Responses to defoliation
of species-rich and monospecific tropical plant communities

B.J. Brown* and J.J. Ewel
Department of Botany, University of Florida, Gainesville, FL 32611, USA

Summary. Floristically rich and monospecific tropical plant communities both responded to partial defoliation with increases in rates of production of new leaf area. Even after 50% of the leaf area had been removed three times, the leaf area increments were still higher in defoliated plots than in controls. Mean leaf area increment after defoliation, on a leaf area per unit ground area basis, was 905 cm^2 m^{-2} d^{-1} in diverse successional vegetation and 536 cm^2 m^{-2} d^{-1} in a cassava monoculture. Although defoliation stimulated leaf area development, on a per unit ground area basis, in both the cassava monoculture and the successional vegetation, the effect was more pronounced in the successional vegetation. On a per unit leaf area basis, leaf area increments following defoliation in both the diverse successional vegetation and the monoculture were approximately five times those of controls. The diverse plant community continued to respond vigorously after repeated defoliation, while the amount of stimulation of leaf area development in the monoculture declined. Because of their ability to respond even after repeated defoliation, diverse communities may in the long term be more homeostatic with respect to leaf area than are monocultures. The enhanced responsiveness of the species-rich community was due to changes in plant species abundance and very rapid leaf area development by some species.

Key words: Defoliation – Diversity – Herbivory – Productivity – Tropical

Much is known about how individual plants respond to defoliation, but responses of whole plant communities to herbivory are less clearly understood. It has been demonstrated that herbivory can shape vegetation physiognomy and composition by altering the competitive balance among species (e.g., Rafes 1970; Harris 1973; McNaughton 1979a; Whittaker 1979; Linhart and Whelan 1980; Belsky 1986). The impacts that herbivory can have on plant species composition are illustrated by instances of successful biological control of plant pests by introduced insects (see DeBach 1974). Such herbivory-induced shifts in dominance may in turn alter aggregate processes such as primary productivity, but these impacts of herbivory have not been thoroughly investigated.

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* *Present address and address for offprint requests:* Institute for Environmental Studies and Department of Botany, University of Wisconsin-Madison, Madison, WI 53706, USA

We predicted that species-rich and species-poor plant communities would differ in their responses to defoliation. Species' responses to herbivory vary, depending on genetics, intensity and frequency of defoliation, the tissues affected, developmental stage at the time of attack, and environmental factors (McNaughton 1979b). Physiological changes induced by herbivory include mortality and reduced growth (Kulman 1971); alteration of resource partitioning (Gifford and Marshal 1973; Detling et al. 1979; Caldwell et al. 1981); increased photosynthetic rate in residual tissue (Pearson 1965; Hodgkinson et al. 1972; Detling et al. 1979; Caldwell et al. 1981; Painter and Detling 1981; Detling and Painter 1983; Nowak and Caldwell 1984; Wallace et al. 1984); changes in reproductive output (Rockwood 1973; Harris 1974; Dyer 1975; Owen and Wiegert 1976; Boscher 1979; Pinter and Kalman 1979; Bentley et al. 1980; Stephenson 1981); increased branching or tillering (Youngner 1972; Saunders 1978; Simberloff et al. 1978; Owen 1980; Belsky 1986); changes in root growth (Dunn and Engel 1971; Whittaker 1979; Richards 1984); delay of plant senescence (Chew 1974; McNaughton 1976); and decreased palatability of remaining leaf tissue (Schultz and Baldwin 1982).

In species-rich communities, response to herbivory is the aggregate of the responses of many species. Changes in the relative growth rates and abundances of co-occurring species can stabilize ecosystem processes, as has been reported for systems ranging from the tropics to the arctic (McNaughton 1977; Chapin and Shaver 1985). If such changes are important mechanisms by which ecosystem-level processes are maintained in the face of herbivore pressure, then species-rich plant communities should be more resilient after defoliation than species-poor communities.

To test this prediction we partially defoliated one species-rich and one monospecific tropical plant community. We measured rates of leaf-area recovery after defoliation in these communities, compared their relative abilities to respond to repeated defoliations, and investigated mechanisms by which plant species richness affects a community's resilience after herbivore attack.

Materials and methods

Artificial defoliations were carried out in experimental plots in the Florencia Norte Forest, near Turrialba, Costa Rica. The site is at an elevation of 650 m and, on average, receives 2.7 m of rain per annum. The second-growth forest on the site was felled in January and burned in March 1979. Plant

communities that differed in composition and species richness were then established and used for many studies, including three concerned with plants and herbivores (Ewel et al. 1982; Blanton and Ewel 1985; Brown and Ewel 1987).

Three of the six blocks on the site were utilized in this study. Each block contained four different plant communities that were randomly assigned to 16 by 16 m plots. The defoliation experiment was conducted in two of the four plant communities: (1) successional vegetation that was 13 mo old at the beginning of the study, and (2) a monoculture of cassava (*Manihot esculenta* Crantz) that was 5 mo old. In each of three plots of successional vegetation and of cassava, two 4.5 by 9.5 m subplots were established. One of the subplots, in a portion of the plot designated for herbivory studies, was partially defoliated; the other, in a portion of the plot set aside for nondestructive sampling, served as an undefoliated control.

The successional vegetation was the natural regeneration from seeds and sprouts on plots that received no postburn experimental manipulations. At the beginning of the defoliation study, the leaf area index (LAI) of the successional vegetation was 1.7. Approximately 90% of the leaf area was less than 3 m from the ground, although some leaves were growing at heights of up to 7 m. The six subplots of successional vegetation, with a total area of 256.5 m^2, contained 51 species at the beginning of the study. Thirty-two of these species were common to the control and treatment plots and accounted for 89% and 93%, respectively, of total LAI in these plots.

The cassava monoculture, grown from stem cuttings planted in November 1979 at a spacing of 1 m by 1 m, was weeded regularly. The cassava was similar in height and LAI to the successional vegetation at the beginning of the study: it was about 3 m tall and its LAI was 1.7.

Three partial defoliations were carried out at 4 wk intervals, beginning in April 1980. At each defoliation, approximately 50% of the leaf area in each plot was removed by hand. Entire leaves were removed by excising the petioles of alternate leaves along each stem. Harvested leaves were weighed, subsampled for dry weight determination, and returned to the plots. The high target-level of defoliation (50%) and short regrowth period (4 wk) were chosen to simulate extreme herbivore pressure. Based on LAI measurements immediately before and after each defoliation, the amount of leaf area removed was slightly greater than 50% for the first defoliation (62% and 65% in the successional vegetation and the cassava monoculture, respectively) and slightly less than 50% for the second defoliation (43% and 49%) and the third defoliation (46% and 47%).

The rate of recovery of leaf area, measured as the increment in LAI after defoliation, was used to compare the responses of the two plant communities to defoliation. We used a method described by Ewel et al. (1982) to measure LAI. For each measurement we lowered a plumb-bob vertically from the top of the canopy to the ground, then counted interceptions of leaf and string. Interceptions were recorded by species and by height above the ground in intervals of 25 cm.

The vertical plumb-bob method yields an accurate estimate of LAI only when all foliage is horizontal, and the error increases as a function of foliage angle (Warren Wilson 1960). To estimate the degree to which our measurement technique underestimated leaf area, we determined the specific leaf area of all important species in each plot

and used these data to convert the biomass of foliage removed to leaf area. In the cassava monoculture, the mean ($n=9$) ratio of our plumb-bob estimate of LAI to our mass-derived estimate was 0.88; in the successional vegetation, which included species that displayed their foliage at many angles, the mean ($n=9$) ratio was 0.54.

There are two mitigating factors that we feel justify the use of plumb-bob-derived estimates of LAI in our study. First, petioles were included in the leaf biomass determinations. The relatively high mass per unit area of petioles would lead to an overestimate of mass-derived LAI. It is likely, therefore, that our two estimates do not differ as widely as the ratios between the two indicate. Second, we apparently underestimated the LAI of the successional vegetation to a greater degree than that of the cassava. Therefore, differences in response to defoliation would be conservatively biased in favor of the monoculture.

Leaf area measurements were made in the defoliated and control plots immediately before and after each of the three defoliations, at the midpoint of each regrowth period (2 to 3 wk after defoliation), and approximately 4 wk after the last defoliation. On each sampling date we made 75 LAI measurements per plot (five from each of 15 regularly spaced locations) and used the mean value as an estimate of LAI for the plot. Leaf area increments for each plot were calculated by subtracting LAI immediately after each defoliation from LAI immediately before the next defoliation. The values were then converted to mean daily increments for each time interval.

The experimental design was a split plot in time and space with three replications. Analysis of variance was employed to determine the effects of plant community (cassava monoculture or diverse successional vegetation), treatment (defoliated or control), and time (first, second or third defoliation) on leaf area increment. Analyses were performed on leaf area increment data expressed both on a per unit ground area basis and on a per unit leaf area basis.

To determine whether changes occurred in biomass allocation after defoliation, above- and below-ground biomasses of cassava were estimated when the edible tubers were harvested (at age 10 mo, approximately 3 mo after the third defoliation). Above-ground biomass was estimated from the harvest of eight randomly selected individuals from each of the three defoliated plots and from each of six non-defoliated plots (the three plots used in this study, plus three additional plots of the same size that were a part of the larger ecosystem study). The harvested vegetation was weighed in the field, then subsamples were dried to constant mass at 70° C to obtain fresh- to dry-mass conversions. Fresh mass of tubers was estimated from the harvest of all plants in the three defoliated plots and in the six non-defoliated plots.

Results

Leaf area development

Development of new leaf area was rapid after each defoliation, both in the successional vegetation and in the cassava monoculture (Fig. 1). Analysis of variance tests, based on data from three replications of each treatment, showed that leaf area increment (both on a per unit ground area basis and on a per unit leaf area basis) was significantly greater
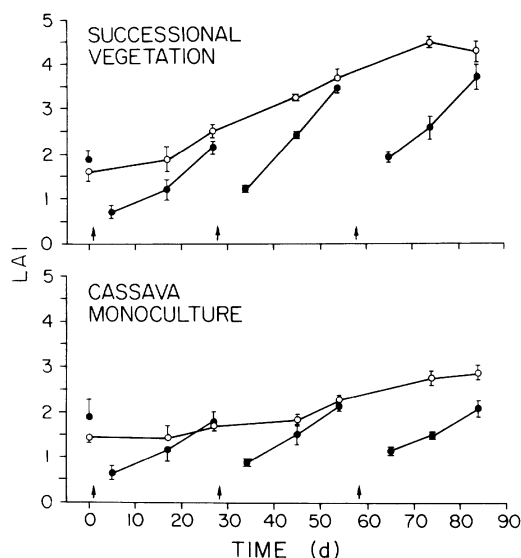
Fig. 1. Leaf area index in defoliated plots (closed circles) and in non-defoliated plots (open circles). Each point ($\bar{x}\pm$SE) is based on LAI values from three replicate plots. Arrows show when each partial defoliation occurred

significant community X treatment interaction in the analysis of variance with data expressed on a per unit ground area basis ($P<0.05$). On a per unit leaf area basis, the magnitude of the stimulatory effect of defoliation on rate of leaf area development was not significantly different in the diverse successional vegetation and in the monoculture (community X treatment interaction not significant). On the average, defoliation stimulated leaf area development per unit leaf area by a factor of five.

The timing of the stimulatory responses of the diverse successional vegetation and the monoculture differed. In the per unit ground area analysis, the significant community X time X treatment interaction ($P<0.01$) indicates that the two systems responded differently to repeated defoliations. In the cassava monoculture, leaf area increment was more than six times that in non-defoliated plots after the first defoliation, but dropped to less than three times that of controls after the second and third defoliations (Table 1). The trend was the opposite in the species-rich successional community, where the rate of leaf area development increased with successive defoliations, until leaf area increment was five times that of controls after the third defoliation. On a per unit leaf area basis, the timing of responses of the successional vegetation and the monoculture were not significantly different at the 0.05 level, but the general trend was the same: the response of the diverse successional vegetation increased after repeated defoliations, while that of the cassava monoculture declined (Table 1).

in defoliated plots than in plots that were not defoliated ($P<0.01$): defoliation stimulated leaf area development in both the cassava monoculture and the successional vegetation.

Mean leaf area increment in the defoliated successional vegetation, on a per unit ground area basis over the 3 mo defoliation period, was 905 cm^2 m^{-2} d^{-1}, compared to 321 cm^2 m^{-2} d^{-1} in control plots. On a per unit leaf area basis, leaf area increments were 819 and 152 cm^2 m^{-2} d^{-1}, respectively, in defoliated and control plots of successional vegetation. Similarly, defoliated cassava had a greater leaf area increment than did non-defoliated cassava on a per unit ground area basis (536 cm^2 m^{-2} d^{-1} and 165 cm^2 m^{-1} d^{-1}, respectively) and on a per unit leaf area basis (645 and 92 cm^2 m^{-2} d^{-1}, respectively).

Although defoliation stimulated the rate of leaf area development in both the cassava monoculture and the successional vegetation, the effect was more pronounced in the successional vegetation. This result is indicated by the

Species responses

For nine species, or groups of species, in the diverse community, mean leaf area increment was significantly greater in defoliated than in control plots (Table 2). For five of these nine, the net change in leaf area did not differ in defoliated and non-defoliated plots; these species regained the leaf area lost to defoliation and in addition produced as much new leaf area as did the same species in control plots. Other species did not recover LAI to the level of non-defoliated plots, even though their rates of leaf area development were stimulated significantly by defoliation. The cassava growing in the monoculture had less leaf area at the end of the study in defoliated than in non-defoliated plots, even though defoliation stimulated its rate of leaf area development significantly. None of the species moni-

Table 1. Leaf area increments in defoliated and non-defoliated plots. Time periods 1, 2, and 3 are the 1-mo regrowth periods following defoliations 1, 2, and 3. Each leaf area increment is the mean of values from three replicate plots ($\pm$SE)

Community type	Time period	Leaf area increment per unit ground area (cm^2 m^{-2} d^{-1})			Leaf area increment per unit leaf area[a] (cm^2 m^{-2} d^{-1})		
		Defoliated (D)	Not Defoliated (ND)	D:ND	Defoliated (D)	Not Defoliated (ND)	D:ND
Cassava monoculture	1	491 $\pm$ 58	79 $\pm$ 46	6.22	784 $\pm$ 133	59 $\pm$ 36	13.3
	2	618 $\pm$ 12	220 $\pm$ 37	2.81	706 $\pm$ 47	131 $\pm$ 26	5.4
	3	498 $\pm$ 96	196 $\pm$ 23	2.55	445 $\pm$ 93	85 $\pm$ 8	5.2
Successional vegetation	1	651 $\pm$ 17	339 $\pm$ 29	1.92	1026 $\pm$ 208	226 $\pm$ 48	4.5
	2	1125 $\pm$ 38	435 $\pm$ 79	2.59	927 $\pm$ 39	175 $\pm$ 34	5.3
	3	940 $\pm$ 159	188 $\pm$ 130	5.00	503 $\pm$ 91	55 $\pm$ 36	9.2

[a] Calculated as: [(change in LAI during interval)/(LAI at beginning of interval)] $\times$ (10,000/number of days in interval)

Table 2. Leaf area increments and relative dominance of common species in defoliated and non-defoliated plots. Leaf area increment is the mean of three 1-mo intervals

Vegetation type	Species	Leaf area increment[a] per unit leaf area ($cm^2\ m^{-2}\ d^{-1}$)		Net change in leaf area per unit ground area (cm^2/m^2)[b]		Percent of total LAI[g]			
						Defoliated		Not defoliated	
		De-foliated	Not De-foliated	De-foliated[e]	Not De-foliated[f]	Initial	Final	Initial	Final
Successional	*Bocconia frutescens* L.	1435***	332	+3423	+ 3777	7.5 (3)	13.4 (2)	4.8 (6)	10.7 (2)
	Clibadium surinamense L.	756**	159	+5911	+ 5911	20.2 (1)	26.7 (1)	19.0 (1)	21.0 (1)
	Cordia inermis (Mill.) Johnst.	448*	178	+ 755*	+ 2088	2.7 (9)	3.5 (7)	2.2 (9)	5.8 (6)
	Cyperaceae spp.[c]	776*	366	− 89	+ 489	1.2 (13)	0.4 (12)	1.4 (10.5)	1.7 (13)
	Frantzia pittieri (Cogn.) Pittier	−228	26	− 311***	+ 2045	1.9 (10)	0.1 (13)	6.4 (5)	7.2 (4)
	Gouania lupuloides (L.) Urb.	688	396	+ 534	+ 755	1.7 (11.5)	2.4 (9.5)	1.1 (12.5)	2.2 (11)
	Gramineae spp.[d]	452	100	+ 444	+ 2000	5.8 (5)	4.2 (5)	11.5 (2)	9.0 (3)
	Ipomoea neei (Spreng.) O'Don.	921**	342	+ 623**	+ 1466	2.9 (8)	3.2 (8)	1.1 (12.5)	3.9 (7)
	Ipomoea tiliacea (Willd.) Choisy	1408	106	+1111	+ 756	1.7 (11.5)	4.0 (6)	1.4 (10.5)	2.3 (10)
	Lasiacis procerrima (Hack.) Hitchc.	487*	85	− 134**	+ 1156	12.9 (2)	6.2 (4)	9.0 (4)	6.1 (5)
	Panicum trichoides Sw.	532***	148	− 45*	+ 667	4.8 (7)	2.4 (9.5)	2.8 (8)	2.6 (9)
	Phytolacca rivinoides Kunth & Bouche	435	19	− 755**	− 89	5.3 (6)	0.6 (11)	10.6 (3)	3.8 (8)
	Solanum umbellatum Mill.	518**	65	+1156	+ 267	6.1 (4)	6.3 (3)	3.9 (7)	2.1 (12)
	Other species combined (n = 56)	911**	147	+5778	+ 5289	25.3	26.6	24.8	21.6
Monoculture	*Manihot esculenta* Crantz.	628**	9	+1689***	+13911	100.0	100.0	100.0	100.0

[a] Differences between defoliated and non-defoliated treatments based on one-tailed paired t-tests (asterisks indicate probability levels)
[b] Differences between defoliated and non-defoliated treatments based on chi-square tests (asterisks indicate probability levels)
[c] Includes several sedge species indistinguishable by vegetative parts
[d] Includes several grass species indistinguishable by vegetative parts
[e] Calculated as total leaf area produced after defoliations minus total leaf area removed by defoliations
[f] Calculated as final leaf area minus initial leaf area
[g] Based on vertical line intercept measurements. Numbers in parentheses are relative dominance rankings of thirteen common species. Initial values are pre-defoliation; final values are at end of regrowth period following third defoliation

* $P<0.10$ ** $P<0.05$ *** $P<0.01$

tored had significantly lower rates of leaf area development in defoliated than in control plots.

Vegetation structure

The vertical distribution of leaves in the canopy changed after defoliation in both the species-rich community and the monoculture (Fig. 2). Leaf tissue was removed in equal proportions from all heights in the canopy at each defoliation. However, leaf regrowth after defoliation was not distributed evenly throughout the canopy. In species-rich vegetation the amount of leaf area near the ground increased after successive defoliations, while most of the leaf regrowth in the cassava occurred at the tops of the plants.

To determine whether the vegetation structural changes were attributable to the defoliation treatment, the changes in vertical distribution of leaf area in defoliated vegetation in the diverse community were compared to those in non-defoliated vegetation using chi-square tests. The vertical distribution of leaf area produced during the three month study differed significantly between defoliated and non-defoliated successional vegetation ($P<0.01$). The defoliated plots gained proportionally more leaf area than did control plots in the interval from 0 to 1 m and relatively less leaf area at greater heights. The most striking difference between the defoliated and non-defoliated successional vegetation was the larger increase in LAI at ground level (0 to 0.25 m) in the defoliated plots (Fig. 2 A). This probably occurred
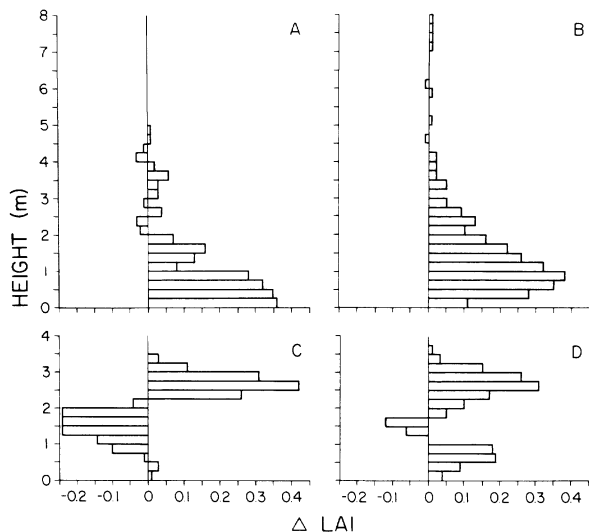
Fig. 2A–D. Net changes in LAI during the 3 mo study period in defoliated (**A**) and non-defoliated (**B**) successional vegetation and in defoliated (**C**) and non-defoliated (**D**) cassava monoculture. Net change is final LAI minus initial (pre-defoliation) LAI, based on pooled data from three replications

because defoliation opened the canopy and allowed more light to reach the ground, thus stimulating seed germination, facilitating the survival of seedlings that would have died in the shade, and enhancing the growth of understory plants.

In the cassava, which continuously adds new foliage at its apices and sheds its shaded leaves, most new leaf area in both defoliated and control plots was concentrated at the top of the canopy. It appears that some of the leaves removed by defoliation would have been lost by the plants even without defoliation. In both defoliated and non-defoliated cassava, the leaves lost were replaced by leaves at the tips of growing shoots higher in the plant canopy.

Although most new leaf area in cassava occurred at the top of the canopy, differences in the vertical distribution of new leaf area in defoliated and non-defoliated cassava plots were statistically significant ($P < 0.01$). The major difference between defoliated and control cassava was a substantial increase in leaf area in the 0 to 1 m interval in only the control plots (Fig. 2D). Some cassava plants in the control plots, especially those growing on slopes, lodged. The woody stems, unable to support the plants' crowns, were bent to the ground by heavy rains and wind gusts. Lodged plants either uprooted or suffered stem damage at the base, so resprouting occurred near the ground. In contrast, reduced leaf area made the defoliated cassava less vulnerable to damage from wind and rain, so they incurred very little lodging, even on moderate slopes.

Height growth was depressed by defoliation. The height of both the non-defoliated cassava and species-rich communities increased 1 m during the 3-mo study, while the defoliated cassava grew 0.75 m and the defoliated successional vegetation grew 0.50 m during the same period.

Species composition

The LAI measurements were used to rank plant species in the species-rich vegetation by relative dominance and to assess changes in species composition. Both the defo-

Table 3. Changes in species richness over a 3 mo period in defoliated and non-defoliated successional plant communities. Species richness is the number of species intersected by a total of 225 LAI measurements in three 42.75 square meter plots

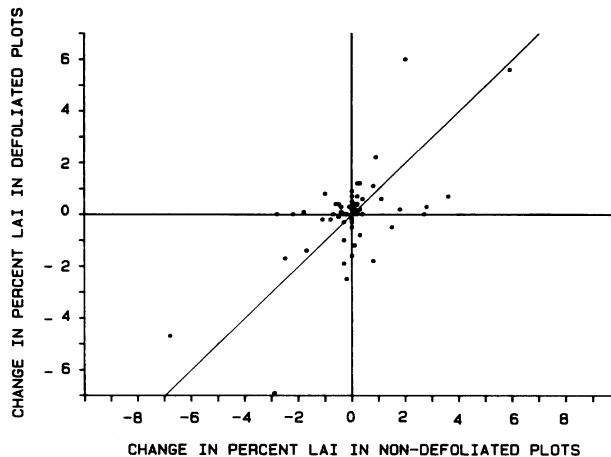|	De-foliated	Non-De-foliated	Common to both
Initial species richness	40	43	32
Final species richness	46	51	39
Number of species gained	15	18	9
Number of species lost	9	10	4

Fig. 3. Changes in per cent LAI of species in defoliated and non-defoliated successional vegetation during the 3 mo study period. Each point is one species. Values are based on pooled data from three replications

liated and non-defoliated species-rich communities gained several new species and lost several species during the 3 mo study period, but some of the species involved were different in plots subjected to different treatments (Table 3). The net result of gains and losses was an increase in species richness in both defoliated and non-defoliated plots. Although species richness increased, both the defoliated and the non-defoliated communities were more strongly dominated by a few very common species at the end of the study than at the beginning (Table 2). Two species, *Bocconia frutescens* and *Clibadium surinamense*, together accounted for a substantial fraction of total LAI at the end of the study both in defoliated plots (40.1%) and in control plots (31.7%).

Several species in the diverse communities showed significantly different patterns of leaf area development in defoliated and non-defoliated plots (Table 2). The LAI of three species increased significantly in the control plots and decreased in defoliated plots: *Panicum trichoides, Lasiacis procerrima,* and *Frantzia pittieri.* The LAI of *Phytolacca rivinoides* decreased significantly more in defoliated than in control plots, and the LAI of *Ipomoea neei* and *Cordia inermis* increased significantly less in defoliated than in control plots.

The net result of different species' responses to defoliation was a change in relative species dominance (measured as per cent of total LAI) in defoliated plots. To evaluate the impact of defoliation on species composition, we compared the changes in species dominance in defoliated and in control plots (Fig. 3). Relative dominance (per cent LAI)

Table 4. Cassava biomass at harvest (age 10 mo) in defoliated plots ($n = 3$) and non-defoliated plots ($n = 6$). Values are $\bar{x} \pm$ SE. For all biomass compartments, F tests of treatment differences were not significant

Cassava component	Mass (g/m^2)[a]	
	Not Defoliated	Defoliated
Leaves	89.3 ± 27.3	97.2 ± 67.1
Stems	624.9 ± 128.2	500.6 ± 121.4
Standing dead material	23.5 ± 11.7	15.6 ± 9.0
Tubers	1088.3 ± 264.2	1219.6 ± 137.9

[a] Dry mass reported for above-ground components; fresh mass reported for tubers

of 33 species increased (or did not change) in both control plots and defoliated plots (upper right quadrat of Fig. 3); relative dominance of 12 species decreased in both the control and defoliated plots (lower left quadrat of Fig. 3). For example, the per cent LAI of *Bocconia frutescens* increased substantially during the 3 mo period (5.9% increase in both defoliated and control plots), and the per cent LAI of *Phytolacca rivinoides* decreased (4.7% and 6.8% decreases in defoliated and control plots, respectively).

Relative dominance of ten species decreased in defoliated plots, but increased (or did not change) in control plots (lower right quadrat of Fig. 3). For 14 species, relative dominance increased (or did not change) in defoliated plots, while it decreased in control plots during the same period (upper left quadrat of Fig. 3).

The differences in species compositional changes between defoliated and non-defoliated plots are indicated in Fig. 3 by deviations from the diagonal line. Points above the diagonal represent species that increased more (or decreased less) in relative dominance in defoliated plots than in non-defoliated plots. For example, *Clibadium surinamense* increased from 20% to 27% of total LAI in defoliated plots, but only from 19% to 21% in control plots. Similarly, points below the diagonal line represent species that responded negatively to defoliation. For example, *Lasiacis procerrima* decreased 7% (from 13% to 6% of total LAI) in defoliated plots, but only 3% (from 9% to 6%) in control plots. The changes in relative dominance rankings for the 13 most common species in the successional communities are shown in Table 2.

Cassava yields

We hypothesized that defoliated plants would use a greater proportion of available energy for production of new leaf area than would plants that were not defoliated, and that this reallocation of resources following leaf removal would result in a reduction in biomass production of other plant organs. The data on cassava did not support this hypothesis. There were no significant differences in mean biomass of cassava leaves, stems, standing dead material or tubers in defoliated and control plots (Table 4).

Discussion

A plant community's response to herbivores may be evaluated in terms of its resistance to herbivore attack or its resilience, i.e., its ability to regain functional characteristics rapidly after large losses to herbivores. In another study on the same site, we measured herbivory rates in the floristically complex and simple communities (Brown and Ewel 1987). Although one herbivore showed a strong preference for plants grown in monoculture (Blanton and Ewel 1985), we found that in general the complex and simple communities were equally resistant to herbivore attack. If diverse communities incur as much damage from herbivores as do simple ones, why then do agricultural polycultures often appear to offer advantages over monocultures with respect to herbivory? The results of this study indicate that they may be more resilient to repeated loss of foliage than are monocultures. High rates of leaf area development may result from the ability of species mixtures to use resources more fully than monocultures (Trenbath 1974; Harper 1977).

Herbivory stimulated leaf area development in both simple and diverse plant communities. Even after three consecutive defoliations, which resulted in the removal of more than five times the amount of foliage than is normally lost to herbivores (Brown and Ewel 1987), the rate of leaf area development was greater in defoliated plots than in non-defoliated plots. Increased growth following defoliation has been reported for many plant species (e.g., see Pearson 1965; Hodgkinson et al. 1972; Gifford and Marshal 1973; Detling et al. 1979; Painter and Detling 1981; McNaughton et al. 1983; Solomon 1983; Wallace et al. 1985). Our results indicate that a stimulatory effect occurs at the plant community level as well. Similar responses of whole plant communities to grazing have been well-documented for African grasslands (McNaughton 1985).

The abilities of the diverse successional vegetation and the monoculture to replace lost leaf area after herbivory may be compared in absolute or in relative terms. Proportional increases in leaf area, relative to the rates of leaf area development of controls, were similar in the defoliated diverse community and the defoliated monoculture. Nevertheless, because the rate of leaf area development was generally higher in the intact diverse vegetation than in the intact monoculture, the total amount of new leaf area stimulated by herbivory was greater in the diverse vegetation.

Defoliation changed the species composition of our diverse system by favoring those species best able to respond. The data indicate that a change in the competitive balance among co-occurring species was an important determinant of this community's response to herbivory. Some species recovered completely, i.e., they regained the leaf area lost to defoliation and also produced additional leaf area equal to that produced by control plants during the same period. Other species did not recover completely, although leaf area development was more rapid in defoliated plants than in control plants. No species produced leaf area at a lower rate in the defoliated plots than in control plots. These results suggest that the resilience of the diverse community was due to rapid regrowth of some of its many species and not to any emergent property of the whole system.

A key difference between the diverse community and the monoculture was in the timing of their responses to herbivory. Maximum stimulation of leaf area development occurred after repeated defoliation of the diverse system, while the amount of stimulation declined after repeated defoliation of the monoculture. If such trends continue over extended periods of exposure to herbivores, we may expect

that, in the long term, diverse communities will be more homeostatic with respect to leaf area than are monocultures.

Continued response of the diverse community, even after repeated defoliation, occurred in part because many species were present at the site and because many complements of species could utilize equally well the available space and resources. Such stabilizing responses by co-occurring species are consistent with other studies, both empirical (McNaughton 1977; Chapin and Shaver 1985) and theoretical (Holling 1973). In the monoculture, the fluctuations in species composition that contributed to the resilience of the diverse system were precluded.

The high resilience of diverse communities after repeated defoliation has important implications for the design of agricultural ecosystems. Even if diverse cropping systems and monocultures on the average incur equal amounts of damage from herbivores, the ability of diverse systems to respond to repeated defoliations may make them more sustainable in the long term. If one crop species succumbs to pest attack, others can compensate through increased growth and the community can continue to take the fullest possible advantage of the site's resources. In agroecosystems the pool of available species is controlled through management, but the principle is the same as in the diverse communities we studied: compensatory growth by co-occurring species may result in the maintenance of energy flow through the system. Because minimizing risk is often as important to a farmer as maximizing yield (Barlett 1980), incorporating resilience into agroecosystems by crop diversification is a critical design consideration.

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