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Source: *Ecology*, Vol. 68, No. 1 (Feb., 1987), pp. 108-116

Published by: Ecological Society of America

Stable URL: <http://www.jstor.org/stable/1938810>

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HERBIVORY IN COMPLEX AND SIMPLE TROPICAL SUCCESSIONAL ECOSYSTEMS¹

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Abstract. To investigate the relationship between herbivory and floristic complexity, we measured losses to herbivores in four 0.1- to 4-yr-old tropical ecosystems: (1) unmanipulated successional vegetation, (2) successional vegetation with higher plant diversity than the unmanipulated succession, (3) an ecosystem of investigator-controlled species composition, designed to imitate the physiognomy and species richness of the successional vegetation, and (4) monocultures of maize, cassava, and *Cordia alliodora*. We measured herbivory rates (loss of leaf area per day) on dominant plant species in each system and aggregated these over species to estimate rates for plant communities. Although herbivory rates varied widely among species, losses to herbivores in terms of mass of leaf tissue lost per unit of ground area were approximately equal in the four systems, 71.5 to 78.5 g · m⁻² · yr⁻¹. Ecosystems with greater plant species richness lost a lower proportion of available leaf area and exhibited lower temporal variability in herbivory. Species-rich ecosystems had relatively constant, predictable rates of herbivory due to counterbalancing of low rates on some species with high rates on others. The rate of herbivory on any species was strongly influenced by the nature of the surrounding vegetation. Although surrounding vegetation often conferred protection upon potential pest targets, in some cases a plant species experienced increased susceptibility to herbivores through association with other species.

Key words: *cassava; Cordia alliodora; Costa Rica; diversity; herbivory; maize; succession; tropical succession.*

INTRODUCTION

The rate of herbivory on a plant is influenced by the composition, density, and diversity of the surrounding vegetation. Recent research, reviewed by Risch et al. (1983) and Strong et al. (1984), illustrates the context dependence of herbivory for numerous plant species in natural and managed ecosystems. Although empirical results vary, a species is often subjected to less herbivory when it is part of a floristically complex plant assemblage than when it is grown in a monospecific stand. Several mechanisms have been proposed to explain this phenomenon. These include decreased concentration of the plant resource in diverse ecosystems (Root 1973); increased abundance of insect predators and parasites (Root 1973); physical interference with insect behavior, due to the structural complexity of diverse ecosystems (Atsatt and O'Dowd 1976, Perrin 1980); chemical inhibition of herbivore colonization by repellent stimuli of associated plants (Tahvanainen and Root 1972); and diversion of polyphagous herbivores from one plant species to other more palatable species (Atsatt and O'Dowd 1976, Cromartie 1981).

Much recent work on herbivory has focused on interactions between a single plant species and a single herbivore species. Although there have been significant

increases in our understanding of evolutionary and ecological impacts of herbivory at the species level (reviewed by Crawley 1983, Denno and McClure 1983, Strong et al. 1984), herbivory patterns for whole ecosystems are not well understood. An important question at this higher level of organization is whether total ecosystem herbivory is related to plant species diversity.

Based on mechanisms operating at the species level, we may predict either higher or lower overall herbivory in floristically diverse than in simple ecosystems. If abundance of insect predators is a major factor controlling herbivory, then diverse ecosystems with many predators should have reduced abundance of both monophagous and polyphagous insects (Risch et al. 1983) and lower herbivory for the ecosystem as a whole. Similarly, we might predict lower total herbivory in diverse plant assemblages if the dominant herbivores are monophagous insects whose host-finding behavior is disrupted by the structural complexity of the vegetation. However, if the major factor reducing herbivory on a species in a diverse ecosystem is diversion of polyphagous herbivores to a nearby, more palatable species, then less herbivory on one species may be offset by more herbivory on another. The net result would be equal (or perhaps greater) overall rates of herbivory in complex than in simple systems.

Although herbivory rates have been estimated for numerous ecosystems (e.g., Teal 1962, Reichle et al. 1973, Sinclair 1975, Boring et al. 1981, Uhl and Mur-

¹ Manuscript received 5 December 1985; revised 9 May 1986; accepted 13 May 1986.

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phy 1981), simultaneous comparisons of herbivory rates in species-rich and species-poor ecosystems in the same environment are lacking. The major objective of this study was to investigate experimentally the relationship between floristic complexity and ecosystem herbivory. We measured herbivory rates on the most common species in four tropical successional ecosystems of different diversity, then aggregated these over species to estimate total leaf loss to herbivores. We used these data to address the following questions: (1) Does total leaf loss differ in floristically simple and complex ecosystems? (2) Are temporal patterns in herbivory related to plant community complexity? (3) Is there a relationship between a plant species' relative dominance and its rate of leaf loss to herbivores? (4) Is herbivory on one species in a community influenced by the palatability of co-occurring species?

METHODS

The study area

The research reported here was conducted as part of a larger ecosystem study designed to test the feasibility of using secondary succession as a model for the design of tropical agroecosystems. The experiments were carried out in the Florencia Norte Forest near Turrialba, Costa Rica. The site, at 650 m elevation in the Tropical Premontane Wet Forest life zone (Tosi 1969), has a long-term mean annual rainfall of ≈ 2700 mm with a pronounced dry season from January through March.

The second-growth forest on the site was felled in January 1979 and burned on 22 March 1979. After the burn, four experimental vegetation types were established in a randomized block design with each treatment on six 16×16 m plots; strips of vegetation ≥ 5 m wide were left uncut between blocks.

The four experimental ecosystems were: successional vegetation, enriched successional vegetation, an imitation of successional vegetation, and a sequence of monocultures.

In the successional vegetation and the enriched successional vegetation, natural regeneration was allowed to proceed. The successional vegetation received no further experimental manipulations. The enriched succession treatment was designed to explore the functional attributes, including herbivory, of an ecosystem that was even more diverse than the species-rich successional vegetation and to answer questions about the invasibility of diverse plant communities. It received periodic inputs of seeds of species not present in the vicinity: a minimum of 10 000 seeds comprising at least 20 species were added to each plot each month.

The imitation of successional vegetation was an ecosystem designed to find out if structural mimicry of a natural ecosystem would result in similar function, including herbivory. The plant species composition was entirely investigator-controlled, and all species not planted by us were removed. The species used to build

this community included cultivars and noncultivars morphologically similar to those found in the successional vegetation, selected through careful observation of the succession plots and using prior knowledge of floristic trends in tropical succession.

The monocultures consisted of maize (*Zea mays*) planted in late March 1979; a second maize crop planted in late July 1979; a shrub, cassava (*Manihot esculenta*), planted in November 1979; and a tree, *Cordia alliodora*, planted in September 1980. The monoculture plots were weeded regularly.

Plant community structure

To estimate relative species dominance, leaf area index (LAI), defined as the area of leaves (one side) per unit ground area, was measured using the plumb-bob method used by Ewel et al. (1982). A thin line was lowered vertically from the top of the vegetation canopy to the ground and the leaves touching the line were counted. This method reduces the sampling area to a single point, and the number of leaves above a point (i.e., the number of intersections of line and leaf) is a measure of LAI. Intersections of line and leaf were recorded by species and height. Our LAI values were based on 30 measurements in each plot in July 1979, November 1979, April 1980, and February 1983, when the plots were 4, 8, 13, and 47 mo old. LAI of the maize monoculture in November 1979 was calculated using leaf biomass/leaf area regressions rather than the plumb-bob method to avoid biases resulting from the uniform spacing of the maize plants. In addition, we used floristic data derived from species surveys taken in each plot in July 1979, November 1979, April 1980, and February 1983.

Leaf losses to herbivores

Consumption of leaf tissue by herbivores was estimated by monitoring amounts of damage incurred over a 3–7 wk period on tagged leaves of dominant species in each of the four experimental ecosystems during four sampling intervals. The intervals began in September 1979 (when the three diverse communities were 6 mo old), January 1980 (10 mo old), June 1980 (15 mo old), and February 1983 (47 mo old). Herbivory was measured on those species that were dominant at each of these four times. The dominants in each ecosystem were defined as those most common species that jointly accounted for at least 80% of total LAI.

The one exception to this general procedure was the February 1983 measurement in the *C. alliodora* monoculture. Leaves (30 from each of the six replications) were harvested and the area of damaged tissue on each was measured. Because *C. alliodora* is deciduous, and using information gained from observation of its phenology, we assigned an age of 300 d to each leaf and assumed that the damage had been inflicted over that period.

At the beginning of each sampling interval five in-

individuals of each dominant species in each treatment were tagged, one in each of five plots. In a few cases, patchy distribution of a species made it necessary to tag more than one individual of that species within a single plot. One unbroken, unbranched stem bearing at least four leaves was arbitrarily selected on each plant. Four to eight consecutive leaves along the stem were marked by small plastic bands placed around the stem. (Pilot studies indicated that the tags did not affect herbivory rates.) Holes in each leaf were measured by placing a sheet of millimetre-ruled graph paper under the leaf and counting the uncovered squares, and the areas of necrotic tissue (brown spots) were estimated visually.

The length of each leaf was measured to the nearest millimetre at the time of tagging. Initial leaf areas were estimated using leaf length/leaf area regressions developed from samples of ≥ 50 leaves per species.

The tagged leaves were harvested 3–7 wk later. Damaged areas (holes and brown spots) on each leaf were traced onto clear plastic using a permanent black marking pen. All areas of missing tissue, plus areas of damage that left only a transparent layer of leaf tissue, were considered to be holes. Brown spots included all other visible damage: that caused by leaf-mining insects, rasping insects, fungi, or viruses, plus the necrotic tissue around the holes. Because it was not possible to separate losses due to plant diseases from losses due to herbivorous insects, both were included in the herbivory estimates. We did not measure damage from herbivores such as sap-sucking insects, stem borers, and root herbivores. Because these types of herbivory may have affected the four experimental ecosystems differently, our results do not necessarily reflect differences in total herbivory.

Residual leaf areas and damage areas were measured using an area meter (Lambda Instruments, LI-3000) that gives the area of opaque surfaces to the nearest 0.01 cm^2 with a precision of $\pm 1\%$. For each leaf, total damage and gross leaf area at the time of leaf harvest were calculated as $(H + B)$ and $(R + H)$, respectively, where H = area of holes, B = area of brown spots, and R = residual leaf area at time of harvest.

Relative loss rate (area of leaf lost per unit leaf area per day) was calculated for each leaf as

$$\{[D(t)/G(t)] - [D(0)/G(0)]\} \times (10^4/n)$$

where $D(0)$ = area of damage present at the beginning of the time interval, $D(t)$ = area of damage present at the end of the interval, $G(0)$ = gross leaf area at the beginning of the interval, $G(t)$ = gross leaf area at the end of the interval, and n = number of days in the interval, with all areas expressed in square centimetres. Because the rate of expansion of holes in a leaf is approximately equal to the rate of expansion of the leaf (Reichle et al. 1973, Coley 1980), estimates of percent loss are not affected by leaf expansion during the monitoring interval.

The absolute loss rate for each species was calculated by multiplying its mean relative loss rate by its LAI. To enable us to convert loss rates from a leaf-area basis to a mass basis, leaf specific mass (mass per unit area of leaf) was estimated for each species from a sample of 50 leaves.

RESULTS

Plant community structure

Species richness increased over time in all three of the diverse ecosystems. The successional vegetation, with a total species richness (i.e., all replications combined) of 233 species at 47 mo, and the enriched successional vegetation, with 268 species, were the most species-rich of the four experimental ecosystems (Table 1). The floristic differences between the successional vegetation and the enriched successional vegetation reflect both the presence of investigator-introduced species in the enriched ecosystems and local heterogeneity in species distributions. At 47 mo, 71 of the species (26%) in the enriched succession plots had been introduced. (Herbivory was measured on three of these, *Manihot esculenta*, *Musa paradisiaca*, and *Erythrina costaricensis*.)

The imitation of succession treatment had no species in common with the succession treatment and only three species in common with the enriched succession treatment (*Ma. esculenta*, *Mu. paradisiaca*, and *E. costaricensis*). This investigator-designed ecosystem had less replication-to-replication variation in species composition than did the succession and enriched succession treatments, so it contained fewer total species (151 at 47 mo). On the average, however, each of its replications contained as many species as a replication of the successional vegetation.

All three species-rich systems were characterized throughout the study period by an abundance of uncommon species with low LAI and a few dominant species with high LAI (Table 2). One exception was a paucity of uncommon species in the imitation treatment at 6 mo.

Mean LAI values during the first year (sampling intervals 1 through 3, Table 1) were highest in the succession (3.3) and enriched succession (3.5) and lowest in the imitation (1.8) and the monoculture (1.2). In sampling interval 3, which occurred during the dry season, LAI values were low in all ecosystems except the cassava monoculture. During a later dry-season sample (interval 4), the LAIs of the four ecosystems did not differ; at that time all ecosystems were dominated by woody perennials.

Leaf loss rates

The frequency distributions of leaf damage were highly skewed for most species, with many leaves of a species receiving little or no damage and a few leaves incurring moderate to large amounts of damage (see

TABLE 1. Vegetation structure and herbivory rates in the four experimental ecosystems.

Ecosystem	Sampling interval		Species richness‡		Leaf area index (m ² /m ²)§	Sample size		Rate of leaf loss to herbivores	
	No.	Age (mo)†	In 6 plots	\bar{X} per plot		No. of species	No. of leaves	Area per unit area of leaf (cm ² ·m ⁻² ·d ⁻¹)	Mass per unit area of ground surface (g·m ⁻² ·d ⁻¹)
Succession	1	6	83	34	4.02	8	96	14.7	0.208
	2	10	81	34	3.63	10	176	23.0	0.244
	3	15	77	33	2.31	12	186	16.6	0.143
	4	47	233	104	3.34	9	189	16.2	0.190
$\bar{X} \pm SE$					3.32 ± 0.37			17.6 ± 1.8	0.196 ± 0.021
Enriched succession	1	6	84	34	4.27	9	87	14.9	0.260
	2	10	97	41	3.72	8	130	15.3	0.231
	3	15	89	40	2.59	11	148	17.9	0.215
	4	47	268	133	3.44	8	148	14.5	0.149
$\bar{X} \pm SE$					3.50 ± 0.35			15.6 ± 0.8	0.214 ± 0.024
Imitation of succession	1	6	10	8	1.78	8	114	27.3	0.191
	2	10	37	18	2.11	7	88	47.8	0.323
	3	15	44	21	1.37	6	56	9.6	0.051
	4	47	151	107	3.33	9	171	28.5	0.295
$\bar{X} \pm SE$					2.15 ± 0.42			28.3 ± 7.8	0.215 ± 0.062
Monocultures									
Maize	1	2	1	1	0.38	1	14	6.2	0.013
Cassava	2	2	1	1	0.85	1		103.4	0.399
Cassava	3	7	1	1	2.30	1		38.2	0.399
<i>Cordia</i>	4	29	1	1	3.34	1	180	2.1	0.044
$\bar{X} \pm SE$					1.72 ± 0.68			37.5 ± 23.4	0.214 ± 0.107

† Age of vegetation (months) at beginning of sampling interval during which herbivory was measured.

‡ Total number of species in six 256-m² plots, mean number of species per 256-m² plot.

§ Leaf area per unit ground surface area.

|| Estimates from Blanton and Ewel (1985).

examples in Fig. 1). Tests of normality were performed on leaf damage data for 14 species in the successional vegetation, 15 species in the enriched vegetation, 12 species in the imitation of succession, and 2 species grown in monoculture. The damage distributions were non-normal in 36 of the 43 tests ($P < .05$, Kolmogorov-Smirnov statistic). The data therefore were normalized by a log transformation. However, the transformed data did not meet the homogeneity-of-variance assumption for the F test of analysis of variance, so non-parametric tests were used for all statistical comparisons between species.

To evaluate the variability in herbivory at the community level, it is important to characterize the range of variability among and within the component species. Rates of loss to herbivores, calculated as the area of leaf lost per unit area of leaf per day, varied widely among species, from 0.6 cm²·m⁻²·d⁻¹ for *Coffea arabica* to 143.0 cm²·m⁻²·d⁻¹ for *Leucaena leucocephala*. The median value for average rate of leaf loss (per unit leaf area available) for all species measured in all ecosystems was 0.139%/d during the first year (measurement intervals 1 through 3, combined) and 0.064%/d in the fourth year. Temporal variation in herbivory

TABLE 2. Species dominance distributions in three experimental ecosystems at four vegetation ages.

Leaf area index†	Age of vegetation (months)											
	Successional vegetation				Enriched successional vegetation				Imitation of successional vegetation			
	6	10	15	47	6	10	15	47	6	10	15	47
	Number of species‡											
<0.10	32	31	33	46	27	34	35	66	5	11	13	42
0.10-0.19	1	3	1	5	2	2	1	1	1	2	1	4
0.20-0.29	2	3	1	2	2	1	1	2	2	1	1	3
0.30-0.39	2	1	0	1	1	0	1	0	1	3	0	1
0.40-0.49	1	0	1	0	0	2	0	0	1	1	0	0
≥0.50	1	2	1	1	3	2	1	1	0	0	1	1

† Leaf area per unit ground surface area.

‡ Based on 180 leaf area index measurements in each ecosystem at each vegetation age.

was high for many species, no matter how diverse the community in which they were growing.

To determine whether herbivory on a species differed among ecosystems, we compared the herbivory rates for those species that were sampled in more than one ecosystem. Of 11 species sampled in both the successional vegetation and the enriched successional vegetation during the same interval, 9 incurred equal amounts of herbivore damage in the two communities (Table 3). This was an expected result because these two ecosystems were very similar in species richness, composition, and LAI. Two species, *Acalypha macrostachya* and *Panicum trichoides*, had different herbivory rates in the enriched successional vegetation and the successional vegetation (Table 3), but the pattern was not the same for both species: *A. macrostachya* incurred more damage in the enriched successional vegetation; *P. trichoides* had its higher herbivory rate in the successional vegetation.

Two of three species monitored in both the enriched successional vegetation and the imitation (*E. costaricensis* and *Ma. esculenta*) had higher median herbivory rates in the imitation treatment ($P < .01$, Kruskal-Wallis test; Table 3). In addition, *Ma. esculenta* had a significantly higher herbivory rate in the imitation than in the monoculture. This species thus had its highest herbivory rate in the ecosystem with intermediate species richness and LAI.

Species' herbivory rates (per unit leaf area) were not significantly correlated with their leaf-specific mass or LAI. However, the species most heavily damaged by herbivores were relatively uncommon species; the abundant species received less-than-average amounts of damage (Fig. 2). For example, *Cymbopogon citratus*, a common grass in the imitation at 15 mo, accounted for more than half of the total leaf area, but <5% of the leaf loss. *Leucaena leucocephala*, on the other hand, received 21% of all damage from herbivores in the imitation at 47 mo, although it made up only 3% of the total leaf area in the system. Other uncommon species that were heavily eaten relative to their leaf area were *Momordica charantia* in the successional vegetation at 10 mo (7% of LAI, 38% of damage) and *Homolepis aturensis* at 47 mo (4%, 16%); *Bocconia frutescens* in the enriched successional vegetation at 15 mo (3%, 9%) and at 47 mo (6%, 26%); *Vernonia patens* in the enriched successional vegetation at 15 mo (2%, 8%); and *Hyptis suaveolens* and *Erythrina costaricensis* in the imitation at 15 mo (9%, 36%; 5%, 31%; respectively).

Ecosystem herbivory rates

Herbivory rates for ecosystems were obtained by assuming that losses from unsampled species equalled the weighted mean of the sampled species, then summing loss rates for all species. Even if losses from unsampled species differed from those of sampled species by as much as 20%, the error resulting from this as-

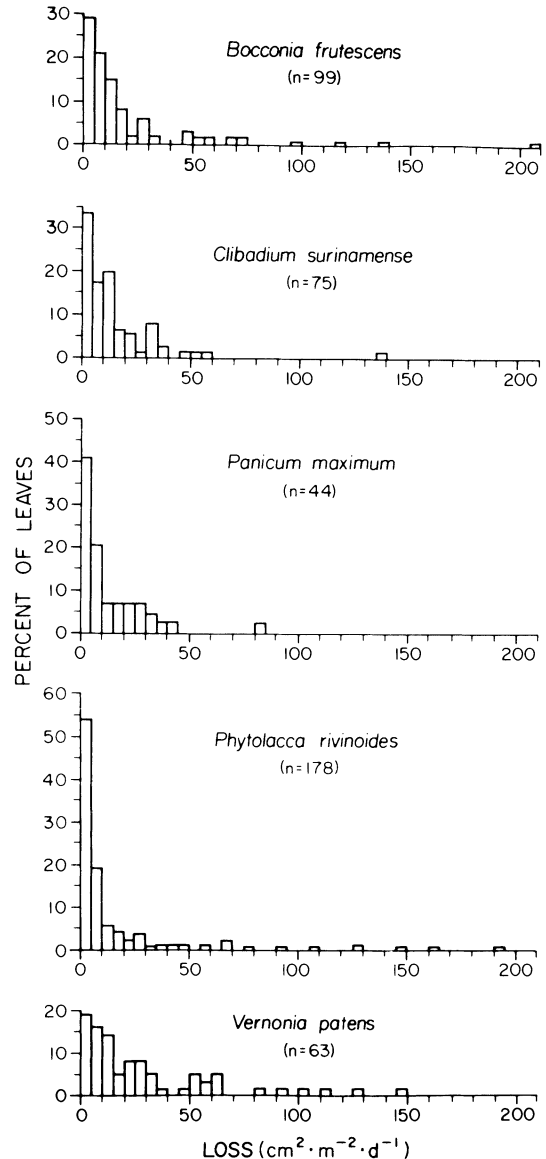


FIG. 1. Frequency distributions of leaf loss to herbivores for five common early successional species, based on samples of n leaves.

sumption had to be <4%, since unsampled species accounted for <20% of ecosystem LAI. The estimate of herbivory used by Blanton and Ewel (1985) for the mature cassava monoculture (obtained by monitoring activity on leaf-cutting ant trails) was used because the method we used (noncontinuous monitoring of selected plants) did not adequately sample the spatially and temporally localized pest attacks by leaf-cutting ants.

Herbivory, expressed as a fraction of available leaf tissue, varied widely among ecosystems and among sampling dates (Table 1). The amount of temporal variability in herbivory differed among the four ecosystems ($P < .01$, χ^2 test); ecosystem-level rates of leaf tissue loss to herbivores were nearly constant in the more

TABLE 3. Herbivory rates for species sampled in two or more ecosystems.

Species	Ecosystem	Year	No. of leaves	Leaf loss per unit area of available leaf material (cm ² ·m ⁻² ·d ⁻¹)†	
				$\bar{X} \pm SE$	Median
<i>Acalypha macrostachya</i> Jacq.	Succession	4	20	1.5 ± 0.6	0.6*
	Enriched	4	19	3.9 ± 1.1	2.9*
<i>Bocconia frutescens</i> L.	Succession	1	52	15.8 ± 2.4	9.8
		4	19	19.7 ± 10.5	6.0
	Enriched	1	47	27.2 ± 5.9	10.7
		4	15	41.3 ± 19.0	7.3
<i>Cestrum panamense</i> Standl.	Succession	4	20	1.6 ± 0.5	0.5
	Enriched	4	21	1.8 ± 0.6	0.7
<i>Clibadium surinamense</i> L.	Succession	1	32	14.9 ± 4.5	6.1
	Enriched	1	43	14.4 ± 2.0	10.7
<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	Succession	4	20	5.1 ± 1.4	2.2*
	Monoculture	4	180	2.1 ± 0.2	1.1*
<i>Erythrina costaricensis</i> Micheli	Enriched	1	24	14.8 ± 4.1	7.4**
	Imitation	1	22	57.5 ± 8.7	45.4**
<i>Gouania lupuloides</i> (L.) Urb.	Succession	4	24	2.5 ± 0.9	0.7
	Enriched	4	20	5.0 ± 2.0	1.8
Gramineae spp.‡	Succession	1	20	33.4 ± 2.7	6.3
	Enriched	1	18	9.4 ± 4.0	1.6
<i>Heterocondylus vitalbis</i> (DC.) King & H. Robinson	Succession	4	22	21.0 ± 8.2	9.6
	Enriched	4	22	7.2 ± 3.8	2.5
<i>Manihot esculenta</i> Crantz	Enriched	1	17	4.0 ± 1.0	2.9**
		1	15	20.5 ± 6.6	7.1**
	Imitation	4	18	2.1 ± 0.5	1.0
		1	72	11.3 ± 3.4	1.3**
<i>Musa paradisiaca</i> L.	Enriched	1	7	2.6 ± 1.0	1.5
	Imitation	1	6	0.8 ± 0.2	0.8
<i>Panicum maximum</i> Jacq.	Succession	1	18	12.0 ± 4.4	6.0
		4	20	20.4 ± 14.1	2.4
	Enriched	1	26	14.4 ± 2.4	9.1
		4	20	6.4 ± 1.2	5.0
<i>Panicum trichoides</i> Sw.	Succession	1	19	21.4 ± 6.0	9.5**
	Enriched	1	16	3.5 ± 1.2	1.7**
<i>Phytolacca rivinoides</i> Kunth & Bouche	Succession	1	96	13.4 ± 2.7	4.1
	Enriched	1	82	16.1 ± 3.6	4.5
<i>Vernonia patens</i> H.B.K.	Succession	1	34	24.2 ± 5.0	11.2
	Enriched	1	60	51.0 ± 5.8	21.8

* $P < .05$ or ** $P < .01$ indicate significantly different medians (Kruskal-Wallis test) for each species and year.

† Year 1 losses (except for monocultures) are pooled over three sampling intervals (6, 10, and 15 mo); year 4 losses are from one sampling interval (47 mo).

‡ Includes several grass species indistinguishable by vegetative parts.

complex systems, while rates in the less complex systems fluctuated widely over time (Fig. 3). Both the lowest and the highest rates of herbivory occurred in the monoculture (0.02%/d in *C. alliodora*; 1.03%/d in 2-mo-old cassava). Herbivory was also low in the maize monoculture (0.06%/d), perhaps because the study plots had not been cultivated for many years and were relatively isolated from agricultural fields. Although leaf loss to above-ground herbivores was low in the maize, root herbivory was extensive, but not measured.

Because of high variability among sampling periods, herbivory rates (per unit leaf area) were not significantly different. However, the successional vegetation and enriched successional vegetation tended to have lower percent losses than the imitation treatment or the monoculture; all rates in the successional and en-

riched successional plots were <0.25%/d, while five of eight rates measured in the imitation and monoculture were >0.25%/d.

Leaf biomass losses to herbivores (mean rates per unit ground area, averaged over all sampling intervals) were similar in the four ecosystems (Table 1). Between-sample variance in herbivory rate differed among ecosystems ($P < .01$, χ^2 test), with highest variances in the imitation and monoculture.

DISCUSSION

The size and close proximity of our plots relative to the mobility of herbivores are important considerations in the interpretation of our results and their extrapolation to larger spatial scales (see Kareiva 1983). For example, the equal herbivory rates for most species

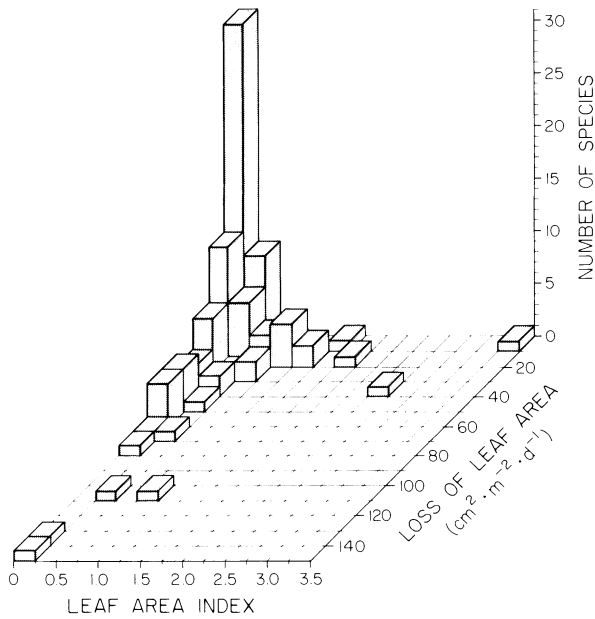


FIG. 2. Relationship between leaf loss to herbivores and species leaf area index.

in the successional vegetation and the enriched successional vegetation might be interpreted to mean that these two ecosystems were identical from the insects' perspective. However, herbivory on several species that occurred in two or more ecosystems differed significantly among ecosystems, indicating that the vegetation of our experimental plots was not perceived as a uniform resource by all of the herbivores.

Ecosystem losses to herbivores

We had originally hypothesized that species-rich ecosystems would incur less herbivory than ecosystems with fewer species. We found, however, that herbivores consumed approximately the same amount of leaf tissue per unit ground area—71.5 to 78.5 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ —regardless of floristic composition, diversity, or amount of leaf tissue available. Wint's (1983) preliminary data indicate that the same may be true of mature tropical forests.

We are aware of only one other study of tropical succession in which herbivory rates were measured for most of the dominants and summed to estimate community-level losses (Uhl and Murphy 1981). Their estimates, from 1- and 2-yr-old vegetation in Amazonian Venezuela, were substantially lower than ours: 3 to 20 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. Although the differences between their values and ours may be attributable to methodologies, it is also possible that the plants on the Amazonian site are less edible than those on our site because the two sites differ in soil fertility and local floristics.

Although herbivory per unit ground area was approximately equal in our four ecosystems, the impact of that herbivory was greatest in the ecosystems with

lower species richness and LAI: these were the systems that lost the highest proportion of their leaf area. This dilution effect has been demonstrated in numerous studies of insect abundance (see review by Kareiva 1983). The key question for agroecosystem design is whether results like ours are caused by abundance of leaf area, species richness, or both. Because LAI and species richness varied together in our study (as they often do in both natural and managed communities), it was not possible to separate the effects of these two factors on herbivory.

In one of the few experiments designed to separate LAI effects from those of diversity, Bach (1980a) found that lower pest abundance in polycultures than in monocultures was a function of plant diversity rather than plant density, but that plant density was important within polycultures. Her findings, coupled with our observations in extremely diverse ecosystems, lead us to conclude that herbivory per unit leaf tissue area might be reduced by increasing either LAI or species richness. Imitating the structural complexity of natural ecosystems may be one way to maintain high leaf area index in an agroecosystem.

Temporal fluctuations

The high temporal variability in leaf loss that we observed for many species did not carry over to total rates of leaf loss in the diverse systems. In the diverse systems we studied, some species incurred high levels of damage at times when other species received little damage. The net result of coupling many low rates of herbivory with many high rates was increased constancy of herbivory for the ecosystem as a whole. Thus what may appear to be diversity-mediated reduction of variability is actually the result of aggregating the herbivory rates of many species and is not a function

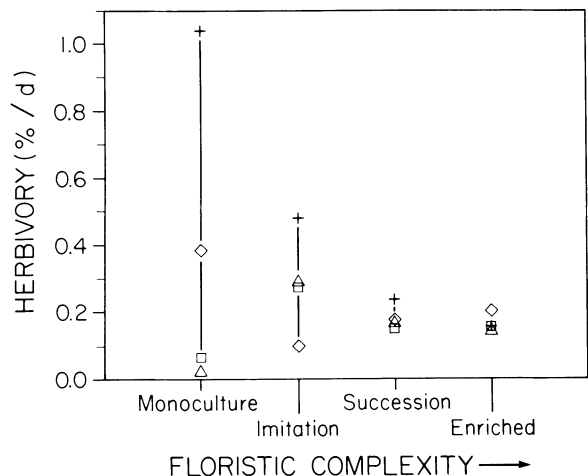


FIG. 3. Total community-wide leaf loss rates in monocultures, imitation of successional vegetation, unmanipulated successional vegetation, and enriched successional vegetation. Sampling intervals 1 (\square), 2 (+), 3 (\diamond), and 4 (\triangle) correspond to vegetation ages given in Table 1.

of the internal spatial arrangement of the community. A group of monocultures of different species, considered as a unit, would probably exhibit a similar reduction in overall temporal variability. Reduced variability in herbivory in species-rich systems is an issue of scale; it occurs regardless of the degree of patchiness in spatial distribution of species.

If all 200-plus species in one of our diverse ecosystems were subjected to high rates of herbivory in one time interval and low rates in another, then the total leaf loss in that system would not be any more constant than that of the monocultures. However, given the immense biological complexity of plant-herbivore interactions, such a sequence of events would be extremely unlikely. We suggest, therefore, that species-rich ecosystems can be expected to have relatively constant, and therefore predictable, rates of herbivory.

The idea that instability at one level of organization in an ecological system may lead to stability at another level has been proposed on theoretical grounds (Allen et al. 1984) and has been supported empirically (McNaughton 1977, Chapin and Shaver 1985). Our data lend further support to this concept. The composite effect of a highly variable population-level process (herbivory on each plant species) was a relatively constant ecosystem-level process (energy flow from plants to herbivores).

Herbivory and species' leaf area

Our observed herbivory rates of individual plant species ranged over at least one order of magnitude; wide ranges of herbivory have been reported for other tropical species (Benedict 1976, Coley 1980, 1983).

The herbivory rate on a particular species could not be predicted by its leaf area. However, very abundant species often received low to moderate levels of damage, while some uncommon species accounted for a disproportionately large fraction of total leaf loss. Elevated rates of herbivory on the less common species may occur because of high population densities—even outbreaks—of one or a few feeding specialists. Alternatively, high rates of herbivory may indicate that the target species are highly palatable to generalist herbivores (i.e., that they have poorly defended, nutritious foliage). If so, then such species may divert herbivores from less palatable species in the same ecosystem (Atsatt and O'Dowd 1976). This would help explain the uniform rates of ecosystem-level herbivory we observed. It may be useful in some cases to incorporate such palatable species into agroecosystems as a mechanism to divert herbivores from crops (Perrin 1980, Cromartie 1981).

Associational susceptibility

Many of the species we studied did not incur less herbivory in floristically complex than in simpler ecosystems. Our data suggest that the degree of herbivory on any species is influenced not by the absolute com-

plexity of the ecosystem, but by the relative herbivory rates on the other species in the system. Furthermore, the influence of associated species may be positive or negative. Just as association with other species may confer some resistance to herbivore attack (Tahvanainen and Root 1972), we propose that a lightly attacked species surrounded by heavily consumed species may experience associational susceptibility to herbivores.

The ecosystems we studied include some species that illustrate this concept of associational susceptibility. Two species, *E. costaricensis* and *Ma. esculenta*, incurred significantly higher levels of damage in the imitation of succession than in the enriched successional community. The plants surrounding an individual *E. costaricensis* or *Ma. esculenta* in the imitation had higher average herbivory rates than did those surrounding an individual in the enriched succession. The same pattern occurred with *C. alliodora*, which had a higher herbivory rate in the successional stand than in the monoculture. Similar results have been reported by others. Bach (1980b) found more beetles on corn when it was grown in a polyculture with cucumbers (a heavily consumed species) than when it was grown in monoculture, and Risch (1981) observed that numbers of beetles were higher in polycultures containing all host species than in polycultures containing at least one nonhost species.

A single species can experience either associational resistance or associational susceptibility, depending on its palatability relative to that of the species with which it is associated. This idea can be illustrated using data derived from cassava, the one species we (and Blanton and Ewel 1985) monitored in three different ecosystems.

Cassava was less heavily attacked in the enriched successional vegetation than in monoculture (0.04%/d compared to 0.11%/d). There are several possible mechanisms (not distinguishable with our data) that might explain how a species such as cassava might benefit if grown in association with other species. These include reduced apparency (Feeny 1976), diversion of herbivores to more palatable species (Atsatt and O'Dowd 1976), and maintenance of predators (Root 1973).

If, however, that same species is grown in an ecosystem in which it is surrounded by species that are even more palatable than it is, it is likely to fall victim to the high populations of polyphagous herbivores that can build up under such favorable circumstances. This may have been the case with cassava in the imitation treatment, where it was most heavily attacked, losing leaf area at a rate of 0.20%/d.

One agricultural implication of these relationships is that increasing the number of crops within a field does not necessarily reduce herbivory on a particular plant species. Herbivory on a single crop may increase, decrease, or remain the same with diversification, as

Risch et al. (1983) showed in a summary of 150 studies of herbivory in monocultures and polycultures. The species composition of the agroecosystem is a key plant-related factor affecting herbivory, and selective diversity is needed to ensure that crops are provided with associational resistance rather than associational susceptibility.

ACKNOWLEDGMENTS

This research was supported by National Science Foundation grants DEB 78-10721, DEB 80-11136, and BSR 85-06373, and by a Research Initiation and Support (RIAS) grant awarded by the Organization for Tropical Studies. The work was part of a joint research project of the University of Florida and the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE). We thank M. Artavia, C. Berish, C. Blanton, A. Coto, N. Price, and L. Williams for their generous help in data collection and analysis; K. Bro, D. Greene, B. Pace, and M. Kelly for assistance with computer-related tasks; G. Fuller, C. Helmholtz, and L. Taylor for illustrations; C. Wall for wordprocessing; T. Allen, M. Rausher, and F. Slansky for useful comments on the manuscript. This paper is University of Florida Agricultural Experiment Station Journal Series No. 6926.

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