SHORT COMMUNICATION

Herbivore and plant demography: a case study in a fragment of semi-deciduous forest in Brazil

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Janzen (1970) and Connell (1971) suggested that heavy predation on juveniles that are in the proximity of adults results in density-dependent mortality amongst rain forest trees and keeps species at densities so low that high species diversity can be maintained. While there are a number of cases reported in the literature where mortality is density-dependent and higher near the parent trees (e.g. Augspurger 1983, Augspurger & Kelly 1984, Clark & Clark 1984, Silva Matos & Watkinson 1998), there are other studies based on spatial relationships that have found little evidence of density-dependence (Clark & Clark 1984 for review). The effect of herbivory depends on the plant developmental phase during which the herbivores' attack occurs. In general, an attack during early stages of plant ontogeny may have the greatest impact on plant populations (Clark & Clark 1985, 1989; Dirzo 1984, Janzen 1970). Changes in size distribution within a plant population and consequent skewness and size inequality might result from selective herbivory (Crawley 1983, Crawley & Weiner 1991, Weiner 1988).

The present study reports the interaction between caterpillars of *Antirrhea archaea* Hübner (Lepidoptera, Nymphalidae, Morphinae) and the tropical palm *Euterpe edulis* Mart. in a fragment of semi-deciduous forest in southeastern Brazil. The issues examined in particular are: (1) the pattern of herbivore attack; (2) the relationship between the plant population density and the rate

of herbivore attack; and (3) the consequences of folivory on survival and transition rates of plants in different size classes.

Euterpe edulis is a tall palm ($\leqslant 15$ m) with a single straight stem and pinnate leaves (Silva Matos 1995). It is distributed in the south, southeast and central-western regions of Brazil and also in Argentina and Paraguay (Silva Matos 1995). In the specific locality of this study *Euterpe edulis* grew in a swampy area periodically flooded in the wet season. *E. edulis* (commonly known as palmiteiro, juçara or jiçara) is intensively exploited due to the quality of the edible heart of palm that it yields, corresponding to the apical meristem of the plant together with the developing new leaves. *E. edulis* has a single apical meristem (heart of palm) whose removal results in the death of the plant.

The genus *Antirrhea* occurs from Guatemala to Amazon basin, southern Brazil and on the eastern slope of the Andes (DeVries 1987). Larvae are bright red and orange and hirsute and feed on leaves of palms. Usually they are found solely on the abaxial face of the lamina. Adults of *Antirrhea archaea* are found in deep forest shade especially in swampy areas, and are camouflaged with the under wing surface resembling litter on the ground. They usually fly slowly and close to the soil and often feed upon juice of rotting fruits attacked by fungi (DeVries 1987).

The study was carried out in a swampy area in a semi-deciduous forest, the Municipal Reserve of Santa Genebra in Campinas, São Paulo (Brazil), where the palm *Euterpe edulis* is abundant. The climate of this region has two distinct periods: the wet season, when 74% of the rainfall occurs, extends from October to March, with a mean temperature of 23 °C while the dry season extends from April to September, with a mean temperature of 17 °C. The mean annual rainfall is 1365 mm.

One hundred 5-m × 5-m plots were randomly placed within 1 ha of this swampy area. Randomness was achieved by choosing random pairs of coordinates through a scientific calculator. In one of the corners of each plot, an area of 1-m × 1-m was demarcated in which all palm seedlings were counted. Seedlings were defined as plants having the first three leaves: the first and the second are a pair of palmate leaves and the third one is intermediate in form between the palmate leaves and the mature pinnate leaves (Silva 1992). All seedlings found were tagged with a numbered label and then checked 1 y later to determine survival and the rate of transition to the next size class, i.e. plants having mature pinnate leaves in form. All individuals of *E. edulis* having more than three leaves within each 5-m × 5-m plot were also tagged and classified for the demographic analysis. A classification system was developed on the basis of number of leaves, stem diameter at soil level and reproductive capacity, which allowed the division of the population into seven classes: class 1 (all seedlings having at most three leaves), class 2 (>0–10 mm diameter), class 3 (>10–20 mm), class 4 (>20–30 mm), class 5 (>30–60 mm), class 6 (>60–120 mm) and class 7 (>120 mm, all being reproductive plants).

Herbivore attack was recorded in January 1991 when the population was censused. The number of leaves of all individuals was counted and the diameter at soil level and height of each plant were measured. All plants were checked for presence of caterpillars and/or damaged leaves. Herbivory was recorded as the number of plants having at least one leaf damaged since the density of herbivores found on a single plant was very low. Caterpillars of *A. archaea* usually eat the leaflets completely, some leaves were found having only the rachis. No other herbivore was found during the period causing the same pattern of injury to leaves of *E. edulis* as that of *A. archaea*. Analysis was thus based on the presence of injury rather than the number of caterpillars. The population was censused again in January 1992 to determine individual survivorship and growth in diameter.

The survival rate of plants in each size-classes (σ_i) in each year was calculated as the number of plants that survived during that year in the size class i (s_i) divided by the number of living plants at the beginning of the year (n_i): $\sigma_i = s_i / n_i$. The transition rate (γ_i) was calculated as the number of plants leaving size class i and appearing, annually, in the next size class (r_i) divided by the number of plants that had been alive in size class i at the beginning of the year and had survived to the next year (s_i): $\gamma_i = r_i / s_i$. Data were analysed using chi-squared test (Zar 1984) for the number of damaged and undamaged individuals which survived and grew during the study period.

The number of individuals showed a marked decrease from seedlings to the larger adults (Table 1). The mean diameter (mm), mean height (cm) and mean number of leaves of plants distributed in size class is shown at Table 1. It was impossible to measure the height for all of the seedlings because most of them had a single leaf (height is measured as the distance from the base to the point of bifurcation of the oldest leaf from the stem). The spatial pattern of the population of *E. edulis*, was revealed to be significantly clumped (6.73) according to the Morisita's index of dispersion (Krebs 1989). The intensity of attack, measured as the number of damaged plants within a size class, varied amongst size classes (Table 1). The behaviour of herbivore adults could explain why herbivore attack concentrated only on the smallest plants. Otero & Marigo

Table 1. The number of plants sampled at the first enumeration (in 2500 m^2), average size ($\pm$ SD) of plants within each size class for diameter, height and number of leaves, percentage of damaged individuals in each size class and the percentage of damaged individuals within all size classes. See text for size classification system.

Size class	Number of plants	Diameter (mm)	Height (cm)	Number of leaves	% damaged	% of total
1	209	2.7 ± 0.8	—	1.8 ± 0.7	5.7	16.6
2	495	5.5 ± 1.6	8.1 ± 3.4	3.1 ± 0.8	9.7	66.7
3	56	15.0 ± 3.0	30.0 ± 28.9	3.4 ± 1.0	16.1	12.5
4	29	25.4 ± 2.8	47.8 ± 12.5	4.1 ± 0.7	6.9	2.8
5	50	45.1 ± 7.8	99.3 ± 53.5	4.3 ± 1.5	2.0	1.4
6	41	86.8 ± 18.2	342.7 ± 116.8	6.8 ± 1.4	0	0
7	65	175.2 ± 31.5	670.9 ± 152.2	9.9 ± 1.4	0	0

Table 2. Comparison of survival and transition probabilities between healthy and damaged plants, calculated as annual rate. n is the number of plants in each size class.

Class	n	Survival		Transition	
		Healthy	Damaged	Healthy	Damaged
1	209	0.6172	0.5833	0.1550	0.2857*
2	495	0.8303	0.8125	0.0754	0.1026
3	56	0.9286	0.8888	0.2692	0.2500

*Significant at $\chi^2 = 6.674$, P = 0.0098.

(1990) reported that herbivore adults are usually found close to the forest floor where they gain protection from predators by being camouflaged on the litter. Also, adults feed on juice of fruits ripening on the ground or on fungi (DeVries 1987, Otero & Marigo 1990). Therefore, small host plants close to the ground provide an available oviposition site due to proximity to the adults' food preferences and flight level.

Analysis of survival and transition rates was only performed for the smaller size classes because few damaged plants were found in the other size classes. Although they were slightly smaller, the survival rates for damaged plants are not significantly reduced by herbivory (Table 2). Apparently, the pattern of herbivore attack in relation to plant size is not a major factor responsible for mortality concentrating on the plants of the smaller size-classes. There are three main reasons for this: (1) herbivory does not affect the apical meristem of the plants; (2) apparently plants are growing in favourable conditions so that competition could be reduced (Silva Matos & Watkinson 1998); and (3) the temporal scale is too small to observe the effects of herbivory on plant survivorship. Oyama & Mendoza (1990) found no mortality of experimentally defoliated individuals of the neotropical palm *Chamaedorea tepejilote*. The role of herbivory in palm mortality might be questionable when herbivory is not damaging the apical meristem of the plant. Architectural characteristics of palms might be considered as a protection from herbivory, for instance the protection of the apical meristem by enclosure within the terminal crown of leaves and the protection of the youngest parts of developing leaves (Tomlinson 1990). So, for palms, defoliation might not be a direct cause of plant mortality.

Conversely, the probability of a plant growing from size class 1 to class 2 between the two recording dates was significantly higher for plants damaged by herbivores (Table 2). Plants of *E. edulis* might be using stored reserves to regrow quickly after being damaged. Compensatory growth was also observed in the palms *Astrocaryum mexicanum* (Mendoza *et al.* 1987) and *Chamaedorea tepejilote* (Oyama & Mendoza 1990) as a consequence of experimental defoliation. This could occur through the use of stored reserves in the root system affecting the competitive ability of both above- and below-ground structures and increasing the risk of plant death. So, it is possible that rapid regrowth would be a strategy for plants to reduce negative impacts of all types of damage, under highly favourable conditions, rather than a strategy to increase fitness after being damaged by herbivory.

The spatial pattern of damaged plants, according to the Morisita's index, was even more clumped (59.4) than the spatial pattern of the overall population. Most plots had either no plants (21%) or damaged plants (45%), and those plots were excluded from this analysis. As the biological interaction depends on the presence of both plants and caterpillars, the absence of one of them in the plots implies an absence of the interaction. No correlation was observed between the number of damaged plants/plot and density of plants (slope = 0.0541, interception = 2.9103 and $r^2 = 0.2450$). The slope is close to zero and so this could mean that the number of damaged plants/plot is constant. It is possible to rewrite the relation in terms of other variables in order to test for this possibility. The linear equation for the number of damaged plants/plot and density of plants is:

$$n_d = a + bn_i \qquad (1)$$

where n_d is the number of damaged plants per plot n_i = number of plants per plot and a and b are constants. Alternatively it can be expressed in terms of the proportion of damaged plants/plot:

$$\frac{n_d}{n_i} = \frac{a}{n_i} + b \qquad (2)$$

or

$$P = ax + b \qquad (3)$$

where P is the proportion of damaged plants per plot and x is $1/n_i$. A significant relationship was observed between the proportion of damaged plants per plot and density using equation 3 ($r^2 = 0.8652$, $a = 0.9209$, $b = 0.0714$, $n = 34$, $P < 0.0001$, Figure 1). As the value obtained for b is close to zero (0.0714), it suggests that the number of damaged plants is constant per plot ($n_d = a$) (equation 1), while the proportion of damaged plants per plot was inversely density responsive (equation 3). An explanation for this result could be that female adults are territorial and lay only a limited number of eggs, in addition to the behaviour of the caterpillars.

The conclusions from the present study are that selective herbivory is one of the causes of skewness and size inequality observed for the population of *E. edulis* (Silva 1992, Silva Matos 1995). Although herbivory is not one of the main density-dependent factors linked to a mortality-mediated spacing process, it seems to be a factor that could decrease the aggregation of plants by increasing the growth probability of plants in lower density stands as verified by Silva Matos & Watkinson (1998). Studies from the herbivore's perspective are also necessary to better understand this interaction and to find out how the fragmentation and isolation of this reserve affect both the populations.
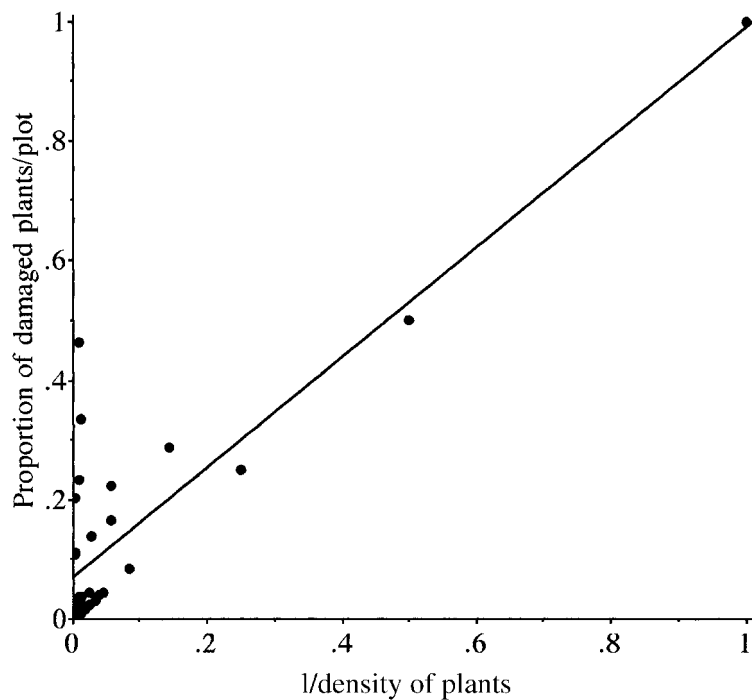
Figure 1. The relationship between the proportion of damaged plants per plot and density of plants. The model obtained is $P = a/D + b$ (where P = proportion of damaged plants per plot, D = density of plants, see text for statistics.

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