LEAF HERBIVORY ON THREE TREE SPECIES IN A MONODOMINANT AND TWO OTHER *TERRA FIRME* FORESTS ON MARACÁ ISLAND, BRAZIL.

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ABSTRACT - The aim of this study was to test the hypothesis that the monodominant non-pioneer *Peltogyne gracilipes*, typically does not suffer density-dependent herbivory (Janzen-Connell model). Two components of intraspecific variation in leaf herbivory were measured: 1) the variation between individuals in the population at the same time and 2) the temporal variation in rates of damage to each individual. The study was carried out on Maracá Island, Roraima, Brazil in three plots (50 m x 50 m) in each of three forest types: *Peltogyne*-rich forest (PRF), *Peltogyne*-poor forest (PPF), and forest without *Peltogyne* (FWP). Two other non-pioneer species (*Ecclinusa guianensis* and *Pradosia surinamensis*) were chosen for comparison because they were fairly abundant and their seedlings could be readily identified. The values of leaf area removed by herbivores of trees and seedlings of the three study species were in the range reported for other tropical tree species (2-16%, standing damage). There were no differences within species between forests. However, there was a significant difference among species but this was not correlated with seedling density. *Peltogyne* seedlings showed no evidence of density-dependent herbivory as predicted by the Janzen-Connell model despite the fact that adult trees were observed to suffer a mass defoliation in April 1992. This result suggests that *Peltogyne* may be dominant partly due to escape from herbivory in the early stages of its life although it may suffer occasional mass defoliation as an adult.

Key words: Amazonia, density-dependent herbivory, monodominant forest, *Peltogyne*, *terra firme* forest

Herbivoria Foliar em Três Espécies Arbóreas em Uma Floresta Monodominante e Duas Outras Floresta de Terra Firme na Ilha de Maracá, Brasil.

RESUMO - O objetivo deste trabalho foi testar a hipótese de que *Peltogyne gracilipes*, espécie climax e monodominante, tipicamente não sofre herbivoria dependente da densidade (Modelo de Janzen-Connell). Dois componentes da variação intraespecífica na herbivoria foliar foram avaliados: 1) a variação entre indivíduos na população no mesmo tempo e 2) a variação temporal na taxa de danos em cada indivíduo. O estudo foi realizado na Ilha de Maracá, Roraima, Brasil em três parcelas de 50 m x 50 m em cada um dos três tipos florestais (Floresta rica em *Peltogyne*, PRF; Floresta pobre em *Peltogyne*, PPF e Floresta sem *Peltogyne*, FWP). Duas outras espécies não pioneiras (*Ecclinusa guianensis* e *Pradosia surinamensis*) foram escolhidas para comparações por serem abundantes nas diferentes classes de tamanho e suas plântulas de fácil identificação no campo. A percentagem de área foliar removida pelos herbívoros está entre os valores reportados para outras espécies arbóreas tropicais (2-16%). Não houve diferenças dentro das espécies entre florestas. Entretanto, existiu uma diferença significativa entre espécies. As plântulas de *Peltogyne* não apresentaram nenhuma evidência de herbivoria dependente da densidade como previsto pelo modelo de Janzen-Connell, embora para árvores adultas tenha sido observado a ocorrência de desfolhamento em massa em abril de 1992. Este resultado sugere que *Peltogyne* pode ser dominante parcialemente devido ao escape da herbivoria nos estágios iniciais de sua vida embora possa sofre ocasionais desfolhamento quando adulta.

Palavras-chave: Amazônia, herbivoria dependente da densidade, floresta monodominante, *Peltogyne*, floresta de terra firme

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INTRODUCTION

The extent of herbivore damage may be affected by factors such as leaf age, leaf quality, plant size (Coley, 1983a; Marquis, 1987; Ernest, 1989; Aide, 1992; Kursar & Coley, 1992; Nascimento 1989; Nascimento & Hay, 1993; Coley & Barone, 1996) and by the composition, density and diversity of the surrounding vegetation (Brown & Ewel, 1987). The number of insects per plant and per unit area and their damage to leaves are usually held to be higher in monospecific stands than in species-rich ecosystems (Crawley, 1983). However, according to Connell & Lowman (1989), a monodominant stand can occur when a species has lower seed predation or superior resistance to pathogens and/or herbivores. It should have also the ability to persist in greater numbers in the understorey and subsequently the canopy, by replacing one canopy element after another (Hart, 1995).

In 1992, a mass defoliation of newly emergent leaves on adult trees of the deciduous *Peltogyne gracilipes* Ducke (Caesalpiniaceae) was observed in *Peltogyne* forests (monodominant or not) on Maracá Island, and was more severe in monodominant stands (Nascimento & Proctor, 1994). The monodominant forests are here referred to as *Peltogyne*-rich forest (PRF), whereas stands where *Peltogyne* is infrequent are called *Peltogyne*-poor forest (PPF), and those without this species are forest without *Peltogyne* (FWP). The younger (< 20 cm dbh) *Peltogyne* individuals are evergreen and neither their young leaves, nor the mature leaves on adult trees, were attacked during the mass defoliation. The mass herbivory (which was not observed in the three subsequent years of recording) fits the hypotheses of density-dependent herbivory (Janzen, 1970; Connell, 1971) and higher herbivory rates in species-poor stands (Crawley 1983). The density-dependent herbivory hypothesis predicts heavy herbivore damage on seedlings that are near adults resulting in density-dependent mortality amongst rain forest trees maintaining species densities so low that high diversity can be reached. In this paper we test the hypothesis that adult *Peltogyne*, as a monodominant species in PRF, is particularly prone to herbivore damage with higher herbivory rates on adult trees than the two other common (but not dominant) tree species, *Ecclinusa guianensis* and *Pradosia surinamensis* (both Sapotaceae), but that *Peltogyne* seedlings do not suffer mortality by density dependent herbivory (Janzen-Connell model). The work also addresses the observations of Brown & Ewel (1987) that simultaneous comparisons of herbivory rates in species-rich and species-poor ecosystems in the same environment are lacking.

MATERIALS AND METHODS

Maracá Island

Maracá Island is a large (100,000 ha) island located in the River Uraricoera, a tributary of the Amazon, at about 3°25'N, 61°40'W in Roraima

State, north-east Brazil. The main features of its climate, from Thompson *et al.* (1992) and Nascimento (1994), are: rainfall, *c.* 1800 mm yr^{-1} with a dry season from October to March; mean monthly maximum temperatures ranging from 35 °C to 41 °C and mean monthly minima ranging from 22 °C to 24 °C.

The forests of Maracá have been described by Thompson *et al.* (1992) and Nascimento *et al.* (1997). The PRF has an average of 26 tree (≥ 10 cm dbh) species per 0.25 ha and a Simpson diversity Index (1/Ds, Brower & Zar, 1977) of 9.11, PPF 32 and 13.28 and FWP 31 and 17.64. *Peltogyne* has the highest percentage basal area in PRF with 53% (≥ 10 cm dbh). For the trees greater than 30 cm dbh, however, the *Peltogyne* monodominance is much more pronounced, reaching up to 91% of the basal area (Nascimento *et al.*, 1997). The average number of *Peltogyne, Pradosia* and *Ecclinusa* seedlings per m^2 in each plot studied by Nascimento & Proctor (1997) ranged from 0 to 5.7 (*Peltogyne)*, 0 to 0.9 (*Pradosia)* and 0 to 0.8 (*Ecclinusa*) in PPF and from 6.1 to 23.3 (*Peltogyne*), 0.4 to 13.8 (*Pradosia*) and 0 to 0.3 (*Ecclinusa*) in PRF.

This study was carried out in 50 m x 50 m plots replicated three times in each of PRF, PPF, FWP and in a medium-sized gap (33 m long and 11 m wide) (Brokaw, 1985) near one of the plots in the PRF.

HERBIVORY ASSESSED FROM LEAVES IN LITTERFALL

In November 1991, all leaves of *Ecclinusa* (from one plot in PRF and all plots in FWP), *Peltogyne* (all plots in PRF and PPF) and *Pradosia* (all plots in PRF and FWP) in the litterfall (collected from 0.33 m^2 traps, n= 11 per plot) were visually assessed for herbivory using an eleven-point scale (percentage of lamina removed): 0, < 10%, 11-20%, 21-30%, 31-40%, 41-50%, 51-60%, 61-70%, 71-80%, 81-90%, and 91-100%. The damage was assumed to have been caused by chewing insects before the leaves fell into the traps. Mean leaf herbivory for each plot was calculated by multiplying the number of leaves within each damage class by the mean of that class to provide a percentage apparent leaf-damage estimate (Wint, 1983).

TEMPORAL VARIATION IN HERBIVORY ON *PELTOGYNE* AND *PRADOSIA* SEEDLINGS

This part of the study was only carried out for *Peltogyne* in PRF, for *Pradosia* in FWP, and for both these species in the gap. On 1-5 August 1991, ten seedlings (≤ 50 cm tall) of each of *Peltogyne* and *Pradosia* were chosen at random in each of the specified study plots and the gap. On each plant, the outlines of at least three leaves were traced onto graph paper and left intact on the plant. The leaves were classified into young and mature age-categories. Young leaves (group 1) were about 14 d old when measurement began, while most of the mature leaves (group 2) had probably been produced in the past wet season and so were about 1 yr old. The group 1 leaves became mature after the first census. After one month (1-5 September 1991) the plants were censused for changes in the damaged area for each traced leaf, and for leaf fall and leaf production. The young leaves which were not fully expanded when marked were redrawn at the second census to allow for their increased area. Further censuses were made every two months until July 1992. Leaf area was measured using a planimeter. The area of insect damage was determined by counting the number of squares (mm^2) visible under the damaged area.

SEEDLING HERBIVORY

On 8-9 June 1992, five seedlings ($\leq$ 50 cm tall) of each study species were chosen randomly in each plot where they occurred. All leaves from each individual were removed and their herbivore damage assessed using the eleven-point scale described above after the leaves had been separated into two age categories: young (not fully expanded, light-green and nearest the branch apices), and mature (fully expanded, dark green and located further from the apices).

A further study was made on *Peltogyne* recruits tagged in March 1993 in five sub-plots (2 m x 1 m) in each study-plot. Herbivory was estimated, on one occasion only, when the plants were about 13 d old and still had both cotyledons and were usually without fully expanded leaves.

Leaf herbivory values were transformed (ln (% damaged leaf area + 1) to obtain a normal distribution (Coley, 1983a; Zar, 1984), and comparisons among species and forest types were made by two-way nested Anova where factor A (forest type) was considered fixed and factor B (plot) random (Zar, 1984). Differences among means were calculated using Tukey's test. A Chi-square test was applied for comparisons of the proportion of damage between young and mature leaves.

RESULTS

HERBIVORY ASSESSED FROM LEAVES IN LITTERFALL

For *Peltogyne* (PRF and PPF) and *Pradosia* (PRF and FWP) there were no significant differences in % leaf area removed by herbivores (t-tests, $p > 0.17$) within species between forests. *Ecclinusa* did not occur in enough plots to be tested. There was a significant difference among species in PRF (one-way Anova, F= 12.6, p= 0.001) reflecting the lower herbivory on *Pradosia* (Tab. 1).

TEMPORAL VARIATION

The proportion of leaves damaged in the gap was significantly smaller for *Peltogyne* than *Pradosia* (Chi-square test= 4.54, d.f.= 1, $p < 0.05$). In the understorey of each forest type the between-species differences were not significant (Chi-square test= 1.45, d.f.= 1, $p > 0.05$). For *Peltogyne* the number of leaves attacked by herbivores was not different between the gap and forest (Chi-square= 1.92, d.f.= 1, p> 0.05), but for *Pradosia* there was a difference between forest and gap (Chi-square test=

4.64, d.f.= 1, p≤ 0.05).

The median herbivory rates on young and mature leaves (Table 2) of *Peltogyne* and *Pradosia* seedlings were not significantly different within species and between species (Mann-Whitney test, p> 0.05). Coefficients of variation ranged from 1.74 to 3.23 (Table 2) indicating that the variation in herbivory between plants was high in both species, with herbivory rates positively skewed so that the modal individuals suffered less damage than the mean. All leaf damage to both species in the forest plots occurred during the wet season. However, in the gap, only 50% (*Peltogyne*) and 35% (*Pradosia*) of the leaf damage occurred in the wet season. The damage to particular individuals was not con-

Table 1. The percentage leaf area removed by herbivores from leaves (collected as litterfall) for three species in three forest types on Maracá Island, Roraima, Brazil. - indicates that the species was not recorded from that replicate plot within the forest type. PRF, *Peltogyne* rich forest; PPF, *Peltogyne* poor forest; FWP, forest without *Peltogyne*.

Forest	*Peltogyne*	*Pradosia*	*Ecclinusa*
PRF			
Plot 1	7.7	6.2	-
Plot 2	11.5	5.3	-
Plot 3	15.1	39.7	12.6
Mean	11.4	7.1	
SD	3.0	1.9	
PPF			
Plot 7	19.5	-	-
Plot 8	17.0	-	-
Plot 9	13.4	-	-
Mean	16.6		
SD	2.5		
FWP			
Plot 10	-	5.0	8.3
Plot 11	-	4.0	11.1
Plot 12	-	6.4	14.2
Mean		5.1	11.2
SD		1.0	2.4

stant over time for both species. For each sample period a different group of individuals was more heavily attacked.

Over the 11-month period, 41% of the *Peltogyne* leaves and 44% of the *Pradosia* leaves were abscised from individuals in the gap. In the understorey, the *Peltogyne* and *Pradosia* seedlings lost 63% of the leaves and the differences between gap and understorey were significant (Chi-square tests, $p < 0.01$). There were no significant differences in leaf loss between species in both site types (Chi-square tests, $p > 0.05$), with both species shedding more leaves during the dry season.

Herbivory was not related to survival, since the dead plants (two for *Peltogyne* and three for *Pradosia*) had no leaf damage during the study.

HERBIVORY ON SEEDLING LEAVES

There were no intraspecific differences in leaf herbivory for seedlings between forests (Table 3). The high coefficients of variation in Table 3 were caused by a small number of heavily damaged individuals while the average extent of damage was low (Fig. 1). The number of *Peltogyne* seedlings with more than 5% leaf herbivory was lower than those found for *Ecclinusa* and *Pradosia*, and only one *Peltogyne* individual (in PPF) suffered more than 10% leaf herbivory (Fig. 1). The number of damaged leaves was higher in mature leaves, except for *Peltogyne* which had a similar propor-

Table 2. Herbivory rates (mean, coefficient of variation and median) per individual of *Peltogyne* and *Pradosia* over an 11-month period in two leaf age categories: group 1, *c.* 14 d old when first censused, and group 2, *c.* 1 yr old at the first census. PRF, *Peltogyne* rich forest; PPF, *Peltogyne* poor forest; FWP, forest without *Peltogyne*.

Species and location	Mean (%/day)	CV (%)	Median (%/day)	% number of damaged leaves
(a) Group 1				
Peltogyne				
Gap	0.0044	252	0.00	25
PRF	0.0005	300	0.00	30
Pradosia				
Gap	0.0352	255	1.94	53
FWP	0.0205	204	0.00	40
(b) Group 2				
Peltogyne				
Gap	0.0011	323	0.00	42
PRF	0	0	0.00	32
Pradosia				
Gap	0.0476	174	0.00	76
FWP	0	0	0.00	39

tion of damaged leaves in young and mature leaves (Tab. 4). Mature leaves were generally more damaged than young leaves (Tab. 4).

HERBIVORY IN *PELTOGYNE* SEEDLING RECRUITS

The herbivory on leaves of new (13 d after germination) seedlings of *Peltogyne* was low in both PRF and PPF. Only six of 81 (PRF) and two of 22 (PPF) newly tagged seedlings were attacked, with most seedlings having less than 5 % of leaf area lost. At this time only 23 % (PRF) and 27 % (PPF) of the individuals had leaves fully expanded.

DISCUSSION

HERBIVORY ASSESSED FROM LEAVES IN LITTERFALL

Table 3. Mean values (with ranges) of percentage leaf area damage from seedlings of three species in three forest types on Maracá Island, Roraima, Brazil. PRF, *Peltogyne* rich forest; PPF, *Peltogyne* poor forest; FWP, forest without *Peltogyne*.

	PRF	PPF	FWP	P
Ecclinusa				
Mean	9.0	11.9	9.5	n.s.
range	(0-24.3)	(1.2-53)	(0-38.6)	
CV	88	119	103	
p	n.s.	n.s.	n.s.	
Peltogyne				
Mean	2.3	3.8	-	n.s.
range	(0-9)	(0-7.7)		
CV	126	82		
Pradosia				
Mean	9.0	7.2	11.9	n.s.
range	(0-22.5)	(0-33.7)	(0-35)	
CV	83	127	95	

CV= Coefficient of variation (%).
p= probabilities, n.s= not significant.

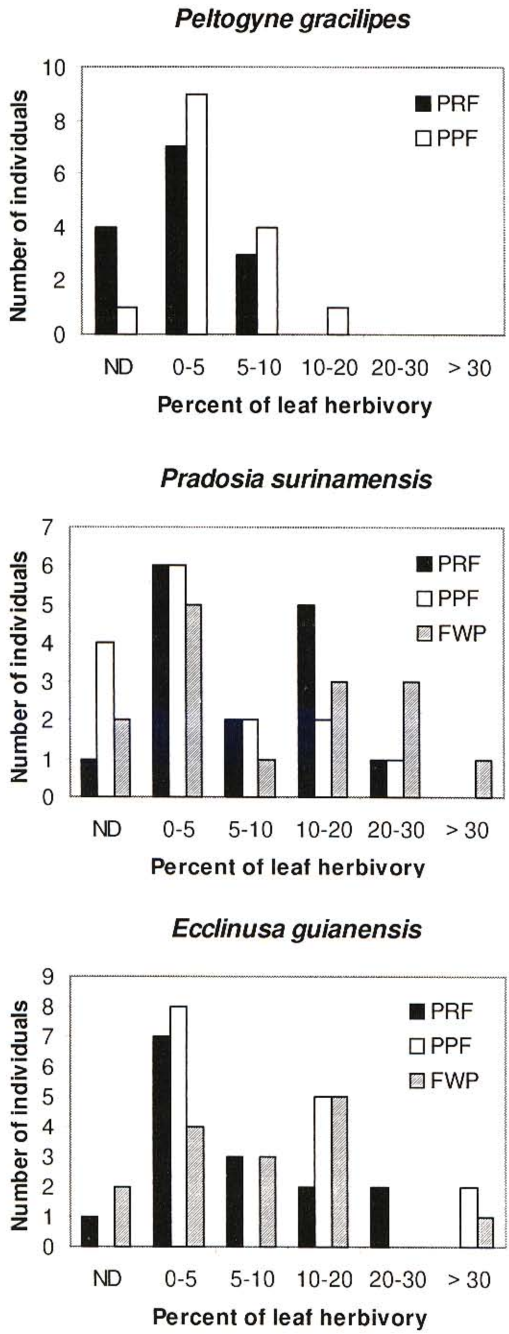

Figure 1. Intraspecific variation in leaf herbivory on seedlings (< 50 cm tall) of three study species in *Peltogyne* rich forest (PRF); *Peltogyne* poor forest (PPF); forest without *Peltogyne* (FWP).

Table 4. The percentage of damaged leaves and mean of percentage damaged area per individual in two leaf age categories (young, YL; and mature, ML) in three forest types on Maracá Island, Roraima, Brazil. PRF, *Peltogyne* rich forest; PPF, *Peltogyne* poor forest; FWP, forest without *Peltogyne*.

	% damaged leaves			% damaged área		
	YL	ML	p[1]	YL	ML	p[2]
Ecclinusa						
PRF	17	57	***	6.3	10.3	**
PRF	16	53	***	0.5	14.2	***
FWP	16	59	***	2.4	11.2	***
Peltogyne						
PRF	12	30	n.s.	0.7	3.3	*
PRF	31	48	n.s.	1.5	4.3	**
Pradosia						
PRF	5	60	***	3.7	13.8	***
PRF	18	54	***	3.0	10.2	n.s.
FWP	33	73	***	3.0	16.3	***

1= Chi-square test
2= t-test
n.s= not significant
*= 0,05, **= 0,01, ***= 0,001

The range (5.1-16%, standing damage) of mean herbivory values for the three species is within the limits recorded (5-15%) for other tropical rain forests (Landsberg & Ohmart, 1989; Sterk *et al.*, 1992). An overall value of 11.3% was found by Scott (1990) for a range of species in a FWP on Maracá. Although Lowman (1984) and Filip *et al.* (1995) remarked that herbivory may be underestimated by the discrete sampling method, comparisons with other studies using the same technique are valid.

SEEDLING HERBIVORY

Coley *et al.* (1985) proposed that slower growing species would be better defended and have lower herbivory rates than faster growing species. The species in this study are slow growing (Nascimento & Proctor, 1997) and their seedling herbivory rates, especially for *Peltogyne*, are relatively low when compared with those of other tree species (Lowman, 1982; Coley, 1983a,b; Lowman, 1984; Marquis, 1987; Nascimento & Hay, 1993). However, as found by Coley (1983b), Marquis (1984) and Nascimento & Hay (1993), variation between plants at any one sample period is high, and rates of damage to a particular individual are not constant. It is striking, however, that the results of seedling herbivory indicate lower rates of herbivory on dense *Peltogyne* seedlings than on much rarer *Ecclinusa* and *Pradosia* and show no density-dependent herbivory for *Peltogyne*, as there was no significant difference between young-plant herbivory in PRF (high density) and PPF (low density). So escape from herbivory could be a factor leading to dominance of *Peltogyne*.

Site differences are one of the factors that are believed to affect herbivory (Brown & Ewel, 1987; Marquis, 1987). No statistical differences in herbivory between forest types were seen in this study, although herbivory on *Pradosia* was significantly higher in the gap.

The difference found by the discrete sampling method for the percentage of herbivory between young and mature leaves probably reflects damage accumulated during leaf development, since the temporal variation method showed that herbivory rates between young leaves and mature leaves were not different.

Many authors consider that the impact of leaf damage decreases with plant age or height or both (Marquis, 1984; Nascimento & Hay, 1994, Coley & Barone, 1996). The low herbivory found for the seedlings of *Peltogyne* suggests that this species might invest more in defense of younger individuals. Their leaves were not eaten during the mass adult defoliation in 1992 (Nascimento & Proctor, 1994).

CONCLUSION

The leaf herbivory rates of trees and seedlings of the three study species were in the range for the tropical plants. There was no evidence for density-dependent herbivory. This is in contrast to earlier observation (Nascimento & Proctor 1994) of extensive lepidopteran defoliation of newly flushed leaves on adult *Peltogyne* and it is suggested that *Peltogyne* may be dominant due to escape from herbivory in spite of sporadic severe defoliation of newly-flushed leaves on adult trees.

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