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Leaf survival in relation to herbivory in two tropical pioneer species

Juan Núñez-Farfán and Rodolfo Dirzo

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Survival, longevity, and herbivory patterns of two leaf cohorts of two pioneer tree species, *Cecropia obtusifolia* and *Heliocarpus appendiculatus*, growing as seedlings in natural canopy gaps, were studied in the rainforest of Los Tuxtlas, Mexico. The leaf cohorts of *C. obtusifolia* did not differ in longevity and mortality pattern, and the leaf populations experienced low levels of herbivory. Herbivory was higher in *H. appendiculatus* than in *C. obtusifolia*; in *H. appendiculatus*, also, the percentage of leaf area lost per day (herbivory rate) was higher for young than mature leaves. The rates of herbivory in *C. obtusifolia* at Los Tuxtlas are lower than those reported for the same species in Panama; while the herbivory rates of *H. appendiculatus* are the highest reported for any pioneer neotropical species. The two leaf cohorts of *H. appendiculatus* differed in their longevity since an episode of intense and sudden mortality of leaves occurred when herbivory approached 70% of leaf area damaged, regardless of the age of the leaves. It is suggested that the mortality pattern and longevity of leaves of seedlings and saplings of *H. appendiculatus* are determined by herbivory but this does not appear to be so in *C. obtusifolia*.

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Introduction

The total amount of carbon gained by an individual leaf in a plant can be limited by the natural longevity of the leaf and by the animals that act as predators on these plant parts (Chabot and Hicks 1982, Mooney and Gulmon 1982, Hartnett and Bazzaz 1984). Moreover, herbivores may affect leaf performance by reducing the leaf area available to capture energy, by removing nutrients and by increasing the likelihood of pathogenic disease (Dirzo 1987) or of death (Dirzo 1984, Pritchard and James 1984). Herbivory affects leaf survival, and thus leaf demography. The demographic behaviour of plant parts (e.g. leaves) could determine, to some extent, the fate of the whole plant (Bazzaz and Harper 1977, Abul-Faith and Bazzaz 1980, Dirzo 1984). Several authors have shown that, for a particular species, the potential leaf longevity (and, hence, amount of carbon gained) is a function of the habitat that the plant occupies (for example a forest gap versus a closed canopy) (see Baz-

z 1984), the type of community (Chabot and Hicks 1982, Mooney and Gulmon 1982, Shukla and Ramakrishnan 1984), and the position of the leaf within the tree (Pritchard and James 1984, Shukla and Ramakrishnan 1984). Species such as tropical gap-filling pioneers may allocate their resources to a large leaf area (see Ashton 1978) and also a high leaf turnover rate (Shukla and Ramakrishnan 1984). Herbivory clearly affects leaf attributes, but the details have been little studied (see Hartnett and Bazzaz 1984), particularly in the tropics.

It has been suggested that tropical plant species from different successional stages (and leaves of different ages) differ in their type and amount of defenses: pioneer plant species and young leaves do not seem to allocate much of their resource budget to defense and escape to herbivores, and herbivory rates are negatively correlated with the investment in defense (Coley 1986, 1988). Apart from these correlations, little work seems to have been done regarding the consequences of herbivory on leaf survival (see Dirzo 1984, Pritchard and

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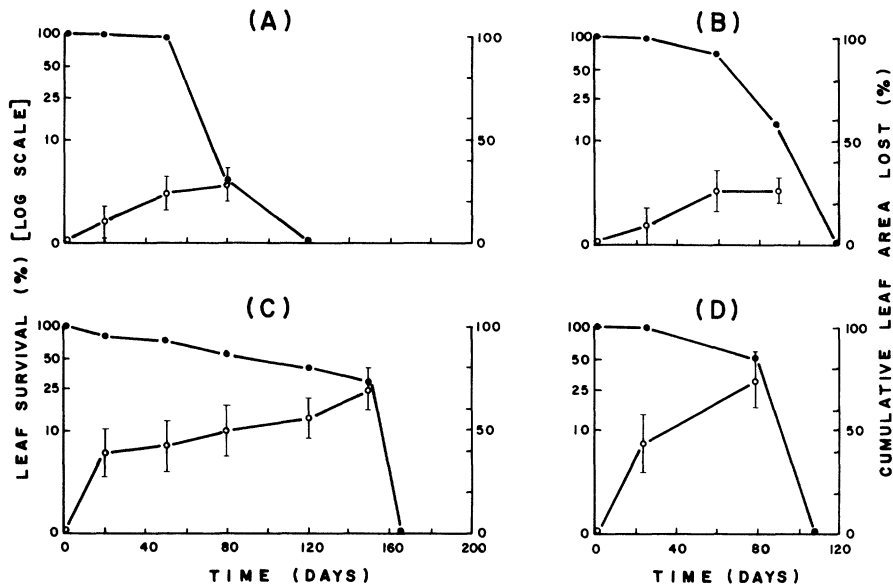


Fig. 1. Survivorship curves (●) and cumulative leaf area lost (○) of two leaf cohorts of *Cecropia obtusifolia* (A and B) and *Heliocarpus appendiculatus* (C and D). Herbivory values are $\bar{X} \pm$ SD for all surviving leaves.

James 1984, Núñez-Farfán and Dirzo 1988). In this paper we report data on longevity and survivorship of leaves, in relation to herbivory, of two pioneer tree species growing under natural conditions in the tropical rainforest of Los Tuxtlas (Veracruz, southeast Mexico). The study was specifically directed to assess the effect of herbivory on leaf survivorship in early colonizing seedlings.

Methods

In September 1982 we marked recently-sprouted plants (>5 cm in height) of two pioneer tree species, *Cecropia obtusifolia* Bertol. (Moraceae) and *Heliocarpus appendiculatus* Turcz. (Tiliaceae), established on two natural large gaps (ca. 600 m²) of recent formation (detailed information about the species and the study site are given in Núñez-Farfán and Dirzo 1988). In December 1982 we tagged, with plastic colour rings, the most recently born leaves (up to 2) of each individual plant (up to 36) of the two species. A second cohort of leaves was marked on July, 1983. Subsequently, recordings of individual leaves were made at 20-d intervals; we registered leaf survival and leaf area lost to herbivores. The herbivores which we observed feeding on these species include: for *H. appendiculatus* ten species of Lepidoptera, two orthopterans, and two hemipterans; for *C. obtusifolia* four species of Lepidoptera. Further information about these herbivores will be presented elsewhere (R. Dirzo, unpubl.). With the measurements of leaf area loss we compared the rate and level of herbivory in the population of leaves between species and, also, the relationship between herbivory and the time-course of survivorship of the population of leaves. Following the fate of the individually labelled leaves of both cohorts prevented underestimation of herbivory

due to the complete consumption of leaves (see Lowman 1984). We counted a leaf as dead when no green tissue remained on it, or when it was detached from the stem.

Results

The results of this study are shown in Fig. 1. The survivorship curves for the leaf populations of *C. obtusifolia* show that for the first cohort (Fig. 1A) (end of the rainy season 1982-beginning of the dry season 1983), maximal leaf longevity was approximately 120 d. During the first two months the mortality rate was close to zero but after that there was a sudden increase in the number of leaves that died. At the same time, the cumulative leaf area removed per leaf rose gradually to values close to 25%. The second cohort (Fig. 1B), in the rainy season of 1983, showed a similar pattern to that of the first cohort; although intense mortality started slightly earlier in the first cohort, the maximal longevity was, once more, close to 120 d. Likewise, the levels of herbivory reached maximum (cumulative) values of 25% of leaf area eaten on average. The survivorship curves for both cohorts appear to be similar and intermediate between I and II of Deevey's type survivorship curves.

The two survivorship curves of *H. appendiculatus* differed in shape both between them and also in relation to those of *C. obtusifolia*. For the first cohort (Fig. 1C) (end of the rainy season-beginning of the dry season), the maximal leaf longevity was about 165 d, while for the second cohort (Fig. 1D), in the rainy season, it was only about 90 d. The percentage of leaf area lost to herbivores by each cohort of *H. appendiculatus* was very similar and these values were higher than those of *C. obtusifolia*, approaching up to 70% of area lost, on average, for each individual leaf. In cohort one (Fig.

Tab. 1. Herbivory rates (% of leaf area lost per day) for two cohorts of leaves of *Cecropia obtusifolia* and *Heliocarpus appendiculatus* at Los Tuxtlas, Mexico.

Census	<i>C. obtusifolia</i>			<i>H. appendiculatus</i>		
	N	Mean	SE	N	Mean	SE
Cohort 1						
Dec 1982	52	0.5605	0.1117	34	1.5100	0.3071
Jan 1983	50	0.3554	0.0741	30	0.2000	0.2672
Feb	14	0.4285	0.1447	22	0.3272	0.1477
Mar		+		16	0.0246	0.0263
Apr				12	0.1805	0.1498
May					+	
Cohort 2						
Jul 1983	50	0.5000	0.1079	45	2.2833	0.3507
Aug	38	0.5092	0.1321	24	0.4875	0.1598
Sep	8	0.2500	0.2800		+	
Oct		+				

+ Only 1 or zero leaves remained.

1C) the proportion of damage rose to about 70%, but at a different rate than that of cohort two (Fig. 1D). Intense and sudden mortality of leaves of the two cohorts occurred when herbivory approached 70% regardless of the age of the leaves. Leaf life-span appeared to be determined by herbivory.

A comparison of the average leaf longevity (arithmetic mean), between the first and second cohorts of *C. obtusifolia* showed no significant differences (means = 74.82 and 67.89 d, respectively; $t = 1.118$, $P > 0.1$). For *H. appendiculatus*, however, there was a significant difference in mean leaf longevity between the cohorts: 94.5 (first) versus 53.66 (second) days ($t = 2.710$, $P < 0.01$). Leaf longevity of *C. obtusifolia* is lower than that reported for the same species in Barro Colorado, Panama (Coley 1988). The difference between species in cumulative mean leaf area lost (per leaf) was highly significant (Mann-Whitney's $U = 42$, $P < 0.002$).

With respect to intraspecific differences in herbivory as a function of leaf age (Tab. 1), in both species there was a tendency for the rate of herbivory (% of the total leaf area consumed per day) to be higher when leaves were younger. The values for young leaves of *C. obtusifolia* are lower than those for *H. appendiculatus* and for *C. obtusifolia* at Barro Colorado (Coley 1980). There was no significant difference in the mean rate of herbivory between cohorts of *C. obtusifolia* (Mann-Whitney's $U = 6.0$, $P > 0.05$). In contrast, *H. appendiculatus* displayed high herbivory rates during the first twenty days after leaf expansion, rising to more than 1.5% per day in the first cohort and more than 2% per day in the second (see Tab. 1). However the rate of herbivory for the second cohort, as a whole, was higher than that for the first one. These values are the highest reported for tropical pioneer species and are even greater than the highest reported on young leaves of some pioneer species (see Coley 1980).

Discussion

The net gain in carbon for a plant is affected by leaf longevity, favorable and unfavorable conditions (seasonality, open versus shaded sites), and by herbivores (Chabot and Hicks 1982, Mooney and Gulmon 1982). The latter reduce leaf area and carbon gain, and also increase the probability of leaf death (Pritchard and James 1984, Núñez-Farfán and Dirzo 1988). Differences in leaves of herbivory, leaf longevity and pattern of mortality were detected between leaf populations of two pioneer species established in natural gaps in the rainforest of Los Tuxtlas. Differences in these variables were also detected between cohorts of one of the two species (*H. appendiculatus*). The pattern of survivorship and the differences in longevity between cohorts in *H. appendiculatus* seem to be explained in terms of the high levels of herbivory suffered by the leaves of this species; in *C. obtusifolia*, in contrast, herbivory appears not to be such an important factor in leaf area loss (see Fig. 1). Although both species co-occur locally as gap-filling pioneers at Los Tuxtlas (Núñez-Farfán and Dirzo 1988), differences among them regarding leaf dynamics and herbivory could reflect two ways they confront the same environment. For instance, *H. appendiculatus* produces branches very early in its life (when it is about 1.2 m in height) and consequently bears numerous leaves with an area of approximately 150 cm² per leaf. In contrast, in *C. obtusifolia* the first branching occurs much later (at a height of > 5 m) and a low (up to 10) and constant number of leaves is maintained during the first two years of growth. These leaves however, are much larger (approximately 1000 cm²) than those of *H. appendiculatus* (Núñez-Farfán 1985). The net result of this is that *H. appendiculatus* has a slightly lower leaf area (for any given height) and a higher (though variable - cf. Fig. 1C,D) turnover rate of leaves that might,

at least proximally, compensate for the higher values of herbivory that this species experiences at all stages of its life-cycle.

On the basis of the present results, the predicted escape in time for young leaves (Rhoades and Cates 1976, Hartshorn 1978) does not seem to hold for these two species at Los Tuxtlas, since damage by herbivores in the early stages of the life of the leaves was greater regardless of the season. This result is in agreement with that of Coley (1980, 1983) for pioneer gap species at Barro Colorado Island, Panama, and also with those that show that short-lived leaves experience more damage by herbivores (Coley 1986, 1988; see also Southwood et al. 1986 for a different type of community).

The results presented here suggest that, through their effects on leaf survival, herbivores may affect the performance and fate of colonizing individual plants of some species in tropical forest gaps.

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