand) into which we insert probes for sampling leachate. The surface horizons constituting the first sequence contain relatively high concentrations of essential elements (Table I), and this is generally true (except for potassium, which decreases in concentration) down through the nine horizons of the uppermost 2 in of soil.

## Experiments

There are three main experiments at the site, each distinguished by its dominant tree species: *Cedrela odorata* (Meliaceae, Spanish cedar), *Cordia alliodora* (Boraginaceae, laurel), or *Hyeronima alchorneoides* (Euphorbiaceae, pilón) (Fig. 1). *Cedrela*, a close relative of mahogany, is a timber tree of considerable value. It is fast growing, but seldom escapes attack by a shoot-boring moth, *Hypsipyla grandella*. *Cordia* is a locally prized timber tree, known for its ability to colonize pastures and abandoned agricultural fields on good

soils. *Hyeronima*, the least studied of the three tree species, is a massive, evergreen species that produces dense, durable wood.

Each experiment contains four treatments, three of which are tree monocultures subject to rotations of 1, 4, or 16 years (Figure 2). The fourth treatment in each experiment is a mixed planting (also subject to a 16-year rotation) of the trees plus three monocots. Two of the monocots are congeneric palms, *Euterpe macrospadix* (palmito de mantequilla, exploited in Costa Rica for its delectable bud) and *E. oleracea* (asaí, from the Brazilian Amazon, where its fruit is widely used in beverages and ice cream). The third monocot is a large perennial herb, *Heliconia imbricata*, which is native to the site and was interplanted when the plantations were a year old to speed the dicot-monocot interaction.

The four treatments within each experiment are replicated in three blocks. Each block occupies 3600 square meters and is zoned for three intensities of research use, ranging from areas where destructive harvesting is permitted to a central zone restricted to non-destructive, observational measurements.

Each tree is planted 2.0 meters from its ix nearest neighbors, and the palms and herb are planted adaptively (1.0 meters from the trees) in every column. To permit us to evaluate the impacts of plant spacing on the thoroughness of resources use, we also established density experiments using a Nelder design, which consists of plants grown along spoke-like radii emanating from a central hub. Plant spacing increases along the radii, enabling us to evaluate plant growth at many densities in a small space.

The 8-hectare facility also includes five other plots. Two of them are more diverse plantations, each containing equal numbers of the three tree genera and the *Euterpe* spp. used in the main experiments. These species rich plantings will provide an opportunity to evaluate more complex combinations of resource sharing and competition, as well as compensatory responses that occur when the nutrients and light freed by the failure of one species are utilized by others. Two other plots follow the same model as the main experiment (dicotyledonous species in monoculture and co-planted with a monocotyledonous specks) but employ plants of naturally shower life spans. One of the plots contains papaya planted alone and together with banana; the other contains cassava planted alone and together with the banana. The fifth plot is allowed to regenerate naturally and serves as a control with which the plantations can be compared.

## Objectives

in this paper we report early findings that deal with soil nutrients and the comparative abilities of the three main tree species to exploit the soil. On most forest soils nitrogen and phosphorus differ greatly in their availabilities. and our site is no exception. As our preliminary data indicate, differences in root architecture may make some tree species more adept for phosphorus exploitation whereas others may be better adapted to forage for nitrogen.

TABLE I CHARACTERISTICS OF WE UPPERMOST SEQUENCE OF THE STUDY SITE SOIL, LA SELVA BIOLOGICAL STATION, COSTA RICA. VALUES ARE MEANS FROM TWO PITS, 400 M APART. CALCIUM AND MAGNESIUM WERE EXTRACTED WITH 1 M POTASSIUM CHLORIDE, AND POTASSIUM AND PHOSPHORUS WERE EXTRACTED USING THE MODIFIED OLSEN METHOD (HUNTER 1974); CATION EXCHANGE CAPACITY WAS DETERMINED WITH A NEUTRAL AMMONIUM ACETATE EXTRACTION, AND pH WAS DETERMINED IN WATER.

<i>Horizon</i>	<i>Depth (cm)</i>	<i>Texture</i>	<i>Organic matter</i>	<i>pH</i>	<i>Ca</i>	<i>Mg K</i>	<i>CEC</i>	<i>Base saturation</i>	<i>P (m g/g)</i>
					<i>(Cmol [+)/kg)</i>				
Ap	0-15	sandy loam	5.2	6.6	9.0	2.8	1.5	55.1	34
					42.6				
Bw	15-25	sandy loam	1.2	6.4	5.8	1.8	1.0	38.5	21
		silty loam			36.4				
C	25-48	sandy loam	0.3	6.2	5.2	1.6	0.9	35.2	21
		silty- loam			31.5				

**TABLE II CHANGES IN SOIL NITRATE AND AMMONIUM CONCENTRATIONS, AND THE RESULTANT NET NITROGEN MINERALIZATION AND NITRIFICATION, OVER DIFFERENT PERIODS OF FIELD INCUBATION AT A DEPTH OF 0-25 CM. VALUES ARE MEAN (STANDARD ERROR) NITROGEN CONCENTRATIONS IN p/G SOIL**

	<i>Incubation period (days)</i>			
	0	14	21	28
ammonium concentration	5.12 (0.38)	1.83 (0.37)	3.54 (0.39)	0.47 (0.27)
nitrate concentration	6.01 (0.35)	11.79 (0.77)	14.51 (0.82)	13.56 (0.71)
nitrogen mineralization		2.49	6.92	2.90

nitrification		5.78	8.50	7.55
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**TABLE III CHANGES IN SOIL NITRATE AND AMMONIUM CONCENTRATIONS, AND THE RESULTANT NET NITROGEN MINERALIZATION AND NITRIFICATION, AT DIFFERENT DEPTHS IN THE SOIL DURING A 21 DAY FIELD INCUBATION. VALUES ARE MEAN (STANDARD ERROR) NITROGEN CONCENTRATIONS IN *m G/G SOIL***

		Depth (cm)		
	0-10	10-25	25-45	
Ammonium				
	initial	5.65 (0.39)	4.69 (0.42)	4.74 (0.38)
	final	5.29 (0.53)	1.93 (0.29)	1.03 (0.20)
	net mineralization	15.81	2.15	-2.22
Nitrate				
	initial	8.05 (0.39)	4.49 (0.37)	3.63 (0.25)
	final	24.22 (0.91)	9.40 (0.71)	5.12 (0.43)
	nitrification	16.17	4.91	49

**TABLE IV PHOSPHORUS FRACTIONS EXTRACTED IN SODIUM BICARBONATE. SOIL WAS SAMPLED AT 0-15 CM VALUES ARE MEAN (STANDARD ERROR) PHOSPHORUS**

## CONCENTRATIONS IN m G/G SOIL

Inorganic	Organic	Microbial
46.0	19.4	18.1
(4.4)	(4.4)	(5.0)

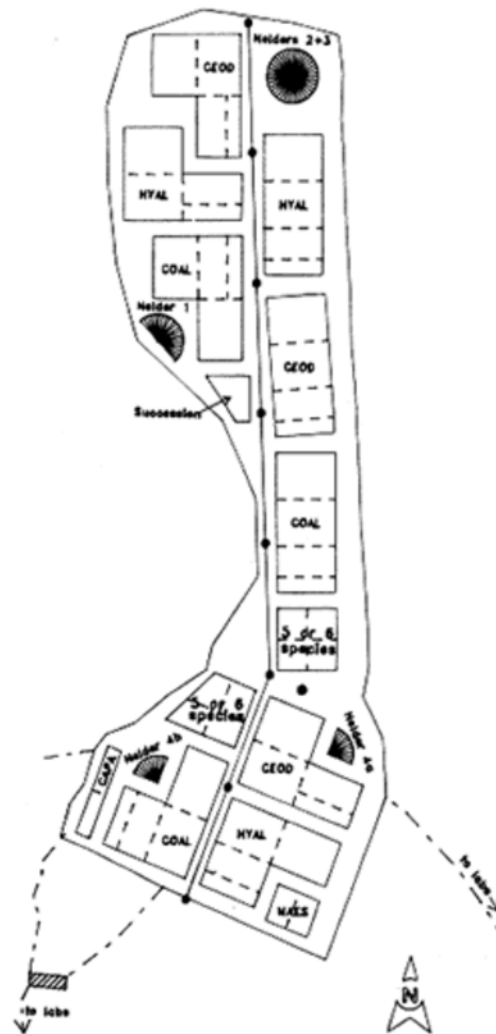
One of the keys to sustainability is the maintenance of soil fertility. Furthermore, determination of the supply of nutrients in the soil is an essential prerequisite to assessment of resource use efficiency by the plantations. The supply of soil nutrients will eventually be interpreted in terms of nutrient uptake by plants and nutrient inputs and outputs from the system, including leaching, which we assume will be the largest flux. Here we focus on two key elements: nitrogen, which is likely to be relatively plentiful in this soil; and phosphorus, which, although relatively plentiful at our site compared with most tropical soils, is likely to be immobilized rapidly on the volcanic alluvium of the study site. Phosphorus is considered to be the most limiting nutrient over much of the lowland humid tropics, and its availability is determined by the interaction of a number of differently bound pools of phosphorus in the soil. Measuring these pools and their changes over time provides a means of defining the effects of different treatments on phosphorus availability.

Dee species growing under the same conditions often have different growth rates, in part because species allocate different proportions of their carbon to leaves, stems, and roots. The distribution to roots determines the volume and intensity of soil exploration. Knowledge of the rate of development and the distribution patterns of root systems may help us interpret the different efficiencies with which species exploit soil resources.

## Methods

Nitrogen supply in the field was assessed by measuring the mineralization of organic nitrogen into ammonium and then nitrification into nitrate. in isolated soil cores (Anderson and Ingram 1989) Before the rate of supply of plant-available nitrogen could be assessed it was necessary to determine the appropriate incubation time and sampling depth for our soil. Net nitrogen mineralization and nitrification were measured over three field incubation periods (14, 21, and 28 days) and over three depths (0-10 cm, 10-25 cm, and 25-45 cm). Nitrogen mineralization was measured by taking pairs of soil cores: one core of each pair was immediately analyzed for nitrate and ammonium concentrations; the other core was isolated inside a 10 cm diameter plastic (PVC) pipe, covered, and returned to the hole from which it came for the period of field incubation before being analyzed for nitrate and ammonium. Nine pairs of cores were taken for each incubation period and each depth.

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CEOD = *Cedrela odorata* (Spanish cedar)

COAL = *Cordia alliodora* (laurel)

HYAL = *Hyeronima alchorneoides* (plón)

EUMA = *Euterpe macrospadix* & *E. oleracea* (palms)

HEIM = *Heliconia imbricata* (giant herb)

CAPA = *Carica papaya* (papaya)

MAES = *Manihot esculenta* (cassava)

MUCV = *Musa cvs.* (banana)

● Rain gauge

▨ Instrument shed

Figure 1. Map of the study site showing the layout of the different experiments.

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Net nitrogen mineralization was then calculated as the difference between the sum of the nitrate and ammonium concentrations in the two cores. Nitrification was also calculated from the difference in nitrate concentrations in the paired cores.

We also carried out an initial assay of the relative amounts of extractable inorganic, organic, and microbially bound phosphorus at the site. Thirty six samples were taken from across the site at a depth of 0-15 cm.

Inorganic and organic phosphorus were extracted with 0.5 M sodium bicarbonate. Microbial phosphorus was estimated by the release of extractable inorganic and organic phosphorus after fumigation with chloroform.

Eight months after planting, sixteen randomly selected trees of each species were harvested to measure leaf, stem, and root biomass and root distribution. The root distribution of each tree was measured by excavating all roots > 2 mm in diameter. During excavation the root system was divided into rows extracted at different distances from the tree and depths in the soil. The horizontal distances were 0-33, 33-67, 67-116, and > 116 cm, and the depths were 0-10, 10-30, 30-50 cm, and continued downward in 20 cm increments to the deepest extent of the root system.

## Results and Discussion

### Nitrogen and phosphorus availability

Net nitrogen mineralization and nitrification measured over three incubation periods appeared to continue up to 21 days (Table II). Thereafter immobilization of ammonium became dominant and nitrate levels stayed the same, although these changes were not statistically significant.

Net nitrogen mineralization rates per gram of soil, measured over three depths, were considerably higher in the top 10 cm than deeper in the soil (Table III). Both net nitrogen mineralization and nitrification rates declined significantly ( $p < 0.05$ ) with depth. Nevertheless, on a per area basis nitrogen mineralization was 1.47 g/ml in the 0-10 cm horizon and 0.35 g/ml in the 10-25 cm horizon. The smaller difference in nitrogen mineralization between 0-10 and 10-25 cm horizons when calculated on a per area basis was in part due to the higher bulk density of the soil in the lower horizon compared to the upper horizon.

The net decline in nitrate plus ammonium at 25-45 cm (Table II) suggests either that ammonium was being immobilized or nitrate was being lost by denitrification. To our knowledge this is the first time that a change down the soil profile from net production to net loss of mineral nitrogen not due to leaching has been identified. Vitousek and Denslow (1986), working on less fertile residual soils at La Selva, found that potential nitrogen mineralization (in laboratory incubations) declined steeply with depth, but was still detectable down to 80 cm. In our field-based study, high concentrations of nitrate and ammonium were present in the subsoil, presumably having previously been leached down from the topsoil, and were available for potential immobilization or denitrification.



Nitrogen mineralization is now being measured in the treatments every two months using an incubation period of 21 days and cores taken to a depth of 20 cm. These assays will be used to determine the rate at which nitrogen is potentially made available for uptake by plants.

The high levels of inorganic phosphorus at our site (Table IV) were probably due to the ash added to the soil surface during site preparation. The amount of microbial phosphorus was similar to the amount of organic phosphorus, indicating that the microbial biomass probably has a large influence on the dynamics of organically held phosphorus.

### Tree biomass allocation and root distribution

At 8 months *Cordia* had accumulated the greatest biomass, followed by *Hyeronima* and then *Cedrela* (Fig. 3). Biomass allocation by *Cedrela* was very different from the other two specks; A invested relatively more in roots and less in leaves.

Most roots, of course, were concentrated close to the base of each tree and near the soil surface (Fig. 4). Nevertheless, it is the horizontal (Fig. 5) and vertical (Fig. 6) extent of roots beyond those zones of highest concentration that are most revealing about the different ways the three species exploit the soil. *Cordia* had the most extensive root system, while that of *Hyeronima* was most restricted.

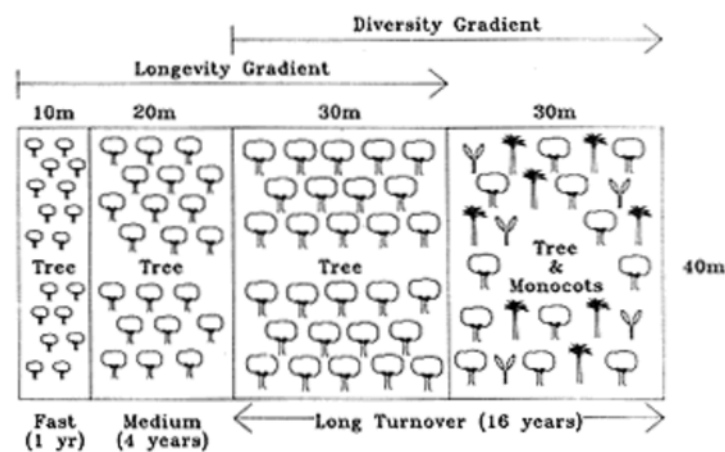


Figure 2. Distribution of the treatments within a block of one of the three main experiments.

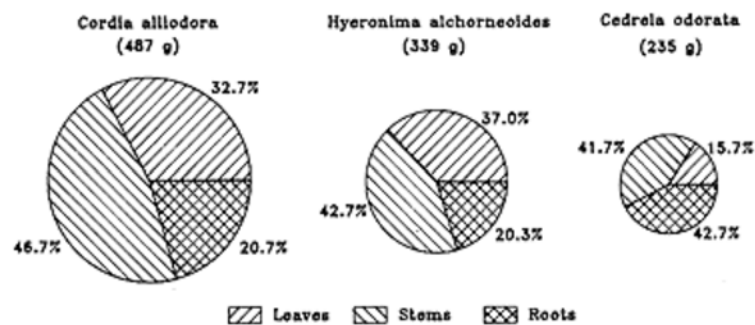


Figure 3. Average biomass of the three dominant tree species 8 months after planting and the allocation of biomass to leaves, stems, and roots.

The occupancy of the soil volume by the root system was not correlated with biomass allocation to roots. It was *Cordia*, with a low root investment, whose roots extended furthest. The high growth rates of *Cordia* were probably due to its ability to invest heavily in leaves, while maintaining an extensive root system through efficient use of the modest amount of biomass allocated to roots.

*Cedrela*, on the other hand, allocated the greatest fraction of its biomass to roots and extended its roots further than did *Hyeronima*. The low growth rate of *Cedrela* may have been caused by a high investment in root biomass at the expense of leaves. *Cedrela* was repeatedly attacked by a stem-boring lepidopteran larva (*Hypsipyla grandella*), which in itself undoubtedly inhibited growth and leaf production. The high allocation to large roots allowed *Cedrela* to store large quantities of starch with which to fuel resprouting after *Hypsipyla* attack.

The extent of the root system determines the volume of soil exploited for nutrients and is particularly important for mobile nutrients, such as nitrate, for which rooting intensity is less important. It is expected that the extensive root system of *Cordia* would enable it to extract the greatest supply of nitrogen from the soil, whereas the compact root system of *Hyeronima* may allow greater quantities of nitrate to escape and be lost through leaching.

## Conclusions

The excess of rainfall over evapotranspiration is a formidable barrier to the maintenance of soil fertility in the lowland humid tropics. On highly weathered soils it is the biota itself that maintains the fertility of the soil through the uptake, storage, translocation, and return to the soil of the nutrient capital. When we simplify the biota to meet human needs (by creating pastures or agricultural fields, for example) we sacrifice some of the fertility-maintaining functions of nature.

A major challenge for the design of sustainable agroecosystems is to determine if it is possible to both simplify the community and sustain soil fertility. We are optimistic that this can be achieved, but we lack the data to prove that it is possible. More importantly,

the biophysical mechanisms that sustain or diminish productivity are so poorly known that generalization is impossible. With our plantations, containing mixtures of plant life forms and subject to different rotations, we hope to provide some of these data.

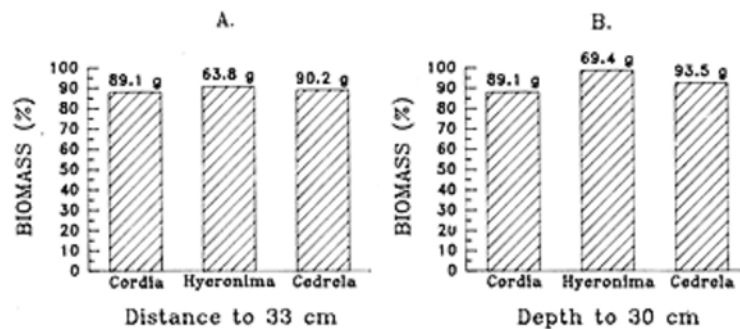


Figure 4. Actual and percentage root biomass near the tree bases and near the soil surface. (A) Roots within 33 cm laterally from the tree. (B) Roots in the uppermost 30 cm of the soil.

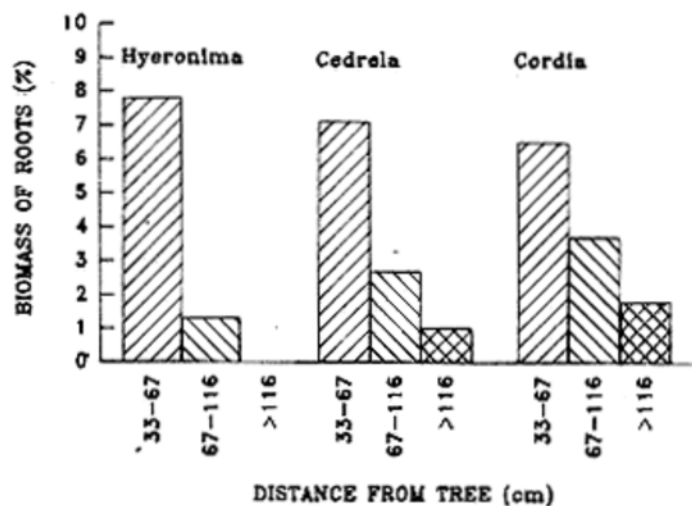


Figure 5. Lateral extent of root. Data include only those roots further than 33 cm from tree bases.

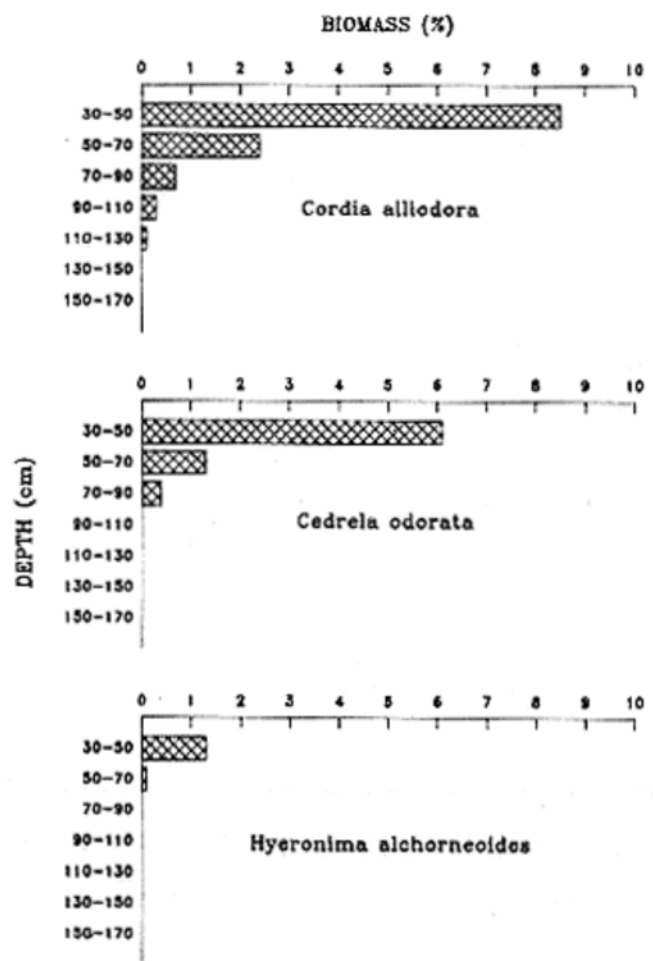


Figure 6. Vertical extent of roots. Data include only those roots deeper than 30 cm.

It is our plan that the investment we have made in plantation establishment, infrastructure, and personnel will provide a long term facility in which to investigate the biophysical basis of sustainability. There is far more to be done than can be accomplished by our small team of researchers, and we hope that many individuals from the international community will join us in these efforts.

## ACKNOWLEDGMENTS

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