

LEAF AREA, LIGHT TRANSMISSION, ROOTS AND LEAF DAMAGE IN NINE TROPICAL PLANT COMMUNITIES

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ABSTRACT

Ewel, J., Gliessman, S., Amador, M., Benedict, F., Berish, C., Bermúdez, R., Brown, B., Martínez, A., Miranda, R. and Price, N., 1982. Leaf area, light transmission, roots and leaf damage in nine tropical plant communities. *Agro-Ecosystems*, 7: 305–326.

The vertical distribution of leaf area by species; transmission of photosynthetically active radiation; root biomass and fine-root surface area; and leaf damage were measured in nine tropical ecosystems: six in Costa Rica and three in Mexico. Ecosystems studied included monocultures of maize (young and mature) and sweet potato; year-old natural succession and vegetation designed to mimic succession; a 2.5-year-old mixture of three arborescent perennials (cacao, plantain, *Cordia alliodora*); 2.7-year-old plantation of *Gmelina arborea*; coffee shaded by *Erythrina poeppigiana*; and an old, diverse wooded garden.

Leaf area index ranged from 1.0 in young maize to 5.1 in natural succession and the gmelina plantation. The vertical distribution of leaves was most uniform in diverse ecosystems, and most clumped in species-poor ecosystems. Light transmission was inversely proportional to leaf area, and two dense-canopied monocultures (sweet potato and gmelina) were nearly as effective at light capture as were some of the more diverse ecosystems. Optical density of the canopy ranged from < 0.5 (35% transmission) in the young maize to > 2.0 ($< 1\%$ transmission) in the natural succession.

Large roots (> 5 mm diameter) accounted for most root biomass in the older ecosystems at a soil depth of 5–25 cm, and fine roots (< 5 mm diameter) were most important in the surface 5 cm in all ecosystems. The range of values for root biomass (39 to 422 g m^{-2} to a depth of 25 cm) were similar to the range of values for leaf biomass (33 to 345 g m^{-2}), and, with the exception of two monocultures, ecosystems with high leaf biomass also had high root biomass. The surface area of the fine roots was lower than leaf area, and ranged from 0.5 to > 2.0 $m^2 m^{-2}$ of ground. Total root surface area increased with

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age and diversity, and the monocultures — even those effective at light capture — had low root surface area.

Herbivore damage on leaves of 35 species ranged from <2 to > 16% of leaf area. Heavily damaged species contributed less to total ecosystem leaf area than did species damaged less than average. Ecosystem-level damage was not well correlated with age or diversity. Leaf damage in all ecosystems ranged from about 2 to 10% of leaf area, or < 2 to > 25 g m⁻² of ecosystem.

Young monocultures do not necessarily capture less light, provide less soil cover, and experience more herbivory than older, more diverse ecosystems. However, root surface area (and therefore possible nutrient-capture ability) is high only in ecosystems that are diverse or old, and this is an important design consideration for agroecosystems appropriate for the humid tropical lowlands.

INTRODUCTION

The efficiency of resource utilization and resistance to pest attack are two key issues in agriculture, especially as fertilizers and pesticides increase in cost. This is particularly true in the humid tropics, where year-round growth permits rapid pest and disease build-ups, high rainfall promotes nutrient leaching, and weeds invade aggressively. Structurally diverse multiple-crop tropical agroecosystems, such as those described by Wilken (1970), Dickinson (1972), and Gliessman et al. (1981), might reduce these problems more than the monocultures now often used. These diverse, structurally complex plant communities might have several desirable features:

(1) Well developed surficial root mats and roots that extend well below the soil surface might impede nutrient loss.

(2) A diverse habitat that houses predators and parasites, and reduces plant apparency, may ameliorate pest attack.

(3) Unbroken canopies lessen the impact of high-intensity rains on the soil (Greenland 1977).

(4) Dense foliage may reduce weed invasion.

(5) Crop mixtures often yield more than the same area divided among monocultures of the component crops, and sometimes even “overyield”, i.e., yield more than an equivalent area of a monoculture of the higher-yielding component (Trenbath 1974).

(6) Diversity may reduce the risk of total crop failure, should one or more components be devastated by pests or weather (Wilken 1975, Innis 1980).

Are such benefits inevitable in complex, diverse agroecosystems? The results of many field and pot experiments comparing simple and complex systems, as well as explanations of the nature of the interactions involved, have been reviewed by Trenbath (1974), Harper (1977, Chaps. 8–11), Kass (1978), and Nair (1979). Increased yield and lowered risk of complete crop failure are common, but not universal, benefits of species mixtures. Yield increases presumably result from increased efficiency of resource utilization (light, water, nutrients, CO₂, and soil O₂), but field data that

directly support this common assumption are few. Some yield increases may also reflect complementary effects among species, such as the maize-bean-*Rhizobium* interactions described by Boucher (1979). Although the idea of reduced pest attack in diverse systems is appealing, both increased and decreased losses to pests can, in fact, occur in polycultures (Murdoch 1975, Litsinger and Moody 1976, Altieri et al. 1978).

To find out if structurally complex ecosystems make better use of resources and experience less herbivory than do simple systems, nine varied agricultural and successional ecosystems were studied, ranging from simple to diverse, herbaceous to woody, short to tall, and young to old. We concentrated on a few study areas to reduce variation due solely to geographic variables; we used identical techniques at all sites; and we made all measurements in a short interval (2 weeks). Measurements included: leaf area index (LAI) by height and by species and optical density of the canopy, both indicators of a system's light-capture ability; root biomass by depth and diameter class, an indicator of ability to exploit root-zone resources; and leaf damage (caused primarily by herbivorous insects) by species, an indicator of resistance to pest attack.

The study areas

Six of the nine ecosystems were on the grounds of the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Turrialba, Costa Rica. CATIE is at latitude 9° 51' N and occupies lands ranging from 600 to 660 m. Mean annual rainfall is about 2700 mm and the dry season extends from January through March. Three of the CATIE study sites were on the Colorado soil series (family: very fine, mixed, isohyperthermic) and the other three were on the Instituto series (family: fine, mixed, isohyperthermic); both soils are Inceptisols (Aguirre 1971).

The other three study sites were in the state of Tabasco, Mexico. Two sites were on the grounds of the Colegio Superior de Agricultura Tropical (CSAT), located 23 km west of the town of Cárdenas (18° 1' N). The other site was at the town of Masateupa (18° 11' N). Annual rainfall averages about 2200 mm at CSAT and about 1600 mm at Masateupa. Both areas experience a dry season from mid-March to mid-May, and bimodal rainfall with maxima in June and September–October. Both areas are on a recent alluvial plain (elevation approximately 10 m). Most soils in the area are Entisols high in clays, principally of the Limón and Nuevo series (Mejía 1978), and are subject to frequent water logging during the wet season.

Each of the nine ecosystems studied is briefly described below. Systems 1–3 were at CATIE on the Instituto soil; 4–6 were at CATIE on the Colorado soil; 7 and 8 were at CSAT on the Limón soil; and 9 was at Masateupa on the Nuevo soil.

(1) Sweet potato

This was a 48-day-old, 2000 m², unfertilized monoculture of *Ipomoea batatas* (variety C-15). The plot was nearly weed-free, having been weeded 22 days after planting. The canopy was low, dense, and uniform. Insecticide had been applied three times.

(2) Cacao-plantain-Cordia

This was a 2.5-year-old, 450 m² experimental planting of *Theobroma cacao* (varieties EET400 × SCA 12, UF29 × IMC27, and Catongo × Pound 12), at 3 × 3 m (1111 individuals per ha), *Musa × paradisiaca* (variety pelipita) at 3 × 3 m, and *Cordia alliodora* (a fast-growing native timber tree) at 6 × 6 m (278 individuals per ha). The plot was weeded during its first year, both manually and using herbicides. No insecticide had been applied, and routine maintenance consisted of occasional light pruning of the *Cordia* and thinning of the plantain shoots.

(3) Shaded coffee

This was a 25-year-old, 2 ha planting of *Coffea arabica* at 1 × 2.3 m (4348 bushes per ha), with an overstory of *Erythrina poeppigiana* at a spacing of about 8.3 × 4.2 m (287 trees per ha). Fungicides are applied annually in April, June, and August, and herbicide is applied sparingly every 2 months. The coffee is pruned annually in March, and the *Erythrina* (a nitrogen-fixing legume) is pruned in January–February and July–August each year, but had not yet received its January–February pruning for 1980 at the time of our measurements.

(4) Gmelina

This was a 2.7-year-old, 0.8 ha planting of *Gmelina arborea*, a fast-growing pioneer tree, native of India and South-East Asia, that is planted in the humid tropics for timber and paper pulp. This planting was in two blocks, one spaced at 2 × 1 m (5000 trees per ha) and the other at 2 × 3 m (1667 trees per ha). During its first year part of the gmelina was interplanted with maize and another part with beans (*Phaseolus vulgaris*). During that first year, only the maize-gmelina intercrop was weeded and received inputs of insecticide and herbicide. The gmelina were pruned at 1.5 and 2.5 years, and at the time of our measurements averaged about 10 m tall with trunks 14 cm in diameter.

(5) Succession

This vegetation was a diverse mixture of species that recolonized three 256 m² plots in a second-growth forest that had been felled 14 months and burned 11 months earlier (Ewel et al. 1981). The vegetation was about 5 m tall, and consisted of a dense mixture of vines, shrubs, large herbs and small trees. The three plots (all located within 1 ha) contained > 100 plant species.

(6) *Mimic of succession*

This vegetation had identical site location, history, and plot size as the succession, but consisted of species planted by the investigators, rather than those introduced through natural processes of dispersal and coppicing. It contained about 40 species, including both economic and non-economic species. This mimic is being developed as part of a larger project designed to test the feasibility of building agroecosystems that imitate the structure and function of natural successional ecosystems. At the time of this study the mimic vegetation was about the same height but less dense than the natural successional vegetation it was designed to imitate.

(7) *Young maize*

This was a 2-month-old, 0.12 ha test planting (local variety criollo blanco) on a site that had been cultivated continuously, using machinery, since forest clearing 12–15 years earlier. Beans and maize had been planted in rotation on the site each June and December, respectively, for the three previous years. Planting was in furrows 0.92 m apart, with 4–5 seeds deposited every meter, giving an initial density of about 44,000–50,000 plants per ha. The site was fertilized with 80-40-40. Weeds were controlled with a preemergence herbicide followed by mechanical cultivation three weeks after planting.

(8) *Old maize*

This was a 3.5-month-old, 0.5 ha planting (of the same variety) established by students using traditional farming methods of the region. The soil was prepared 2 years earlier with machinery, but had since been left fallow; the vegetation was cleared with machetes prior to planting. Planting was done by placing 4–5 seeds in 10–12-cm-deep uncovered holes, about 1 m apart. This resulted in an initial density of 40,000–50,000 plants per ha. A light application of urea was made at planting and again at 30 days, but no insecticides or herbicides were used. The plot was weeded by machete 30 days after planting. At the time of sampling the maize was 3–4 m tall, the ears were well formed yet still green, and the weed cover was dense.

(9) *Wooded garden (huerto familiar)*

This plot, of ca. 0.5 ha, was more than 40 years old, and contained a diverse mixture of useful plants, ranging from timber trees (e.g., *Cedrela mexicana*, *Colubrina* sp.) and fruit trees (avocado, coconut, mango) to light-demanding herbs (e.g., tomato, chili). It was typical of such gardens in Tabasco, as described by Gliessman et al. (1981). The structure and floristic composition of these multi-layered gardens are carefully manipulated by their owners, who harvest both cash crops and products for home consumption from them. The most conspicuous species in the plot sampled were coconut, cacao and coffee, but a cursory inventory revealed the presence of 38 species.

METHODS

Leaf area

The leaf area index (LAI), defined as the area of leaf (one side only) per unit area of ground, was measured in each agroecosystem using a plumb-bob method. Using this method, the unit ground area is reduced to a point, and each measurement consists of the number of leaves touching a thin cord, marked at 25 cm intervals and extended vertically through the vegetation. Each intersection of cord and leaf was recorded by species and height above the ground. This method underestimates true LAI by an amount dependent on leaf angle (deviation from horizontal).

In most of the systems, sampling locations were chosen using randomly determined paired coordinates. In the natural succession and the mimic it was necessary to work from existing trails, and points were chosen randomly along the trails. At each of nine sampling locations, six (two at the ninth location) LAI measurements were made, giving 50 determinations per ecosystem. The six points at which the cord was extended through the vegetation were evenly spaced about the sampling location, at a distance of 1–2 m.

In the wooded garden, the height of the vegetation created special problems. The plot was divided into nine subplots of equal size. Within each subplot, the measurements were made from a tall tree, with the cord extended vertically 3 m from the tree trunk. In a few cases it was necessary to estimate the number of leaves above the top of the cord.

Light transmission

Photosynthetically active radiation ($PAR = 400\text{--}700\text{ nm}$) was measured using a LiCor meter (LI-185A) coupled to two sensors (LiCor 190S) via a switching box. One sensor was placed in a fixed position in a clearing; the other was placed on the soil surface in the ecosystem, leveled, read, and immediately moved to a new position.

One hundred near-simultaneous pairs of readings (clearing/under vegetation) were made in each ecosystem. Sampling points were selected by twice extending a 25 m tape along the ecosystem floor (at an oblique angle to plant rows, where present) and placing the sensor along it at 50 cm intervals.

Each pair of readings was converted to a percent light transmission and optical density (OD), where: $OD = \log_{10} (PAR_C/PAR_V)$, PAR_C = light in clearing, and PAR_V = light beneath vegetation. Optical density was calculated as it is linearly related to absorbance plus reflectance by the vegetation. All statistical comparisons were made using optical density, rather than percent transmission.

Roots

Twelve root samples were taken from each of two depths (0–5 cm in-

cluding litter, and 5–25 cm) in each ecosystem. Sample points were determined using randomly selected coordinates. Shallow roots were sampled by driving a sharp edged, 5.5 cm diameter bulk density sampler into the soil. In all six Costa Rica ecosystems, deeper roots (5–25 cm) were sampled with a long, 4.2 cm diameter corer, designed by D. Santantonio of Oregon State University. In Mexico, deeper roots were sampled in the young maize and wooded garden using a sharpened, 4.6 cm diameter pipe, and in the old maize by excavating 5 × 5 cm cores.

Each soil core was soaked briefly in water containing a dispersing agent (household detergent), then placed in a tank containing an overflow spout. Water was circulated into the bottom of the tank, and the flotsam, including roots, was collected on a 0.5 mm sieve placed beneath the overflow spout.

Roots were separated from all other flotsam, then separated into six diameter classes (in mm): < 1, 1 to < 2, 2 to < 5, 5 to < 10, 10 to < 20. Live and dead roots were not distinguished, but no obviously dead large roots were encountered. Roots in the smallest size class were rewashed to ensure removal of all external mineral matter, including soil particles bound to the roots by mycorrhizae. The clean root samples were dried to constant weight at 70° C and weighed to 0.0005 g.

Root mass for the three smallest diameter classes was converted to surface area using linear regressions developed by C. Berish (unpublished) based on > 120 root samples taken from the successional vegetation and mimic (plus other sites) in Costa Rica. The length: biomass regression equations (L = length (mm), M = dry mass (g), and subscripts indicate diameter classes (mm), were:

$$L_{<1} = 10103 M_{<1}$$

$$L_{1-2} = 1392 M_{1-2}$$

$$L_{2-5} = 341 M_{2-5}$$

Lengths were then converted to surface area by assuming that all roots were cylinders having a diameter equal to the midpoint of the diameter class.

Leaf damage

In each ecosystem, 1 to 11 dominant species were chosen for measurement of leaf damage. Dominance was determined by the LAI measurements, and the species selected accounted for 60 to 99% (\bar{x} = 79) of the total LAI of each ecosystem. Damage was measured on a total of 35 species.

For each species for which damage was assessed, individual plants and/or branches were chosen arbitrarily (if individuals were few) or randomly (most species). Once a branch or plant was selected, leaves were chosen randomly from among all potentially acceptable leaves using the method described by Ward (1974). Any fully expanded leaf that had not been damaged by human activity was potentially acceptable, regardless of the amount of damage it had experienced. No more than two leaves were collected per plant, except

for species having few individuals, where an effort was made to include more than five individuals of varying ages, sizes, and locations. Thirty leaves per species were collected in this manner. With a few exceptions, damage was measured for complete leaf blades, including all leaflets in the case of compound leaves. For eleven large-leaved species, fractions of leaves were either randomly or systematically chosen for damage measurements.

A clear plastic sheet was laid over each leaf, and damage traced and filled in with a permanent black marking pen. Two kinds of damage were distinguished, and traced onto separate plastic sheets. All missing tissue, plus damage that left only a transparent layer of leaf tissue, was recorded as holes. All other damage, including that caused by leaf miners, piercing-sucking insects, pit feeders, viruses, etc., plus the necrotic tissue around holes, was recorded as brown spots.

Area determinations were made with a portable area meter (LiCor LI-3000) equipped with a high speed belt drive. This instrument measures area to the nearest 1 mm² and is accurate to within 1%. For each leaf, three area measurements were made: holes (*H*), brown spots (*B*), and residual area of the leaf (*R*). Percent of leaf area damaged was then calculated as:

$$\text{Damage} = [(H + B)/(R + H)] \times 100$$

All leaves of each species from the same ecosystem were pooled, oven dried to constant weight at 70°C, and weighed to 0.05 g. The leaf specific mass (mass per unit area of leaf) of each species was then calculated so that damage could be expressed on a mass basis as well as an area basis.

RESULTS

The species richness, leaf area, cover, leaf biomass and mean leaf specific mass of the nine ecosystems are summarized in Table I. The species richness shown includes only species intercepted during LAI measurements, so under-

TABLE I

Species richness and leaf parameters of the nine ecosystems studied. Number of species includes only those species intercepted during the leaf area index (LAI) sampling

Ecosystem	Number of species	LAI (S.D.)	Patchiness (S ² \bar{x}^{-1} of LAI)	Cover (%)	Leaf biomass (g m ⁻²)	Mean leaf specific mass (g m ⁻² of leaf)
Young maize	7	1.0 (1.2)	1.45	56	33	31
Mature maize	20	2.6 (1.6)	0.98	88	107	41
Sweet potato	8	2.9 (1.3)	0.60	100	100	35
Cacao-plantain- <i>Cordia</i>	4	3.4 (3.0)	2.56	84	312	91
Wooded garden	18	3.9 (2.7)	1.82	100	307	78
Shaded coffee	7	4.0 (2.9)	2.13	96	272	68
Mimic of succession	27	4.2 (2.2)	1.16	98	204	49
Gmelina	8	5.1 (2.5)	1.20	98	345	68
Succession	35	5.1 (3.5)	2.39	96	248	48

estimates true species richness, especially in the more diverse ecosystems. The eleven month-old succession, for example, was known to contain more than 100 species at the time our measurements were made.

LAI ranged from 1.0 in the young, clean-cultivated maize to 5.1 in the natural succession and the gmelina plantation. LAI in the wooded garden might have been higher had our measurements been taken in the rainy season, when the deciduous overstory tree, *Cedrela mexicana*, would have been in full leaf.

Canopy patchiness, calculated as the ratio of estimated LAI variance to mean LAI (Ewel 1977), was lowest in the dense, uniform planting of sweet potato, and highest in the shaded coffee, succession and cacao-plantain-*Cordia*. Cover, calculated as the number of LAI sample points where LAI > 0, divided by 50 (the total number of sample points), was > 80% in all ecosystems except the young, clean-cultivated maize.

Total leaf biomass was calculated as the sum of leaf specific mass times LAI, for the species selected for damage assessment, plus an adjustment for unsampled species. Ecosystems with high LAI did not necessarily have equally high leaf biomass (Table I) due to differences in leaf specific mass (ecosystem means ranged from 31 to 91 g m⁻² of leaf). Thus, leaf biomass should be used with caution as a measure of an ecosystem's potential for photosynthesis.

Leaf area

The vertical distribution of leaf tissue in each ecosystem, including the amount contributed by some of the dominant species, is shown in Fig. 1. Leaf tissue was most equitably distributed vertically in the wooded garden, cacao-plantain-*Cordia*, and shaded coffee. Leaf tissue was most concentrated in the gmelina plantation (at about 7–8 m), and in the sweet potato planting (0–0.5 m).

Although total leaf area in the succession (LAI = 5.1) was only about 20% greater than that of the successional mimic (LAI = 4.2), the vertical distribution differed considerably in the two communities. The mimic had a dense cover of leaves near ground level (primarily squash and sweet potato) and a gap at 1–2 m, whereas leaf area in the natural succession increased steadily from the top of the canopy (ca. 5 m) to ground level.

Light transmission

Optical density of the nine canopies ranged from > 2.0 (< 1% transmission) in the natural succession to < 0.5 (> 30% transmission) in the young maize (Fig. 2.). Although radiation not transmitted may have been either absorbed or reflected, it is likely that the differences measured were due more to differential absorption than to differential reflectance. Although plant species and canopies vary considerably in their reflectance properties (Billings

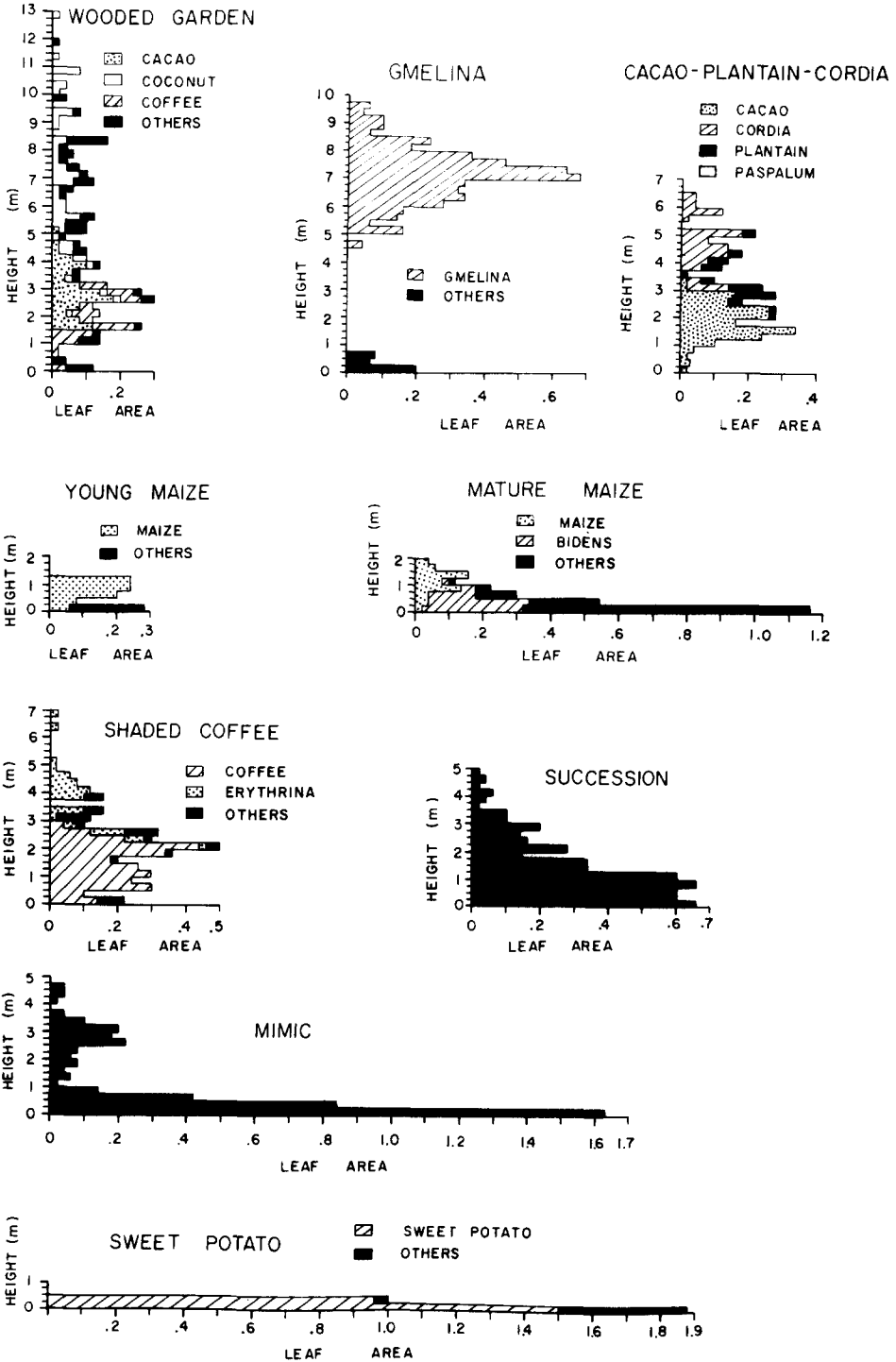


Fig.1. Vertical distribution of leaf area in the nine tropical agricultural and successional ecosystems. Diagrams are based on means of 50 measurements per site.

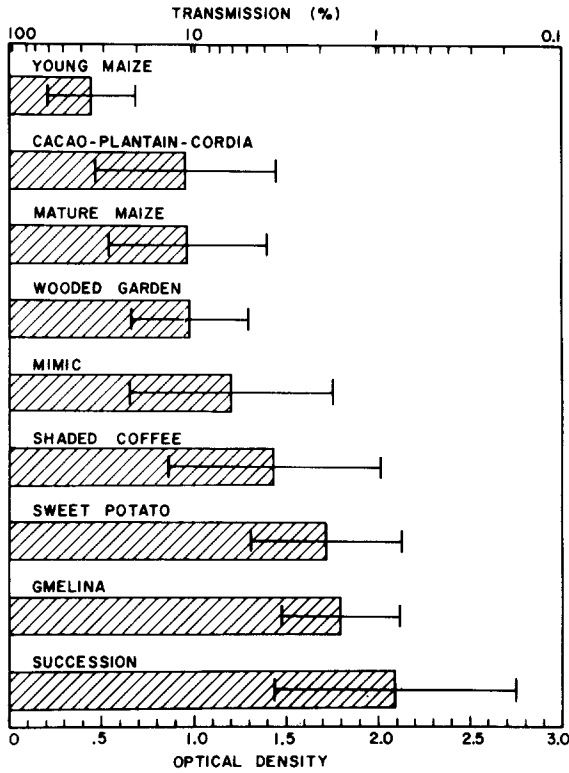


Fig. 2. Transmission of photosynthetically active radiation (PAR = 400–700 nm) and optical density of the canopy of the nine tropical agricultural and successional ecosystems. Hatched bars are means of 100 readings per site; narrow bar is \pm standard deviation.

and Morris 1951, Reifsnnyder and Lull 1965), it is unlikely that this would account for much of the huge difference in light transmission observed among the nine ecosystems.

Two of the monocultures — the sweet potato field and the gmelina plantation — had surprisingly dense canopies. Both transmitted $< 2\%$ of the PAR (400–700 nm). Other low-diversity communities, however, were among the least effective at light capture because of their open canopies.

Roots

The root biomass data are summarized by depth and size class in Table II. Total root biomass to 25 cm ranged from about 40 g m^{-2} (young maize, sweet potato) to over 300 g m^{-2} (wooded garden, successional mimic). The high root biomass of the successional mimic was due primarily to large roots of cassava. Three large ($> 20 \text{ mm}$ diameter) cassava storage roots were intercepted by our corer at 5–25 cm, but excluded from the results reported in Table II and Fig. 3. If these three roots had been included, the mass of the

TABLE II

Root biomass in the nine ecosystems studied. Values for the two depth intervals are g per m² of ground per cm of soil depth; values for ecosystem totals by size class are g per m² of ground. Values in parentheses are 1 standard deviation; *n* = 12

Ecosystem	Depth (cm)	Diameter class (mm)					Total
		0-1	1-2	2-5	5-10	> 10	
Young maize	0-5	3.1 (5.9)	1.3 (3.5)	0.2 (0.7)	0	0	4.6 (10.0)
	5-25	0.6 (0.3)	0.2 (0.2)	0	0	0	0.7 (0.4)
	Total	27.5 (31.7)	10.2 (20.8)	1.0 (3.5)	0	0	38.7 (55.6)
Sweet potato	0-5	3.0 (2.3)	0	0	0	0	3.0 (2.3)
	5-25	0.7 (0.7)	0.5 (1.2)	0.0 (0.1)	0	0	1.3 (1.4)
	Total	29.6 (21.3)	10.6 (23.6)	0.4 (1.5)	0	0	40.6 (32.5)
Mature maize	0-5	5.5 (2.9)	2.3 (3.8)	0.3 (0.9)	2.3 (8.2)	0	10.4 (13.2)
	5-25	2.3 (1.3)	0.7 (0.8)	0.1 (0.3)	0	0	3.1 (1.4)
	Total	73.9 (35.2)	25.3 (21.6)	3.9 (8.6)	11.8 (40.7)	0	114.9 (73.9)
Gmelina	0-5	5.2 (4.5)	1.5 (1.9)	0	1.2 (4.1)	0	7.9 (5.0)
	5-25	1.4 (0.8)	0.4 (0.6)	0.5 (1.5)	2.2 (6.6)	0	4.5 (7.0)
	Total	54.2 (32.3)	14.6 (12.2)	10.0 (29.4)	49.7 (132.4)	0	128.5 (143.0)
Succession	0-5	7.0 (2.7)	2.6 (4.0)	3.7 (7.8)	0	2.1 (7.4)	15.4 (15.7)
	5-25	1.3 (0.8)	0.8 (1.2)	0.4 (1.0)	3.5 (12.1)	1.0 (3.5)	7.0 (13.8)
	Total	60.9 (20.2)	30.2 (40.7)	25.5 (45.3)	69.9 (242.2)	31.0 (107.2)	217.5 (292.7)
Shaded coffee	0-5	7.0 (5.8)	3.3 (5.1)	2.2 (4.7)	0	1.6 (5.5)	14.1 (12.9)
	5-25	1.5 (1.3)	1.9 (1.4)	3.0 (3.7)	0.1 (0.5)	1.7 (5.9)	8.2 (6.6)
	Total	64.4 (47.7)	53.9 (36.5)	71.5 (73.6)	2.7 (9.3)	42.3 (119.5)	234.8 (139.9)
Cacao-plantain- <i>Cordia</i>	0-5	9.6 (3.8)	3.0 (3.4)	5.9 (10.9)	1.4 (4.8)	0	19.9 (14.8)
	5-25	1.6 (0.8)	0.8 (1.4)	2.3 (6.1)	3.9 (12.7)	0	8.6 (13.7)
	Total	79.3 (22.9)	31.8 (29.7)	75.9 (122.8)	84.7 (252.1)	0	271.7 (294.9)
Wooded garden	0-5	6.3 (6.0)	3.7 (3.7)	2.3 (4.5)	0	0	12.3 (11.0)
	5-25	3.0 (1.9)	2.8 (3.5)	2.0 (2.3)	2.0 (3.9)	2.5 (5.9)	12.3 (8.1)
	Total	90.7 (44.9)	74.9 (70.6)	51.0 (57.0)	40.2 (78.4)	50.4 (117.0)	307.2 (177.4)
Mimic of succession	0-5	3.9 (2.8)	2.8 (5.2)	1.2 (3.2)	0	8.4 (29.0)	16.3 (28.5)
	5-25	1.3 (0.9)	0.5 (1.1)	3.6 (5.0)	4.7 (9.9)	6.9 (24.0)	17.0 (26.0)
	Total	45.6 (20.9)	23.8 (33.8)	78.8 (111.7)	92.9 (198.6)	180.7 (489.6)	421.8 (532.8)

> 10 mm diameter class would have increased to 155.8 g m^{-2} per cm depth, and total root biomass per m^2 of ground from 422 to 3398.

In all ecosystems the roots, especially those in the smallest diameter classes, were most concentrated in the surface 5 cm (Fig.3). All ecosystems

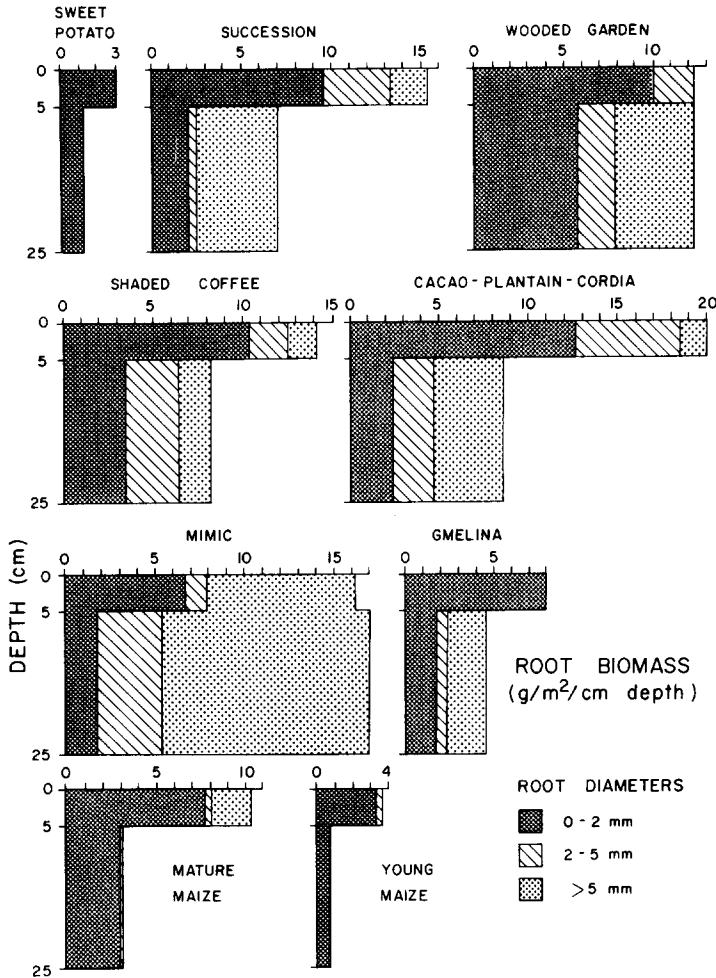


Fig. 3. Vertical distribution of root biomass, by size class, in the nine tropical agricultural and successional ecosystems. Values are means of 12 samples per site.

lacking woody structure also lacked deep roots ($< 5 \text{ g m}^{-2}$ per cm depth root concentration), and the only woody system with few deep roots was gmelina (4.5 g m^{-2} per cm depth). Root biomass concentration from 5–25 cm depth was the same or greater than that from 0–5 cm in only two systems: successional mimic and the wooded garden.

TABLE III

Leaf area and damage, by species, in the nine ecosystems studied

Ecosystem	Species	LAI	Percent of total LAI	Leaf specific mass (g m ⁻² of leaf)	Damage	
					g m ⁻² of ecosystem	Percent LAI
Young maize	<i>Zea mays</i> L.	0.8	78.8	31	0.81	3.1 ^a
	(Others)	0.2	21.2	31	0.22	3.1
Mature maize	<i>Bidens pilosa</i> L.	0.8	30.8	29	1.98	8.5 ^a
	<i>Zea mays</i> L.	0.6	22.3	48	3.60	12.9 ^a
	<i>Cyperus setul-ciliata</i>	0.2	8.5	66	1.61	11.1 ^a
	<i>Paspalum fasciculatum</i>					
	Willd. ex Fluegge	0.2	7.7	42	0.86	10.2 ^a
	(Others)	0.8	30.8	41	3.43	10.4
Sweet potato	<i>Ipomoea batatas</i> L.	2.5	85.4	35	1.42	1.7
	(Others)	0.4	14.6	35	0.24	1.7
Cacao-plantain-Cordia	<i>Theobroma cacao</i> L.	1.8	52.0	89	10.94	6.9
	<i>Cordia alliodora</i>					
	(Ruiz & Pav.) Cham.	1.1	31.0	100	10.27	9.7
	<i>Musa × paradisiaca</i> L.	0.6	16.4	81	3.96	8.7 ^a
	(Others)	0.0	0.6	90	0.15	8.1
Wooded garden	<i>Cocos nucifera</i> L.	1.1	27.0	120	4.37	3.4 ^a
	<i>Theobroma cacao</i>	1.0	26.5	48	2.44	4.9
	<i>Coffea arabica</i> L.	0.8	19.9	62	1.19	2.5
	(Others)	1.0	26.5	78	3.01	3.7
Shaded coffee	<i>Coffea arabica</i> L.	2.7	67.3	78	2.70	1.3 ^a
	<i>Erythrina poeppigiana</i>					
	(Walp.) O.F. Cook	0.8	19.6	36	1.55	5.5
	(Others)	0.5	13.1	68	0.79	2.2

TABLE III (continued)

Mimic of succession	<i>Cymbopogon citratus</i> Stapf.	0.7	16.7	78	1.16	2.1 ^a
	<i>Hyptis suaveolens</i> (L.) Poit.	0.4	10.5	34	1.19	7.9 ^a
	<i>Phaseolus vulgaris</i> L.	0.4	9.0	26	0.17	1.7
	<i>Manihot esculenta</i> Crantz	0.3	7.1	45	0.46	3.4 ^a
	<i>Cajanus cajan</i> (L.) Druce	0.3	6.7	47	1.36	10.3 ^a
	<i>Sorghum bicolor</i> (L.) Moench	0.2	4.3	44	1.29	16.4
	<i>Secchium edule</i> Sw.	0.2	3.8	32	0.17	3.4 ^a
	<i>Ricinus communis</i> L.	0.1	3.3	48	0.76	11.3 ^a
	<i>Carica papaya</i> L.	0.1	1.9	37	0.07	2.5
	(Others)	1.5	36.7	49	4.17	5.6
Gmelina	<i>Gmelina arborea</i> Roxb.	4.8	93.3	68	12.79	4.0 ^a
	(Others)	0.3	6.7	68	0.91	4.0
Succession	<i>Citbadium</i> sp.	0.6	12.5	60	1.64	4.2
	<i>Panicum maximum</i> Jacq.	0.6	10.9	66	1.87	5.1 ^a
	<i>Cestrum panamense</i> Standley	0.4	7.0	28	0.94	9.4
	<i>Bocconia frutescens</i> L.	0.3	6.6	54	1.01	5.5 ^a
	<i>Phytolacca rivinoides</i>					
	Kunth & Buche	0.3	5.1	38	1.08	10.7
	<i>Frantzia pittieri</i> (Cogniaux)					
	Pittier	0.2	4.7	32	0.28	3.6 ^a
	<i>Ipomoea neei</i> (Spreng)					
	O'Donnell	0.2	4.7	24	0.35	6.0 ^a
	<i>Solanum umbellatum</i> Mill.	0.2	4.3	56	0.91	7.5
	<i>Hymenachne</i> aff. <i>amplexicaulis</i>					
	(Rudge) Nees	0.1	2.0	57	0.54	9.5 ^a
	<i>Ipomoea</i> sp.	0.1	1.6	30	0.25	10.1
	<i>Momordica charantia</i> L.	0.0	0.4	15	0.01	3.1 ^a
	(Others)	2.1	40.2	48	6.31	6.3

^a More than 50% of the damage was brown spots (caused by leaf miners, piercing-sucking insects, pit feeders, fungi, viruses, necrosis around holes, etc.).

Leaf damage

The leaf area and damage are summarized by dominant species for each of the nine ecosystems in Table III. The coffee in the shaded coffee stand was the least-damaged species (1.3% of its leaf area), and the sorghum in the mimic suffered the greatest damage (16.4%). The unweighted mean damage per species was 6.5% of leaf area.

Biomass loss on a per-leaf-area basis was calculated by multiplying a species' percent leaf loss by its leaf specific mass. When this value is multiplied by the species' LAI, leaf biomass loss on a per-ground-area basis results. Greatest biomass loss per m^2 of ecosystem occurred in species that were either dominant and/or had leaves of high specific mass. For example, gmelina and coffee, both of which had leaves of relatively high specific mass and dominated their respective ecosystems, lost nearly 13 and 3 $g\ m^{-2}$ of ecosystem, respectively, even though neither species was heavily attacked (4.0 and 1.3% of LAI, respectively). Some species were heavily consumed (e.g., *Phytolacca rivinoides*, 10.7% of LAI and *Ipomoea* sp., 10.1%, both in the natural succession), yet accounted for little total biomass loss because they accounted for less than 7% of the total LAI and had leaves of low specific mass.

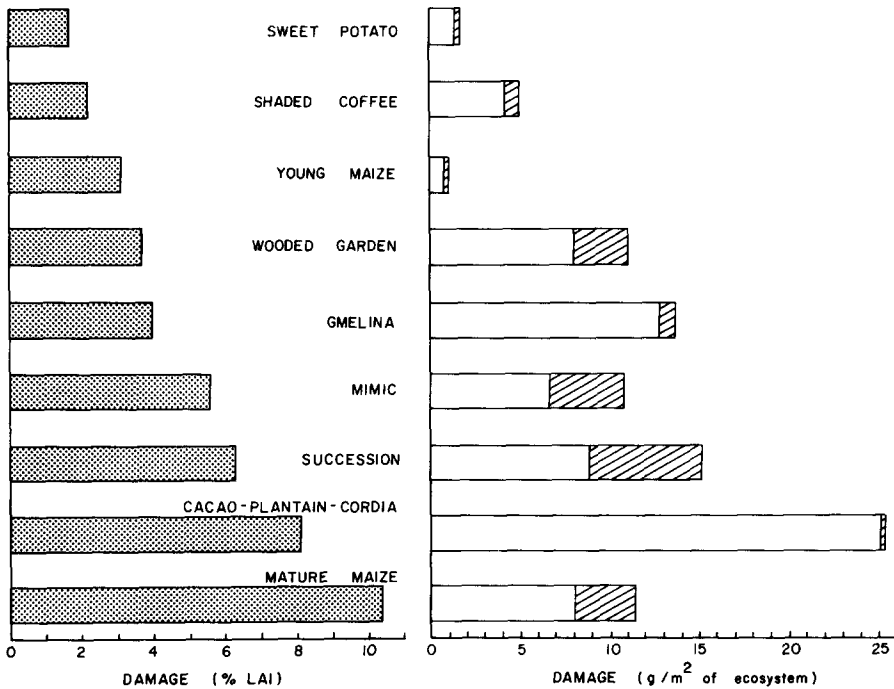


Fig. 4. Leaf damage in the nine tropical agricultural and successional ecosystems. Cross-hatched portion of biomass-loss bars (right-hand side) indicates the portion estimated, based on amounts determined from direct measurement (open portion of bar). Values are based on measurements on 30 leaves from each of 35 species.

Whole-ecosystem leaf damage is summarized in Fig. 4. To calculate ecosystem loss rates, species loss rates (percent leaf area or g m^{-2} leaf) were weighted according to the species' LAI. It was assumed that the mean leaf specific mass and percent leaf loss in unsampled species equalled the LAI-weighted mean of the sampled species. Ecosystem loss rates calculated using weighted means were compared with results obtained using unweighted means (not reported), and the two results did not differ significantly.

Leaf area loss ranged from $< 2\%$ in the sweet potato plot to $> 10\%$ in the mature maize. The sweet potato had received three insecticide applications, whereas many of the leaves (of both maize and *Bidens*, the dominant weed) in the old maize planting were senescent. Biomass loss was lowest in the young maize ($< 2 \text{ g m}^{-2}$) and highest in the cacao-plantain-*Cordia* ($> 25 \text{ g m}^{-2}$). Damage expressed as the percent of total LAI was not well correlated with biomass loss because of differences in total LAI and in leaf specific masses among ecosystems. However, the three ecosystems that lost the lowest fraction of their total LAI (sweet potato, shaded coffee, and young maize) also experienced the lowest biomass loss.

DISCUSSION

The values for total root biomass (30 to 422 g m^{-2} , to 25 cm depth) were remarkably similar to those for leaf biomass (33 to 345 g m^{-2}): in the case of the wooded garden they were identical (307 g m^{-2}). High leaf biomass in an ecosystem was usually associated with high root biomass. The two exceptions were the monocultures gmelina and sweet potato, which had substantially more leaf biomass than root biomass.

The surface area of small, metabolically active feeder roots is a better measure of root function than root biomass. The surface area of small roots ($> 0\text{--}5 \text{ mm}$ diameter to a depth of 25 cm) is shown in Fig. 5. Root area index (RAI = m^2 of small-root surface area per m^2 of ground) is smaller than LAI, but was > 1 in six of the ecosystems.

In spite of all the difficulties associated with the measurement of light and its relationship to canopy architecture (e.g., Saeki 1960; Anderson 1964, 1966), LAI was moderately well correlated with optical density ($r = 0.78$). The gmelina monoculture, with its high LAI (5.1), was nearly as effective at light capture as the diverse succession, even though the leaves in the gmelina were concentrated near the top of the canopy, while those of the successional vegetation were well distributed vertically. The sweet potato planting did not have a particularly high LAI (2.9), but it was remarkably effective at light capture. The sweet potato canopy was very uniform, with the lowest patchiness index of any of the ecosystems studied (0.6, Table I), and close to the ground, leading to less marked penumbral effects around sunflecks.

Ecosystem-level amounts of leaf damage (mean of 4.9% of LAI) were lower than species-level damage (mean of 6.5%), indicating that species that incur less-than-average amounts of damage are more dominant than

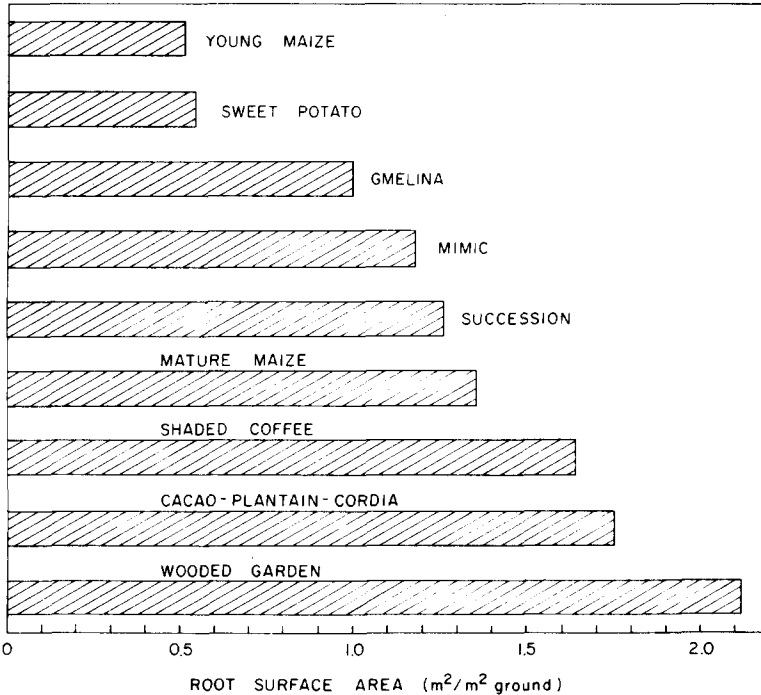


Fig.5. Surface area of small-diameter (≤ 5 mm) roots to a depth of 25 cm in the nine tropical agricultural and successional ecosystems.

species that incur greater-than-average amounts of damage. In the natural succession the low susceptibility of some abundant species to herbivores may account, in part, for their dominance.

Damage was not correlated with leaf specific mass ($r = -0.03$ on a species-by-species basis). Some leaves of high specific mass (e.g., cacao, *Cordia*, plantain) were heavily damaged, whereas some leaves of very low specific mass were practically undamaged (e.g., papaya, *Momordica*, one bean species). Damage reflects many factors, including leaf turnover rates; leaf anatomy, morphology and chemistry; and herbivore abundance and behavior. The amounts of leaf damage measured are similar to others reported for natural tropical ecosystems (Odum and Ruíz-Reyes 1970, Leigh 1978), but like many others in the literature they cannot be used to estimate herbivory rates because the time over which the damage was inflicted was not measured.

Ecosystem trends

Three of the variables examined can be considered as functional responses that would be desirable to incorporate into agroecosystem design: (1) resistance to pest attack (measured as the inverse of the amount of leaf damage), (2) light-capture ability (measured as optical density), and (3) nutrient-cap-

ture ability (measured as fine-root surface area). It was our initial hypothesis that these responses would be positively correlated with either or both of two "independent" variables: ecosystem age and species diversity. Although some trends are discernible, there was no consistent relationship between the three response variables and age or diversity.

To examine the relationships between the response variables and diversity, we used both species richness (Table I) and the Shannon index (for reasons described by Pielou 1977, Chapt. 19). To calculate the Shannon index we did not use numbers of individuals as a measure of abundance, but rather the number of times a species was intersected during LAI measurements. Values (\log_2) ranged from < 1 in the gmelina and sweet potato monocultures to > 4 in the mimic and natural succession.

Leaf damage was remarkably similar in all ecosystems, even though there were substantial differences on a species-by-species basis. Our results do not indicate that the overall damage inflicted to the entire ecosystem is tightly controlled by diversity. Rather, herbivore consumption seems to be a nearly constant proportion of the total amount of leaf area present.

Manipulation of diversity might afford protection to certain species by reducing their apparency to herbivores (Feeny 1976, Cates 1980). In this study, damage was measured in two systems for each of three species: maize, coffee, and cacao. Damage to maize was much higher (12.9% LAI) in the complex mature maize system than in young maize (3.1% LAI). Cacao damage was lower in the wooded garden, where this species comprised 26.5% of ecosystem LAI (damage = 4.9% LAI) than in the less complex cacao-plantain-*Cordia*, where it contributed over half the ecosystem LAI (6.9% damage). Leaf loss in coffee was low in both systems where it was measured (2.5% leaf loss in the wooded garden and 1.3% loss in the shaded coffee, where it was the most common species). On the basis of these comparisons, it does not appear that complexity always confers protection to individual species by reducing their apparency.

Ecosystem damage was not well correlated with age, even when the young sweet potato monoculture, which had received insecticide application, was excluded from the calculations ($r = -0.35$ with sweet potato and -0.50 without). The kinds of factors that might act to decrease damage with age (elimination of the most susceptible plants over time; replacement of species with soft, poorly protected, short-lived leaves by species with tough, well protected, long-lived leaves; build-up of predator populations; etc.) are apparently mitigated by other factors. These mitigating factors may include population build-ups of specialized herbivores; increased probability of physical damage (caused by branch fall and wind, for example) as mean leaf life span increases; and decreased rates of species turnover. It should also be borne in mind that a given percent leaf area loss in ecosystems having long-lived leaves may actually represent a lower herbivory rate than it would in a system having shorter-lived leaves.

Just as age and diversity do not necessarily lead to decreased herbivory,

nor do they necessarily result in increased effectiveness of light capture. The youngest, most species-poor ecosystem studied — sweet potato — was quite effective at intercepting PAR. Sweet potato is a non-woody vine and has relatively large leaves, so it is extremely effective at covering a site completely, regardless of the initial planting density. This may explain why it is often used as a cover crop in mixed cropping systems in regions like Tabasco and Costa Rica. Maize, on the other hand, due to its upright growth habit, is not very effective at covering a site completely at the densities normally planted by farmers in Latin America. High light penetration may have been a decisive selective pressure in the development of the corn/bean/squash polyculture so common in Mesoamerica. In the old maize monoculture, much of the light capture was by weeds. The monoculture of gmelina was also quite effective at reducing PAR transmission, which may explain, in part, why this weedy, fast-growing tree has been such a successful plantation species. The ecosystems that were best at light capture were among the most diverse, but this is probably more a function of their high leaf area than their diversity.

Species-poor ecosystems — including the young maize and sweet potato plantings, as well as the older gmelina plantation — had limited amounts of root-surface area ($RAI < 1$). Increased diversity was associated with increased amounts of root area, even in the weed-rich older maize planting. Even though some of the monocultures (e.g., sweet potato and gmelina) were effective at light capture, their limited amounts of fine-root surface area indicate that they may not be equally effective at nutrient capture. Older ecosystems, even those that were relatively simple floristically (such as the shaded coffee) tended to have high root-surface area. The highest RAI (2.0) was found in the wooded garden, the oldest, most diverse ecosystem studied.

Even though canopy architecture and root-system architecture are, in some ways, analogous, they differ with respect to the nature of the resources they capture. A monolayer of leaves 10 m above the ground intercepts the same resource as does a monolayer of leaves at a height of 1 m. The resources available to root systems at different depths are very different, however, and different species are characterized by different rooting depths (Nelliat et al. 1974). Increased species diversity may enhance an ecosystem's nutrient capturing ability. The maintenance of root systems having high surface area of absorbing roots well distributed in the soil profile may be one of the most important features to strive for in designing agroecosystems appropriate for the humid tropics, where soil-nutrient storage is often low and leaching rates are high. Such root systems can be achieved by designing systems that are diverse and long-lived.

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