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Seeds and seedlings of two neotropical montane understory shrubs respond differently to anthropogenic edges and treefall gaps

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Abstract Edges resulting from forest clear-cutting and treefall gaps can affect plant populations and consequently the distribution of species across landscapes. These two types of disturbance might interact to exacerbate or ameliorate "edge effects", a rarely tested possibility. We focused on the effects of distance from forest edge (0–10, 30–40, 60–70, and 190–200 m) and habitat within forest fragments (treefall gaps and intact forest) on the early stages of development of *Palicourea gibbosa* and *Faramea affinis*, two common shrubs of montane forests in southwest Colombia. Seed germination and seedling growth did not change with distance from forest edge. Within forest fragments, however, seed germination and seedling growth were higher in treefall gaps than in intact forest understory for both species. In contrast, seed predation was influenced by distance from forest edge and in *P gibbosa* it depended on habitat. Seed predation was highest in the forest interior (190–200 m from forest edge) and in *P. gibbosa* this was true only in treefall gap habitats. These results suggest that animal mediated processes such as post-dispersal seed predation are more likely than physiological processes to be affected by anthropogenic edges. Our results provide some evidence that treefall gaps may interact with "edge effects", however, they are inconclusive as to whether they exacerbate or ameliorate them.

Key words Anthropogenic edges · Treefall gaps · Seed germination · Seed predation · Seedling growth

Introduction

Edges resulting from forest clear-cutting can affect the distribution of plants: some species may increase, others may decrease, and still others may experience no change from forest edge to forest interior (Auclair and Cottam 1971; Wales 1972; Ranney et al. 1981; Williams-Linera 1990; Matlack 1994; Restrepo et al. 1999). In many ecosystems, these responses can be ameliorated or exacerbated as a result of the interaction between edges and other types of disturbance (Noss 1991; Wiens 1995; Laurance et al. 1998). In fact, it has been suggested that the importance of such interactions for plant populations are likely to increase as forest fragments become smaller. For example, Janzen (1983) suggested that weeds and second-growth species can increase in forest fragments through the interaction between anthropogenic edges and treefall gaps.

The actual mechanisms driving these changes, however, remain poorly understood. In some instances plants respond to variation in abiotic conditions resulting from disturbance, in others to variation in biotic conditions, including the distribution of predators (e.g., Piñero and Sarukhan 1982; Sork 1983; Schupp and Frost 1989; Sizer 1992; Brown 1993; Burkey 1993; Kapos et al. 1993; Esseen 1994). Variation in these conditions, and thus their effect on plants, may be influenced by type of disturbance. For example, the effects of edges resulting from forest clear-cutting are likely to be greater than those resulting from treefall gaps: anthropogenic edges not only affect larger areas but also persist for longer, so that plants can be affected through several or all stages of their life cycle (e.g., Sork 1983; Blanchard 1992). Although plants can be affected by disturbance at almost any stage, it is the seeds and seedlings that are most vulnerable; moreover, the performance of plants at these stages may largely determine patterns of recruit-

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ment within plant populations (Harper 1994). This might be particularly true for understory shrubs, which, unlike canopy trees, are buffered from the direct effect of some abiotic factors such as sun radiation.

In Neotropical ecosystems, shrubs and herbs become more abundant and diverse with increasing elevation (Gentry 1992a, 1992b). Because in many tropical regions rates of forest clear-cutting also increase with elevation (Cavelier and Etter 1995; Denniston 1995), there are concerns that a disproportionate number of species may be lost from montane ecosystems (Henderson et al. 1991). Understanding the mechanisms that may drive changes in the distribution of plants due to forest clear-cutting may help conservation efforts in these areas. In this paper we concentrate on two Neotropical montane understory shrubs, *Palicourea gibbosa* and *Faramea affinis*, and ask how seed predation, germination, and seedling growth are affected by the combined effect of anthropogenic edges and treefall gaps. *P. gibbosa* and *F. affinis* belong to the Rubiaceae, one of the most speciose families of Neotropical montane forests, and are the dominant species in the understory of some of these forests (Taylor 1989; Gentry 1992a; A. Gentry, unpublished work). Thus, changes in their distribution may not only have a major impact on the structure of montane forests but also on the assemblage of understory frugivores that feed on their fruits.

Methods

The site

This study was conducted at the Reserva Natural La Planada, a transitional tropical premontane wet to rain forest (Holdridge 1967), located at 1800 m in the department of Nariño, southwest Colombia (78°00′W, 1°10′N). La Planada encompasses 3200 ha of mature forest interspersed with second growth and selectively logged areas. In the northwest portion of the reserve where this study took place, forest abuts pastures devoted to cattle grazing. Mean annual rainfall and temperature are 4437 mm and 19°C, respectively; rainfall is distributed in two wet seasons, interrupted by a mild (February-March) and a stronger (June-August) dry season (Reserva Natural La Planada, unpublished work).

La Planada and the surrounding forests are characterized by a high plant diversity, partly due to the presence of an unusual number of endemic herbs and shrubs in the families Araceae, Gesneriaceae, Orchidiaceae, and Rubiaceae (Orejuela 1987). In a 0.1-ha inventory plot 121 species of plants with diameter at breast height (dbh) over 2.5 cm were recorded: *Quararibea*, *Elaegia*, *Hieronyma*, *Alchornea*, *Billia*, *Inga*, *Otoba*, and *Ocotea* were among the most common genera of trees; *Faramea*, *Prestoea*, *Aiphanes*, *Geonoma*, *Palicourea*, and *Miconia* were among the most common genera of subcanopy trees and shrubs (Gentry 1992a; A. Gentry, unpublished work).

The species

Palicourea gibbosa and *Faramea affinis* are found at middle elevations from Panama to Ecuador (Dwyer 1980; C. Taylor, personal communication). In the mountains of southwest Colombia, *P. gibbosa* and *F. affinis* are the commonest understory shrubs (< 4 m height) and treelets (< 7 m height), respectively, in second growth and mature forests (Arias 1993; A. Gentry, unpublished work). In this region, *P. gibbosa* flowers and fruits three times per year: the flowers are pollinated by hummingbirds (*Ocreatus underwoodii*, *Aglaiocercus coelestis*, and *Haplophaedia lugens*) and the seeds dispersed by birds (*Myadestes ralloides*, *Pipreola riefferi*, *Atlapetes brunneinucha*, *Masius chrysopterus*, and *Tangara arthus*; Arias 1993; C. Restrepo and N. Gómez, unpublished work). Ripe fruits of *P. gibbosa* are dark blue to purple, 7 mm long, and contain one or two seeds each measuring 5.0 × 4.9 mm. *F. affinis* flowers and fruits twice per year: the flowers are also visited by hummingbirds (*Coeligena wilsoni*) and the seeds dispersed by birds (*Andigena laminirostris*, *Lipaugus cryptolophus*, *Pipreola riefferi*, *Semnornis ramphastinus*, and *Trogon personatus*; Samper 1992; C. Restrepo and N. Gómez, unpublished work). Ripe fruits of *F. affinis* are blue, 20 × 18.2 mm, and contain a single seed measuring 10.4 × 7.6 mm.

Sampling design

We chose four sites in the northwest portion of La Planada to conduct this study. At three of these sites (Célimo I, Célimo II, and Pialapí) the pastures contiguous to the forest were created around 1950, whereas at the fourth site (Hermógenes) around 1982. Pastures at all but one site (Pialapí) were active; the pasture contiguous to the forest in Pialapi was left fallow in 1982 (Restrepo et al. 1999). At each site we established a 100 × 200 m (2-ha) plot with the long axis perpendicular to the forest edge. Within each plot we delimited four strips (100 × 10 m) running parallel to and located at four distances from the forest edge to the forest interior: 0–10 (D1), 30–40 (D2), 60–70 (D3), and 190–200 (D4) m (Restrepo et al. 1999). Treefall gaps, i.e., canopy openings penetrating down to within 2 m of the ground (Brokaw 1982), were mapped at each of the four distances to evaluate the combined effect of habitat (gap versus intact forest) and distance from forest edge on the distribution of fruiting individuals, seeds, and seedlings of *F. affinis* and *P. gibbosa*.

Canopy structure

We used a LAI-2000 plant canopy analyzer (Li-Cor, Inc.) to estimate leaf area index [LAI = foliage area (m^2)/ground area (m^2)] and characterize the structure of the canopy. Since estimates of LAI obtained with this instrument are based on the transmitted fraction of incident radiation on the canopy they often underestimate true LAI (Chason et al. 1991; Hannan and Bégué 1995). Nevertheless, in the context of this study these values are useful to describe relative changes in canopy structure across the pasture-forest edge. In October 1993 we laid down three transects at each of three edges (Célimo I, Célimo II, and Pialapí), the transects running perpendicular to the edges and extending 10 m into the pasture and 210 m into the forest. The transects were separated from each other by 50 m. LAI readings were made every 5 m in the first 50 m of the transects, every 10 m in the next 130 m, and every 20 m in the last 40 m. At each point we made four consecutive below-canopy readings that together were paired with a single reading taken in an area devoid of trees and shrubs in the nearby pasture. The four readings were averaged to obtain a single value per sampling point. We always kept the lens and optical sensor covered by a 45° view cap, pointing in the same direction, and 1.5 m above the ground.

Distribution of fruiting individuals

We subdivided each of the four 100 × 10 m strips within each plot into five 20 × 10 m quadrats (Célimo I, Célimo II, and Pialapí). The 20 × 10 m quadrats were further subdivided into four 10 × 5 m subquadrats, and two of these per quadrat were chosen at random to census fruiting individuals of *F. affinis* and *P. gibbosa*. Each subquadrat was assigned to either gap or intact forest habitat: a subquadrat was classified as "gap" if it was within a treefall gap or located < 5 m from a treefall gap edge, and as "intact forest" if it was located 35 m from the nearest treefall gap edge at the time the study began (Restrepo et al. 1999). Sampling took place over a 12-month period (September 1992–August 1993, excluding December).

Seed predation and seed germination

We selected four treefall gaps that were paired with intact forest habitats at each distance per site (Hermógenes, Célimo I, and Célimo II) to evaluate the combined effect of distance from forest edge and habitat (gap versus intact forest) on seed predation and seed germination. For each plant species we placed two aluminum trays (15 × 7 cm) in each treefall gap and paired intact forest habitats: one tray was used in the seed predation and the other in the seed germination experiment. The trays were punctured to prevent water from accumulating, filled with soil, and positioned flush with ground level. Intact, cleaned seeds from fresh, ripe fruits of *P. gibbosa* and *F. affinis* (1440 and 720 seeds, respectively) were sown in the trays: ten into each of the *P. gibbosa* and five into each of the *F. affinis* trays. Trays used to evaluate germination rates were covered with galvanized mesh (5 × 5 mm) to protect seeds from vertebrates whereas those used to evaluate predation rates were left uncovered. The germination and predation experiments were run simultaneously. We placed eight trays for each plant species per distance per edge per experiment (384 trays in total).

The trays were checked weekly in order to establish the number of seeds that had survived (predation experiment) and germinated (germination experiment). Seeds in which the hypocotyl was at least 3 mm long were recorded as germinated. The predation experiments lasted 42 (*P. gibbosa*, July 1993–August 1993) and 108 (*F. affinis*, August 1993–December 1993) days at each site. The germination experiments lasted 105 (*P. gibbosa*, July 1993–November 1993) and 252 (*F. affinis*, August 1993–April 1994) days at each site. We concluded the seed predation experiments when seeds stopped being removed and the seed germination experiments when 90% of the seeds had germinated. Throughout this paper we assume that seeds that were missing from the trays were taken by vertebrates and that this constituted predation.

Seedling growth and leaf production

Seedling growth and leaf production were monitored at three distances [0–10 (D1), 30–40 (D2), and 60–70 (D3) m] at each of three sites (Célimo I, Célimo II, and Pialapí). We located a total of 397 *P. gibbosa* and 431 *F. affinis* seedlings (23 ± 5 seedlings per species per habitat per distance, each measuring 5.8 ± 1.1 cm, mean ± 1 SD). In order to standardize measurements, we marked the seedling's stems with yellow vinyl paint (*c.* 1.5 cm above soil surface) and their youngest pair of leaves with threads of flagging tape tied around the petioles. A first measurement of the seedling's height from the yellow mark to the base of the meristem and of the number of leaves was taken in October 1992 and this procedure was repeated in April 1993. A final count of new leaves was done in October 1993.

Seedling growth is expressed in terms of absolute and relative growth rates. The former represents the increment in height between the first and last measurement per number of days elapsed between measurements; the latter represents the increment in height between the first and last measurement per unit height per number of days elapsed between measurements. Leaf production is expressed as the number of new leaves produced between the first and last period of observation per number of days elapsed between the observations (Sizer 1992). In all cases increments are expressed on a yearly basis.

Analyses

Data were analyzed with ANOVAs for mixed factorial designs (Winer et al. 1991; Girden 1992). In the ANOVA tables we specify the type of design, which includes as factors of interest distance from edge, habitat, and month. We averaged growth and leaf production rates for all seedlings per species per habitat per distance per edge to improve the normality of the data sets, reduce their dimensionality, and eliminate problems associated with unbalanced data sets (number of seedlings per gap and intact forest habitats differed). We verified the assumption of compound symmetry for repeated measure ANOVAs and report *P*-corrected values based on the liberal Huynh-Feldt method (Girden 1992). In addition, we plotted the residuals as a function of fitted *y* values to detect any violation of assumptions for ANOVAs (Manly 1992).

Results

Canopy structure

LAI differed from pasture to forest interior (repeated-measure ANOVA with edge and distance included as between and repeated factors, respectively; $F_{25,150} = 4.7$, $P = 0.0001$; Fig. 1). The effect of distance on LAI, however, was exclusively due to the LAI-pasture values: once these were removed from the ANOVA, LAI did not change from the forest edge to the forest interior. This indicates that at our three edges, canopy structure 1.5 m above the ground does not vary in a predictable way from the forest edge towards the forest interior, perhaps reflecting an uneven canopy resulting from frequent treefall gaps.

Distribution of fruiting individuals

The distribution of *F. affinis* did not vary from forest edge to forest interior in gap or intact forest habitats; however, we found a higher number of individuals in fruit in intact forest than in gap habitats (replicated goodness-of-fit test, $df = 3$, $G_{\text{Heterogeneity}} = 30.8$,

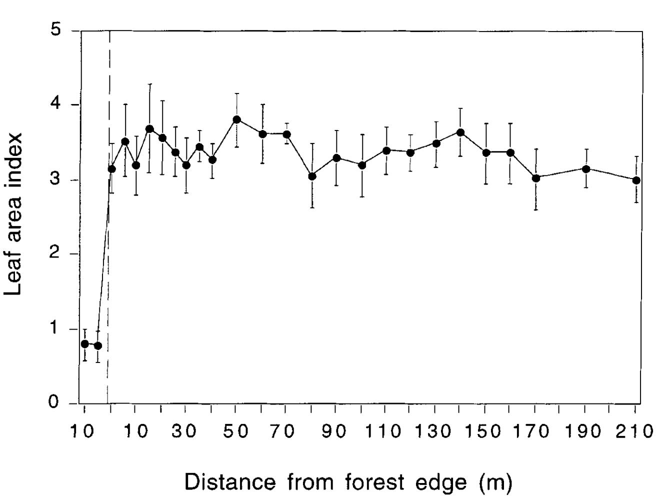

Fig. 1 Variation in leaf area index (LAI) across pasture/forest edge. Each *point* represents the average of 9 readings per distance (3 transects × 3 edges). The *dashed line* indicates position of forest edge. *Points* represent means and *bars* ±1 SE

$P < 0.001$; Fig. 2). *P. gibbosa* showed a different pattern: the distribution of individuals in fruit varied from forest edge to forest interior in gap but not in intact forest habitats (replicated goodness-of-fit test, $df = 3$, $G_{\text{heterogeneity}} = 9.5$, $P < 0.05$; Fig. 2). Variation among the four distances in gap habitats, however, suggests a bimodal distribution.

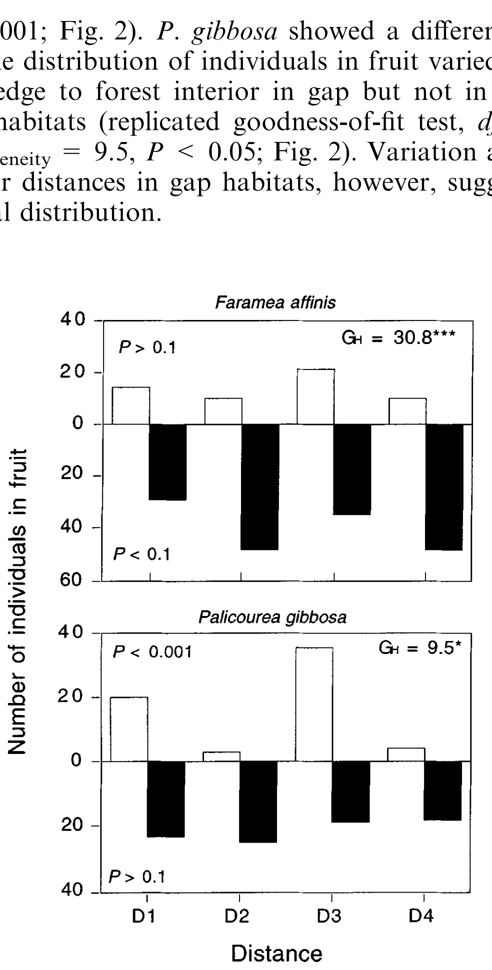

Fig. 2 Distribution of *Faramea affinis* and *Palicourea gibbosa* individuals in fruit from edge to forest interior as a function of habitat. A significant *G*-statistic for heterogeneity (G_H) indicates that the two samples (gap and intact forest) were different. The *P* values are associated with a *G*-statistic comparing the observed distribution among the four distances either in treefall gaps (*open bars*) or intact forest (*filled bars*) against a uniform distribution (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$)

Seed predation and seed germination

Patterns of seed predation differed between *P. gibbosa* and *F. affinis*: seeds of *F. affinis* had higher survival rates than those of *P. gibbosa* (Fig. 3). Distance from forest edge influenced the proportion of seeds that survived in both species. In *F. affinis*, the proportion of seeds that survived over time varied with distance (ANOVA, week × distance effect, $P = 0.002$; Table 1, Fig. 4) and it was lower in the trays at D4 (190–200 m) than at D1 (0–10 m). In *P. gibbosa*, the proportion of seeds that survived over time also varied with distance, but unlike *F. affinis* it depended on habitat (ANOVA, week × distance × habitat effect, $P = 0.007$; Table 1). By week 6, for example, the proportion of seeds that had survived was lowest at D4 in treefall gap than in intact forest at the same distance (Fig. 5). At D2, on the other hand, seed survival was higher in treefall gap than in intact forest habitats.

Patterns of seed germination also differed between *P. gibbosa* and *F. affinis*: seeds of *P. gibbosa* germinated faster than those of *F. affinis* (63 versus 224 days for half

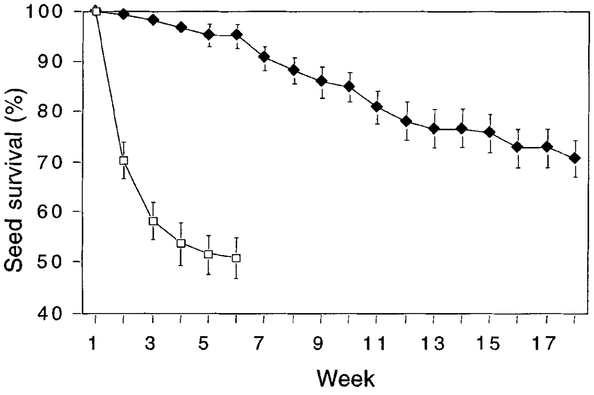

Fig. 3 Seed predation in *F. affinis* (*filled diamonds*) and *P. gibbosa* (*open squares*) over time. *Points* represent means and *bars* ±1 SE

Table 1 Results of four ANOVAs on predation and germination of *Faramea affinis* and *Palicourea gibbosa* seeds. The ANOVAs are for a split-plot design with one repeated measure (week). *Distance (D)* and *Habitat (H)* represent the plot and subplot levels, respectively. *Edges (E)* are the replicates

	Predation						Germination					
	F. affinis			*P. gibbosa*			*F. affinis*			*P. gibbosa*		
	df	MS	*F*	*df*	MS	*F*	*df*	MS	*F*	*df*	MS	*F*
Distance	3	11.28	1.45	3	2.54	0.09	3	2.41	1.73	3	5.08	1.04
Edge (Distance)	8	5.30		8	27.27		8	1.39		8	4.89	
Habitat	1	2.64	0.46	1	12.99	3.05	1	3.19	4.58^a	1	20.78	5.41*
H × D	3	8.31	1.44	3	16.63	3.91*	3	0.71	1.01	3	4.51	1.17
H (D × E)	8	5.78		8	4.26		8	0.70		8	3.84	
Week	17	6.27	40.93***	5	86.50	268.31***	35	25.81	502.29***	14	242.40	658.89***
W × D	51	0.25	1.60*	15	0.17	0.13	105	0.11	0.86	42	0.53	0.46
W × E (D)	136	0.17		40	1.31		280	0.12		112	1.15	
W × H	17	0.24	1.49	5	0.72	2.24^a	35	0.11	2.11*	14	1.26	3.41***
W × H × D	51	0.18	1.19	15	0.86	2.68**	105	0.06	1.12	42	0.27	0.74
W × H (D × E)	136	0.15		40	0.32		280	0.05		112	0.37	

***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, $^a P < 0.1$, *P*-values for the effects of the repeated measures corrected using the Huynh-Feldt method

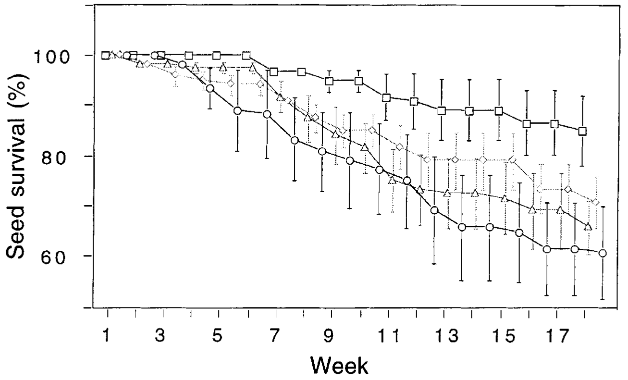

Fig. 4 Variation in seed predation in *F. affinis* as a function of distance from forest edge over time, for distances D1 (0–10 m, *squares*), D2 (30–40 m, *triangles*), D3 (60–70 m, *diamonds*), and D4 (190–200 m, *circles*). *Points* represent means and *bars* ±1 SE

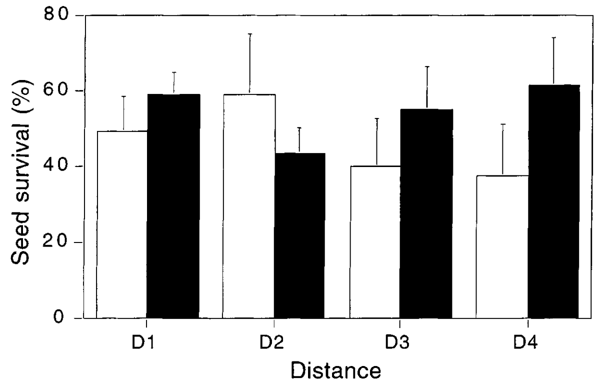

Fig. 5 Variation in seed predation in *P. gibbosa* as a function of distance from forest edge and habitat by the last week of the experiment (W6). Treefall gaps and intact forest habitats are represented by *open* and *filled bars*, respectively (mean +1 SE)

of the seeds to germinate; Fig. 6). In both species, habitat but not distance influenced the number of seeds that germinated over time (ANOVA, week × habitat effect for *F. affinis* and *P. gibbosa*, $P = 0.02$ and $P = 0.003$, respectively; Table 1). A higher percentage of seeds germinated in gap than in intact forest habitats (Fig. 7). In *F. affinis*, however, these differences were less pronounced and disappeared by week 36.

Seedling growth and leaf production

Seedlings of *P. gibbosa* and *F. affinis* also differed: those of *P. gibbosa* grew faster and produced more leaves than those of *F. affinis* (Tables 2, 3). In both species, habitat but not distance influenced absolute growth rates of seedlings (ANOVA, *F. affinis* and *P. gibbosa*, $P = 0.05$ and $P = 0.03$, respectively; Table 2). Seedlings grew faster in gap than in intact forest habitats, but the effect of habitat was stronger in *P. gibbosa* than in *F. affinis* (Table 3). Neither relative growth rates nor leaf production was influenced by distance or habitat in either species.

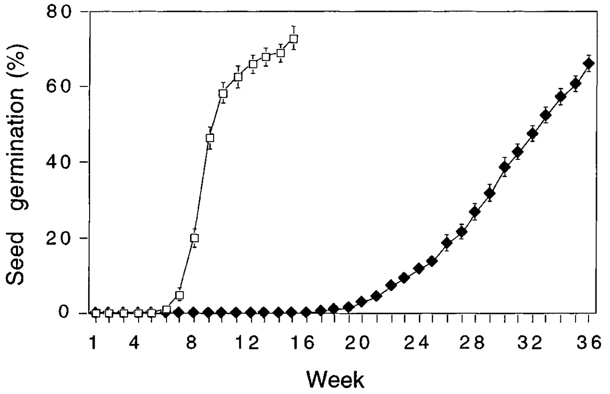

Fig. 6 Seed germination in *F. affinis* (*filled diamonds*) and *P. gibbosa* (*open squares*) over time. *Points* are means and bars ±1 SE

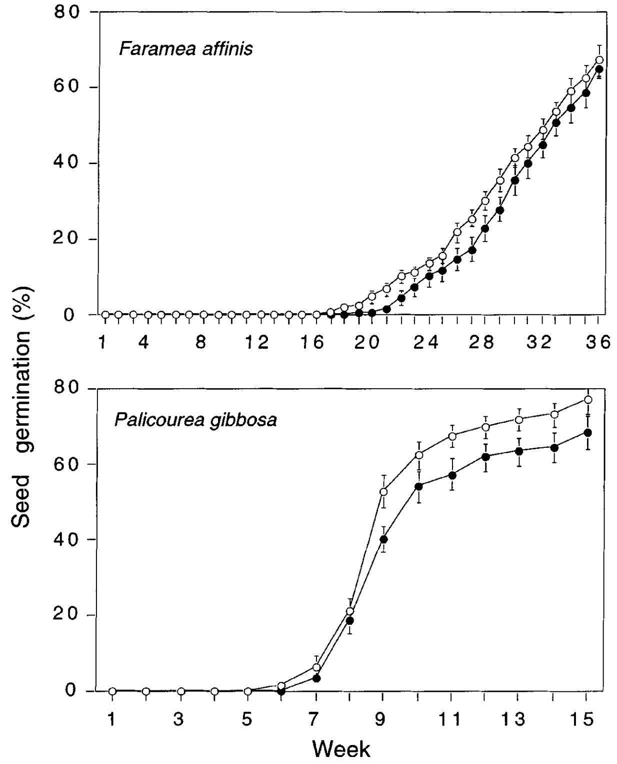

Fig. 7 Variation in seed germination in *F. affinis* and *P. gibbosa* as a function of habitat: treefall gaps (*open circles*) and intact forest (*filled circles*)

Discussion

Even though seed predation, seed germination, and seedling growth rates differed between *F. affinis* and *P. gibbosa*, suggesting variation in their life histories, the two species responded in similar ways to the creation of edges and treefall gaps: seed predation was influenced by distance from forest edge whereas seed germination and seedling growth were influenced by habitat. These results suggest that animal-mediated processes such as post-dispersal seed predation may be more likely than

Table 2 Results of six ANOVAs on absolute and relative growth rates and leaf production of *F. affinis* and *P. gibbosa* seeds. The ANOVAs are for a 0-between, 2-within repeated-measure design. *Distance (D)* and *Habitat (H)* represent the repeated measures. *Edges (E)* are the replicates

		Absolute growth rates				Relative growth rates				Leaf production			
		F. affinis		*P. gibbosa*		*F. affinis*		*P. gibbosa*		*F. affinis*		*P. gibbosa*	
	df	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Edge	2	4.3×10^{-4}		1.1×10^{-5}		0.1		2.6		1.0×10^{-5}		1.6	
Distance	2	0.001	1.75	4.0×10^{-4}	0.09	0.001	0.003	0.3	0.1	3.9×10^{-6}	1.9	7.2	0.4
D × E	4	3.5×10^{-4}		0.004		0.2		2.0		2.1×10^{-6}		1.7×10^{-5}	
Habitat	1	0.001	18.4*	0.02	33.4*	0.05	3.66	4.3	8.7[a]	6.6	2.5	8.2	1.2
H × E	2	4.8×10^{-5}		4.6×10^{-4}		0.01		0.5		2.6×10^{-6}		6.8	
H × D	2	1.8×10^{-4}	1.04	1.7×10^{-4}	0.17	0.001	0.025	0.5	2.1	1.0	0.8	7.3	2.4
H × D × E	4	1.8×10^{-4}		0.001		0.1		0.2		1.2		3.0×10^{-6}	

***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, [a]$P < 0.1$, P-values for the effects of the repeated measures corrected using the Huynh-Feldt method

Table 3 Growth rates, relative growth rates, and leaf production in *F. affinis* and *P. gibbosa* as a function of habitat (mean ± 1 SE)

	Absolute growth rates (mm year^{-1})		Relative growth rates (mm mm^{-1} year^{-1})		Leaf production (number of leaves year^{-1})	
	F. affinis	*P. gibbosa*	*F. affinis*	*P. gibbosa*	*F. affinis*	*P. gibbosa*
Gap	29.52 ± 2.16	66.96 ± 5.76	1.07 ± 0.10	3.71 ± 0.4	5.04 ± 0.36	9.72 ± 0.36
Intact forest	24.96 ± 1.80	46.08 ± 2.88	0.97 ± 0.08	2.73 ± 0.25	4.68 ± 0.36	9.36 ± 0.36

physiological processes to be affected by anthropogenic edges.

Seed survival was lowest in the forest interior (190–200 m, D4) than at the forest edge (0–10 m, D1). In *F. affinis*, seed survival was lowest in the forest interior irrespective of habitat. These results are in agreement with those obtained by Samper (1992) at La Planada for *F. affinis* and 12 other species showing that seed predation was not affected by the creation of treefall gaps (but see Schupp 1988 for *F. occidentalis* in the lowlands of Panama). In *P. gibbosa*, however, seed survival was lowest in the forest interior but only in treefall gap habitats. Differences between *F. affinis* and *P. gibbosa* in the combined effect of distance and habitat may be related to differences in seed size, and thus seed predator size: seeds of *F. affinis* (10.4 × 7.6 mm) are much larger than those of *P. gibbosa* (5.0 × 4.9 mm) and large and small seed predators may respond differently to gaps of different size (Hulme 1994; Sanchez-Cordero and Martínez-Gallardo 1998). These results suggest that changes in the biotic conditions, i.e., distribution of seed predators, may be responsible for the observed patterns. Specifically, vertebrates that feed on *F. affinis* and *P. gibbosa* seeds may be avoiding forest edges. The few other studies that have examined how distance from forest edge influences seed survival have found results similar to ours (Sork 1983; Burkey 1993; Osunkoya 1994; but see Holl and Lulow 1997; Ostfeld et al. 1997).

The germination experiments showed that seeds of *F. affinis* and *P. gibbosa* have dormancy periods of 112 and 35 days, respectively, falling within the range reported for other rubiaceous species (Lebrón 1979; Garwood 1983; Schupp 1988). In spite of differences in seed dormancy, seed germination rates were higher in treefall gap than in intact forest habitats for both species (results, however, were more robust for *P. gibbosa*); distance from forest edge did not have any effect. Seedlings responded in a similar way to seeds: habitat but not distance had an effect on seedling growth. We did not monitor seedlings in the forest interior (D4, 190–200 m), opening the possibility that distance could have had an effect on seedling growth. However, because factors affecting seed germination and seedling growth are similar, we conclude that the trends shown by the seedlings regarding the influence of habitat rather than distance on growth would have been maintained if seedlings had been sampled at D4. These results would be in agreement with other studies showing a strong effect of treefall gaps on seed germination and/or seedling growth for a variety of species (e.g., Lebrón 1979; Denslow et al. 1990; Raich and Wooi-Khoon 1990; Samper 1992; Ellison et al. 1993).

Our results differ from others that have shown differences in seed germination and seedling growth from edge to forest interior (Sork 1983; Sizer 1992). Reduced variation of abiotic conditions resulting from edge creation and/or reduced susceptibility of *F. affinis* and *P. gibbosa* seedlings to existing conditions may explain differences among studies. For example, we found that LAI, which provides an estimate of canopy opening, did not change from edge to forest interior. Also, the area covered by treefall gaps did not vary among the four distances (repeated-measures ANOVA, $F_{3,12} = 0.2$, $P = 0.8$; C. Restrepo, unpublished work). In another study conducted north of our study area, Murcia (1993) found that soil moisture changed little from forest edge to forest interior (up to 10 m and only during the dry season). These findings from montane tropical areas suggest that changes in abiotic conditions from edge to forest interior may not be as pronounced as in the lowlands (Laurance et al. 1997, 1998; Benítez-Malvido 1998).

An interaction between edges of anthropogenic origin and treefall gaps was supported by the seed predation experiment in *P. gibbosa*. In a parallel study, Restrepo et al. (1999) found that fruit production was influenced both by distance from forest edge and habitat: fruit numbers were lowest at D4 in treefall gap habitats. It was suggested that either lower fruit production or higher removal rates at D4 than at the other distances could explain these results. Whether treefall gaps are ameliorating or exacerbating the effect of edges is difficult to establish. Increased seed predation and possibly fruit removal rates at D4 in treefall gap habitats, suggest that treefall gaps may exacerbate the effect of edges. On the other hand, variation in the distribution of individuals in fruit of *F. affinis* and *P. gibbosa* between habitats (treefall gap versus intact forest) from edge to forest interior suggests that the random creation of treefall gaps within forest fragments may ameliorate the effect of edges. From a plant or animal perspective, fragmented landscapes may not just represent forest and clear-cut areas separated by well-defined edges; in some instances, the characteristics of the immediate surroundings may override the effects of edges.

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