

# Effects of flooding and herbivores on variation in recruitment of palms between habitats

MANOEL A. W. PACHECO\*

Department of Biological Sciences, University of Illinois at Chicago, 845 W. Taylor Street, Chicago, Illinois 60607–7060, USA

## Summary

**1** It is widely recognized that negative effects of anaerobic stress on growth and survival of flooded plants influence the distribution of numerous species. Less explored is the possibility that heterogeneity in abundance of plants between habitats with distinct flooding regimes may also result from variation in rates of herbivory or in the ability of plants to tolerate losses to herbivores.

**2** Flooding and herbivores were tested as factors underlying variation in abundance of two tropical forest palms, *Socratea exorrhiza* (which is associated with lowlands adjacent to streams) and *Oenocarpus bacaba* (which is more abundant on plateaux and upper edges of slopes).

**3** In a bench experiment, seeds of both palms were either completely immersed in water for a period of 101 days or not subject to inundation. Flooding inhibited germination of both species but, as expected, the adverse effects were much stronger on *Oenocarpus*.

**4** In a field experiment, seeds of both palms were planted with increasing levels of protection against herbivores on plateaux and in lowlands. Seeds were either not protected or placed within poultry-netting enclosures, half of which were sprayed with insecticide.

**5** After 17 months, only *Oenocarpus* had experienced differential mortality between habitats, and this was clearly associated with the negative effects of flooding on seed germination in lowlands. In contrast, growth differed between habitats only for *Socratea* seedlings, where average above-ground biomass was greater in lowlands.

**6** Although protection with enclosures and insecticide increased survivorship of both species, herbivores caused similar proportions of mortality on plateaux and in lowlands, and had no significant effect on seedling growth. Therefore at this site, herbivores do not appear to influence variation in abundance of species between habitats.

*Key-words:* Amazon, germination, plant distribution, seed predation, tropical forest.

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## Introduction

Heterogeneity in the abiotic environment is frequently associated with variation in abundance of plants. On a continental scale, climatic conditions reliably predict the structure of the vegetation and broad patterns in the distribution of species (Holdridge 1947; Woodward 1987). Changes in the availability of water and nutrients on a regional or local scale correspond with shifts in abundance of species, and the composition and diversity of plant communities (Gentry 1988; Tuomisto *et al.* 1995). Studies of mechanisms underlying the

responses of plants to environmental heterogeneity therefore generally emphasize the direct effects of abiotic factors on survival, growth or reproduction.

Topography is a widespread source of environmental heterogeneity. When excessive rain causes water to overflow from rivers, streams and channels, inundating adjacent areas, variation in elevation along small-scale gradients controls the period over which plants are subject to flooding. Flooding restricts the availability of oxygen to plants because oxygen diffusion coefficients are much lower in water than in the air. Differences among species in levels of tolerance to anaerobic stress (Blom & Voesenek 1996; Vartapetian & Jackson 1997) promote clear changes in composition and diversity of plant communities along gradients of flooding intensity (Junk 1989). In areas subject to long periods of inundation, anaerobic stress reduces survival or growth

\*Present address and correspondence: M.A.W. Pacheco, Applied Biomathematics, 100 North Country Road, Setauket, NY 11733, USA (tel. +631 751-4350; fax +631 751-3435; e-mail MPacheco@ramas.com).

of most plants (Kozłowski 1984), and so limits the distribution of numerous species (Crawford 1992). Plants that are adapted to such extremely anoxic conditions become dominant in the community.

This pattern is very conspicuous in tropical forests, where inundated areas with relatively few species occur in close proximity to elevated sites with high diversity of plants (Lieberman *et al.* 1985; Junk 1989). Species that are associated with habitats that are frequently inundated are expected to be more tolerant of flooding. Unfortunately, there is little experimental evidence demonstrating that flooding has more negative effects on survival or growth of those tropical forest plants that are associated with plateaux (Joly & Crawford 1982; ter Steege 1994).

Other factors may influence variation in abundance of plants between habitats with distinct flooding regimes. Herbivory can reinforce or overrule the response of plants to environmental heterogeneity (Louda 1982, 1983; Louda *et al.* 1987; Louda & Rodman 1996; Olff *et al.* 1997). Differences in the abiotic environment (Pacheco 1999), the composition of plant species (Lieberman *et al.* 1985; Junk 1989), and levels of predation and pathogen infection (see Fernandes & Price 1992) are likely to result in distinct abundance and foraging behaviour of herbivores in lowlands and on plateaux (Janzen & Schoener 1968; Bodmer 1990). Furthermore, differences in rates of herbivory between these habitats are expected because variation in availability of light, soil moisture and nutrients (Tiessen *et al.* 1994; Pacheco 1999) affects the concentration of nutrients and defence compounds in tissues of plants (see Coley *et al.* 1985; Louda *et al.* 1987; Erelli *et al.* 1998). Herbivores selectively forage on plants with higher concentrations of nutrients and lower levels of defences (Hartley & Jones 1997).

Variation in availability of resources may also determine distinct abilities of plants in lowlands and plateaux to tolerate losses to herbivores. Herbivory is expected to have a more negative impact on growth and survival of plants when environmental variables limit the plant's ability to compensate for losses caused by herbivores (the plant stress hypothesis, Crawley 1997). Strong, negative effects of herbivory are also expected when animals can change their foraging behaviour or abundance in response to the higher susceptibility of stressed plants (Jones & Coleman 1991). In agreement with these predictions, flooded plants often experience higher mortality from more frequent attacks by herbivores and pathogens than plants not subject to inundation (Davison & Tay 1987; Mori & Becker 1991).

I performed two experiments to test the effects of flooding and herbivores on variation in recruitment of two tropical forest palms between habitats at opposite extremes of a small-scale altitudinal gradient (45–80 m above sea level). This study was part of a larger project to test the role of herbivores, water, light and nutrients as mechanisms underlying the contrasting patterns of

abundance of tropical forest palms in lowlands and plateaux (Pacheco 1999).

The first experiment tests the effect of flooding on seed germination of the two palms. It is expected that flooding will have a more negative effect on seed germination of the species associated with plateaux. The second experiment analyses the effects of habitat and protection on recruitment of seedlings. If herbivores promote variation in recruitment of seedlings in lowlands and plateaux, then the difference between the number of seedlings within exclosures and unprotected will be greater in the habitat where each species is less abundant.

## Materials and methods

### STUDY SITE AND SPECIES

This study was developed in reserve 1501 of the Biological Dynamics of Forest Fragments Project (BDFFP), 70 km north of Manaus, Brazil (2°25'S × 59°50'W). Annual precipitation at Manaus averages 2186 mm, with a pronounced dry season from July to September. The reserve (10<sup>4</sup> ha) is within a forest that stretches for hundreds of kilometres, and its elevation ranges from 40 to 110 m above sea level. The vegetation is defined as evergreen, 'terra firme' forest (Pires & Prance 1985) with a mean canopy height of 30 m.

The topography is characterized by level plateaux and small hills interspersed with valleys, which often have small streams running through them. In this study, lowland and plateau, respectively, are defined as flat areas (slope < 20°) adjacent to and more than 5 m above the stream level. At reserve 1501, most lowland areas are less than 40 m wide and experience periodic flooding during periods of high precipitation (December–March). Overflows from the shallow streams (< 2 m deep) rarely inundate all of the adjacent areas, and extended flooding (weeks or months) is generally restricted to sites with lower elevation.

The abiotic environments of plateaux and lowlands differ in many ways. In lowlands, soils have, on average, higher water matric potentials and higher concentrations of phosphorus; low areas adjacent to streams are recurrently flooded, and gaps in the forest canopy above stretches where streams are wide create patches with high intensity of light. On plateaux, soils contain more clay, floods are very rare and restricted in area; light gaps in the forest canopy are usually of smaller size and created by tree-falls (Pacheco 1999). The site is described in more detail by Lovejoy & Bierregaard (1990).

The focal species for this study are two arborescent palms (Arecaceae), *Socratea exorrhiza* (Martius) H. Wendland and *Oenocarpus bacaba* Martius, which are common in tropical forests of the Central Amazon (Henderson 1995). *Socratea* is a slender tree, 8–12 cm in diameter at breast height (d.b.h.) that can reach up to 20 m tall, although it is usually shorter. Stilt roots are

characteristic of this species. Its seeds have a smooth surface, a fresh mass of  $3.42 \pm 0.07$  g (mean  $\pm$  SE,  $n = 49$  for all measures), and are on average  $20.7 \pm 0.1$  mm long and  $15.6 \pm 0.1$  mm wide. Adults of *Oenocarpus* reach similar heights, but have thicker stems (13–18 cm d.b.h.). Seeds are covered with fibres, have a fresh mass of  $1.09 \pm 0.04$  g ( $n = 25$  for all measures), and are on average  $13.5 \pm 0.2$  mm long and  $11.1 \pm 0.2$  mm wide.

#### VARIATION IN ABUNDANCE

In August and September 1989, all reproductive-size plants of both species in a  $1000 \times 100$  m transect (10 ha), running E-W across the middle of a 100-ha plot (Mori & Becker 1991), were located and plotted on a topographic map. The number of reproductive-size individuals of each species (*Oenocarpus* stems  $\geq 4$  m in height and *Socratea* stems  $\geq 7$  cm in d.b.h.) were counted exclusively on plateaux and in lowlands; plants on slopes  $\geq 20\%$  were excluded from the analysis. In February 1995, I counted plants of all sizes in 20 randomly distributed plots ( $10 \times 5$  m) within each habitat.

#### EFFECT OF FLOODING ON SEED GERMINATION

This experiment tested the effect of flooding on germination of *Oenocarpus* and *Socratea* seeds, with germination defined as the unfolding of the first leaf. Each seed was buried in a plastic cup (80 mm high, 60 mm in diameter) filled with washed commercial sand. Cups in the 'control' treatment had small holes on the side and bottom to avoid accumulation of water. Cups containing flooded seeds remained completely filled with water for a period of 101 days. Leaky cups were promptly replaced. Seeds were watered daily. There were 100 replicates for each combination of species and flooding treatment, and all 400 cups were randomly placed on a screened bench located under the canopy of trees next to the BDFFP office at INPA, Manaus. I used similar numbers of seeds from seven *Socratea* and eight *Oenocarpus* trees. Germination was monitored for 615 days after planting seeds.

#### EFFECTS OF HABITAT AND HERBIVORES

I planted seeds of *Oenocarpus* and *Socratea*, at three levels of protection against herbivores, on plateaux and in lowlands to test the effects of habitat, herbivores, and their interaction on recruitment of seedlings. This field experiment had a split-plot design. Initially, I selected 11 plots in lowlands along a stretch of stream extending approximately 1000 m. The selection criteria were to sample a variety of flooding regimes and avoid slopes, while maximizing distance between plots. Each of them was then paired with a plot on the closest plateau. Within each plot, I randomly assigned the position of all possible combinations of the two study

species and three protection levels to six subplots spaced 5 m apart. In each subplot, I planted 20 seeds at 5-cm spacing. Seeds were collected from multiple trees in the habitat where each species is more abundant. The 10 *Oenocarpus* trees were outside my study site, and 10 of 14 *Socratea* trees were within it. I discarded seeds that floated on water before pooling all seeds of each species.

The three protection levels consisted of no protection, poultry netting (2.0 cm mesh) enclosure, which prevented access of mammalian and avian herbivores, and poultry-netting enclosure plus insecticide. Enclosures were approximately 45 cm tall, 40 cm in diameter, closed at the top, and fixed to the ground by a wood stake and two wire pegs. Plants in the enclosure plus insecticide treatment were sprayed every other week with Malathion, an organophosphate insecticide, diluted to 0.2% in water. The litter that had accumulated on top of seeds and plants without protection was removed at each census. Each seed was glued to a 5-cm nail, which was inserted into the ground to place the seed at the level of the soil surface (modified from Schupp 1988). Because seeds were in a fixed position in a grid, I could follow their individual fates. The status of each plant was recorded on monthly censuses for the first 13 months, and at 17 months, just before plants were cut at ground surface, dried and weighed. The experiment started on 4 February 1994 and ended on 7 July 1995.

#### STATISTICAL ANALYSES

##### *Variation in abundance*

To test for association between species abundance and habitat, I compared observed and expected frequencies of *Socratea* and *Oenocarpus* plants on plateaux and in lowlands. Goodness of fit was tested with chi-square analysis. Expected frequencies of reproductive-size plants were calculated assuming that the proportions of individuals in plateaux and lowlands equalled the proportions of total area occupied by each habitat. Expected frequencies of seedlings on the plateau and in the lowland were assumed to be identical, the average of observed frequencies of each species, since I sampled the same area in both habitats.

##### *Effect of flooding on seed germination*

I tested the assumption that flooding has similar effects on the fate, i.e. death or germination, of *Oenocarpus* and *Socratea* seeds with a logit model that excluded a term for interaction between the effects of species and flooding treatment (Agresti 1990). A significantly poor fit of this model would demonstrate that flooding has distinct impacts on germination of *Oenocarpus* and *Socratea* seeds. Similarly, to test for independence between the effects of flooding treatment and time I tabulated the number of control and flooded seeds that

germinated within each of four successive time periods (224, 277, 398 and 615 days after planting seeds), and applied the *G*-test (Zar 1984).

#### Effects of habitat and herbivores

I analysed the effects of habitat, protection against herbivores, species, and interactions among them, on the proportion of seedlings recruited using a split-plot ANOVA model. In this model, the effect of habitat was tested using the plot mean square as the denominator in the *F* ratio. Proportions of recruitment were computed as the number of seedlings alive at the end of the experiment divided by the original number of seeds planted. When effects of the factor species significantly interacted with others, I used contrasts to compare their individual responses to different habitat and protection levels. Since the objective of this experiment was to test for differential impact of herbivory on recruitment of *Oenocarpus* and *Socratea* in lowlands and plateaux, the focus was on the interaction among the effects of species, habitat and protection. For clarity, however, I present the results of interactions between the effects of habitat and protection for each species separately. The same split-plot ANOVA model was used to perform tests on the proportion of seeds that germinated, seedlings that died, and the average above-ground dry biomass of seedlings alive at the end of the experiment. The proportion of seedling mortality was defined by the ratio between the number of seedlings that died and the total number of seeds that germinated. To calculate the average seedling biomass, I divided the total dry biomass of live seedlings by their number. All proportions were arcsine transformed prior to statistical analyses. The experimental design for the proportion of seedlings that died and above-ground biomass was unbalanced due to mortality of all plants in several subplots, most of them with no protection. All statistical tests except the chi-square and *G*-tests, which I calculated in spreadsheets, were performed in SAS version 6.12 (SAS 1989).

## Results

### VARIATION IN ABUNDANCE

Reproductive-size plants of *Oenocarpus* were found mostly on plateaux (Table 1a) and upper edges of slopes. Within the 10-ha transect, not a single adult of this species occurred in lowland areas. However, as lowland represents only a small fraction (1.3%) of the sampled area, the observed frequencies were not significantly different from the expected. In contrast, the majority of reproductive-size plants of *Socratea* were present in lowlands. No seedlings of this species occurred within plots on the plateau (Table 1b). *Socratea* seedlings were observed in very low densities in this habitat (personal observation), whereas densities of *Oenocarpus* seedlings were higher on plateaux than in lowlands.

### EFFECT OF FLOODING ON SEED GERMINATION

The negative impact of flooding on seed germination was stronger for *Oenocarpus*, the species associated with plateaux (Table 2, logit model,  $\chi^2 = 12.39$ , 1 d.f.,  $P = 0.0004$ ). Flooding also delayed germination of *Socratea* seeds: by 277 days, 80% of all germination in the control treatment had occurred compared with only 14% in the flooded treatment (test of independence,  $G^2 = 35.9$ , 3 d.f.,  $P < 0.001$ ).

### EFFECTS OF HABITAT AND HERBIVORES

*Oenocarpus* had higher germination on plateaux (84%) than in lowlands (59%) ( $F_{1,20} = 17.48$ ,  $P < 0.001$ ), but germination of *Socratea* seeds was similar (*c.* 45%) in the two habitats ( $F_{1,20} = 0.01$ ,  $P = 0.90$ , Table 3a). Germination of *Oenocarpus* seeds was clearly lowest in those areas of lowlands that were flooded. Only four of the 11 lowland plots were submersed in water for months, and within each of these not all subplots were equally affected. The overall proportion of *Oenocarpus*

**Table 1** Frequencies of (a) reproductive-size plants and (b) seedlings of *Oenocarpus bacaba* and *Socratea exorrhiza* in forest habitats north of Manaus, Brazil. Expected frequencies of reproductive-size plants were calculated assuming that abundance of species on plateaux and in lowlands was proportional to the percentages of total area (10 ha) occupied by each habitat. Expected frequencies of seedlings  $\leq 25$  cm high in 20 randomly distributed plots (10 × 5 m) within each habitat assumed equal densities because the same area was sampled in plateaux and lowlands

(a) Number of reproductive-size plants					
	Area (%)	<i>Oenocarpus</i>		<i>Socratea</i>	
		Observed	Expected	Observed	Expected
Plateau	76.6	95	93.4	5	28.5
Lowland	1.3	0	1.6	24	0.5
		$\chi^2 = 1.64$ , 1 d.f., $P > 0.10$		$\chi^2 = 1140$ , 1 d.f., $P < 0.001$	
(b) Number of seedlings					
		<i>Oenocarpus</i>		<i>Socratea</i>	
		Observed	Expected	Observed	Expected
Plateau		286	159	0	39.5
Lowland		32	159	79	39.5
		$\chi^2 = 202.9$ 1 d.f. $P < 0.001$		$\chi^2 = 79.0$ 1 d.f. $P < 0.01$	

**Table 2** Number of *Oenocarpus bacaba* and *Socratea exorrhiza* seeds that germinated in the control and flooding treatments. Flooded seeds were submersed in water for 101 days. Seeds in the control treatment were never inundated. I planted 100 seeds of each species in the control and flooding treatments. Seed germination was monitored for 615 days after installation of the experiment

	<i>Oenocarpus</i>	<i>Socratea</i>
Control	67	76
Flooded	1	21

seeds in the lowland that germinated in flooded plots was less than half that in non-flooded plots (33% vs. 75%, respectively). The difference was even greater when flooded and non-flooded subplots were compared (20% vs. 72%, respectively).

Protection against herbivores (exclosures with or without insecticide) greatly enhanced germination of *Socratea* seeds ( $F_{2,100} = 50.09$ ,  $P < 0.0001$ ), but had no significant effects on *Oenocarpus* ( $F_{2,100} = 0.72$ ,  $P = 0.49$ ). The positive effect of protection on *Socratea* germination was similar in lowlands and plateaux ( $F_{2,40} = 0.74$ ,  $P = 0.48$ ). Although application of insecticide tended to increase germination (69% with vs.

55% without), this effect was not significant (Ryan-Einot-Gabriel-Welsch multiple range test).

Overall, 73% of *Oenocarpus* and 24% of *Socratea* seedlings died, resulting in a highly significant difference in mortality ( $F_{1,89} = 84.70$ ,  $P < 0.0001$ ). Protection against herbivores reduced mortality only in *Oenocarpus* seedlings ( $F_{2,89} = 5.53$ ,  $P = 0.0054$ ; for *Socratea*:  $F_{2,89} = 0.61$ ,  $P = 0.55$ ). The overall percentage mortality (protection levels pooled) of *Oenocarpus* seedlings was higher in lowlands (82%) than on plateaux (67%), although this difference was not significant ( $F_{1,20} = 1.92$ ,  $0.10 < P < 0.25$ ). Mortality of *Socratea* seedlings was similar in both habitats ( $F_{1,20} = 0.49$ ,  $P > 0.25$ , Table 3b).

Patterns of seedling recruitment were similar to those for seed germination. While recruitment of *Oenocarpus* seedlings on plateaux (28%) was, on average, 2.5 times higher than in lowlands (11%) ( $F_{1,20} = 23.66$ ,  $P < 0.0001$ ), similar proportions of *Socratea* seedlings recruited in both habitats ( $F_{1,20} = 1.10$ ,  $P > 0.25$ ; Table 3c). Protection against herbivores increased recruitment of both species, but the effects were much stronger in *Socratea* ( $F_{2,100} = 48.68$ ,  $P < 0.0001$ ) than in *Oenocarpus* ( $F_{2,100} = 6.75$ ,  $P = 0.018$ ). Both exclosures and insecticide significantly enhanced recruitment of the two species (Ryan-Einot-Gabriel-Welsch

**Table 3** Mean and standard deviations of percentages of (a) seed germination, (b) seedling mortality, (c) recruitment and (d) above-ground (dry) biomass of seedlings for each combination of species, habitat and level of protection against herbivores

	Plateau			Lowland		
	No protection	Exclosure	Insecticide	No protection	Exclosure	Insecticide
<b>(a) Germination</b>						
<i>Oenocarpus</i>						
Mean	83.2	85.9	83.2	53.2	55.9	69.1
SD	6.8	7.0	8.1	28.7	38.1	24.2
<i>Socratea</i>						
Mean	7.7	57.3	71.8	17.3	52.7	65.9
SD	9.0	18.9	10.3	22.2	26.8	22.0
<b>(b) Seedling mortality</b>						
<i>Oenocarpus</i>						
Mean	77.0	65.6	59.0	93.2	84.6	70.4
SD	14.3	24.4	23.3	14.9	30.2	23.4
<i>Socratea</i>						
Mean	35.3	32.5	25.9	26.3	21.6	14.5
SD	43.6	28.0	23.7	40.0	24.8	17.1
<b>(c) Recruitment</b>						
<i>Oenocarpus</i>						
Mean	19.1	29.5	34.1	3.6	8.6	20.5
SD	11.1	19.9	20.6	4.5	8.1	10.4
<i>Socratea</i>						
Mean	5.5	38.6	53.6	12.7	41.4	56.4
SD	6.9	21.5	17.9	20.4	27.7	24.2
<b>(d) Above-ground biomass (g)</b>						
<i>Oenocarpus</i>						
Mean	27.2	31.9	32.2	25.0	28.1	28.6
SD	6.3	6.8	7.9	19.1	14.1	9.6
<i>Socratea</i>						
Mean	49.7	52.7	53.8	62.3	60.2	69.9
SD	14.0	10.1	4.6	16.1	9.2	17.7

multiple range test). Exlosures were very effective in protecting plants against vertebrate herbivores: out of the 1760 seeds planted within exlosures, only one seed and one seedling were removed. However, insecticide was a less effective method of protection, with at least 25% of plants in the exlosures and insecticide treatment being killed by insects. The impact of insect herbivores on plant survivorship was underestimated, but there is no suggestion that efficiency of the insecticide differed between habitats.

The average above-ground (dry) biomass of live *Socratea* seedlings was higher in lowlands (0.65 g) than on plateaux (0.53 g) ( $F_{1,20} = 5.56$ ,  $P < 0.05$ ), but *Oenocarpus* growth was similar in the two habitats ( $F_{1,20} = 0.19$ ,  $P > 0.50$ , Table 3d). The differential growth of *Socratea* seedlings between habitats was not influenced by herbivores, nor was any interaction among the effects of habitat and protection significant ( $F_{2,28} = 1.10$ ,  $P = 0.35$ ).

## Discussion

### VARIATION IN ABUNDANCE

Abundance of reproductive-size *Oenocarpus* plants was not associated with either habitat, as defined here. This result is surprising, since a test of association between abundance and altitude revealed that the frequency of these plants at low elevations was significantly lower than expected (M. Pacheco, A. Henderson and A. Scariot, unpublished data). Similarly, another study in the same region reported that density of *Oenocarpus* was much lower in lowlands than on plateaux (Kahn & Castro 1985).

The consistent association of *Oenocarpus* and *Socratea* trees with plateaux and lowlands, respectively, in many sites throughout the Amazon basin (Kahn & Castro 1985; Kahn 1987; Scariot *et al.* 1989; Kahn & Mejia 1990; Peres 1994) suggests that similar mechanisms control the distribution of these palms in different areas. Such recurrent spatial patterns in abundance of reproductive plants and similar variation in abundance of seedlings (plants  $\leq 25$  cm) at my study site indicate that ecological factors, rather than human activities (Basnet 1992; Clark *et al.* 1995), determine the distinct distributions of these species.

### EFFECT OF FLOODING ON SEED GERMINATION

In this experiment, as in other tests of physiological mechanisms underlying the zonation of plants along elevational gradients (Grace & Wetzel 1981; Joly & Crawford 1982), the negative effect of flooding on plant performance was stronger for the species associated with the plateau, i.e. *Oenocarpus*. This result was consistent with the lower germination of *Oenocarpus* seeds in flooded subplots of the field experiment. However, there was an apparent contradiction in the results for *Socratea* because the pronounced effect of flooding

on germination was not evident in the field. As only three of the 33 lowland subplots with *Socratea* seeds were submersed in water for months, the effect of flooding on germination in the field may not have been fully evaluated. Two of the flooded subplots were protected by exlosures and had lower germination than expected for this protection level (20% vs. an average of 59%). The extended period over which flooded seeds of *Socratea* germinated is likely to reduce survivorship as mortality rates were higher for seeds than for seedlings.

### EFFECTS OF HABITAT AND HERBIVORES

Differences in the flooding regime, and other physical and chemical variables of plateaux and lowlands, may have indirect effects on growth and survival of plants that are mediated by biotic interactions. Most studies emphasize the role of flooding intensity on the outcome of competition among species (e.g. Grace & Wetzel 1981; Bertness & Ellison 1987). Much less understood is how the abiotic factors influence the impact of herbivores on plant populations. Evidence suggests that availability of light, water and nutrients controls the abundance and foraging behaviour of herbivores (Oksanen *et al.* 1981; Coley *et al.* 1985; Hunter & Price 1992; Hartley & Jones 1997), as well as the ability of plants to compensate for losses caused by these animals (Crawley 1997). Therefore, differences in the abiotic environment can lead to distinct impacts of herbivory.

Although protection against herbivores was the factor that explained most of the variance in recruitment, herbivores did not determine differential mortality or growth of species between habitats. If seed or seedling mortality caused by herbivores influenced the observed patterns in abundance, protection should have promoted higher survivorship of *Oenocarpus* in lowlands and of *Socratea* on plateaux. However, the interaction among the effects of protection, species and habitat on recruitment that would have resulted was not significant.

This result contrasts with the majority of studies, which report significantly lower impact of herbivores on recruitment of tropical forest trees in habitats where reproductive plants occur in high densities (Boucher 1981; DeSteven & Putz 1984; Goldberg 1985; Sork 1987; Forget 1992). A notable exception is documented by Janzen (1975), who found almost identical percentages of seed predation in riparian and hillside habitats. Increased survivorship of seeds and seedlings in areas where many adult plants are present has been attributed to satiation of herbivores (Schupp 1992). Satiation was not expected in the field experiment because few *Socratea* and no *Oenocarpus* trees at this site fruited during the period when seeds germinated.

The significant effect of habitat on germination of *Oenocarpus* seeds persisted throughout the experiment. Germination was reduced in lowlands, particularly in flooded areas, and resulted in lower recruitment. In contrast, habitat had no significant effect on either

seed germination or mortality of *Socratea* seedlings, therefore the higher density of *Socratea* in lowlands cannot be attributed to differential recruitment. Data on the above-ground dry biomass of seedlings, however, indicate that growth rates are higher in lowlands. Growth influences the rate at which a size-structured population increases, and thus its abundance, by determining the time taken to reach the reproductive stage and the time spent in smaller, more vulnerable size classes (Werner & Gilliam 1984).

The results varied drastically with plant stage (seed vs. seedling) and demographic process (survivorship vs. growth). The observed spatial patterns in species abundance were consistent with greater survivorship of *Oenocarpus* seeds on plateaux and higher growth rates of *Socratea* seedlings in lowlands. The absence of differential mortality between habitats was also seen when identical numbers of seedlings were transplanted into the two habitats (Pacheco 1999).

#### THE RELATIVE IMPORTANCE OF HERBIVORES AND FLOODING

As the impact of herbivores on seed germination, seedling mortality and growth of the study species was similar on plateaux and in lowlands, I conclude that these animals did not promote differential recruitment of *Oenocarpus* and *Socratea* between habitats. In contrast, the negative effect of flooding on germination of *Oenocarpus* was evident in both experiments, and is consistent with the higher abundance of this species on plateaux, where flooding is less frequent. The greater growth rate of *Socratea* seedlings in lowlands was determined by factors other than flooding or herbivores.

#### IMPLICATIONS FOR THE STRUCTURE AND COMPOSITION OF PLANT COMMUNITIES

Differences in the individual responses of species to the distinct environments (biotic and abiotic) of plateaux and lowlands, as observed in this study, ultimately result in changes in the structure of tropical forest plant communities (Kahn *et al.* 1987; Tuomisto *et al.* 1995; Clark *et al.* 1999; Svenning 1999). Variation in abundance of species and composition of plant communities along small-scale altitudinal gradients are also well documented in many other vegetation types (e.g. Nelson & Anderson 1983; Loeffers & Larkin-Loeffers 1987; Burke *et al.* 1989).

If the impact of herbivores on plant growth and survivorship is similar on plateaux and in lowlands, as documented in this study and in Janzen (1975), then it is likely that changes in abundance of species and structure of plant communities between these habitats are determined by abiotic variables. Flooding inhibits germination of *Oenocarpus* seeds and has a negative effect on growth and survivorship of many species (Joly & Crawford 1982; Mori & Becker 1991; ter Steege 1994; Losos 1995). Plant diversity in periodically inundated

areas is consistently lower than in adjacent uplands (Lieberman *et al.* 1985; Junk 1989; Ferreira 1997). Additional experiments indicate that drought inhibits growth of *Socratea* seedlings on plateaux (Pacheco 1999). Water may be the most important factor generating variation in recruitment of species between plateaux and lowlands.

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