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Edge Effects on Germination, Seedling Establishment, and Population Structure of *Parkia pendula* in an Atlantic Forest Fragment, NE Brazil

Daniel Piechowski[1*] • Gerhard Gottsberger[2]

[1] Institute of Systematic Botany and Ecology, Ulm University, Albert-Einstein-Allee 11, 89081 Ulm, Germany
[2] Botanical Garden and Herbarium, Ulm University, Hans-Krebs-Weg, 89081 Ulm, Germany
Corresponding author: * **danielpiechowski@web.de**

ABSTRACT

Edge effects on germination, seedling establishment, and the population structure of *Parkia pendula* were studied in a fragment of northeastern Brazilian Atlantic Forest. Germination and seedling survival were observed underneath adult trees in the edge zone and in the forest interior; the population structure was examined in plots with a total area of 1 ha in each environment. The overall germination rate was very low but significantly higher in the forest interior than in the edge zone (0.52% vs. 0.21%). Furthermore, the seedlings' survival time was significantly longer in the forest interior. The probability to survive the first nine months after germination was three times higher in the forest interior. The higher germination rate and the better seedling establishment in the forest interior seem to be the reasons for the significantly higher seedling density within the forest interior. However, the patterns of saplings and juvenile trees differed from the seedling pattern. The sapling density was similar in both environments, but the density of juvenile trees was three times higher in the edge zone. Seedling density is therefore an improper prediction for the pattern of later size-classes.

Keywords: Fabaceae, forest fragmentation, Mimosoideae, seed dormancy, seedling survival, tropical forest
Abbreviations: dbh, diameter at breast height; **rcd**, root collar diameter

INTRODUCTION

Parkia pendula is a typical (Andrade-Lima 1960; Ferraz *et al.* 2004) and abundant (Guedes 1998; Siqueira *et al.* 2001) species of the northeastern Atlantic Forest. Its density in this region is much higher than in the Amazonian forests (Peres 2000; M.J.G. Hopkins pers. comm.).

The results published so far about the germination ability and survival rates of *P. pendula* differ widely. According to Rizzini (1977), seeds of *P. pendula* "refuse to germinate under any experimental set of conditions" including e.g., mechanical scarification. Similar observations were made by Teppner (pers. comm.). On the other hand, Alencar and Magalhães (1979) obtained a germination rate of 58.5% using untreated seeds and Barbosa and collaborators (1984) got germination rates of *ca.* 70% using different pre-germination treatments including mechanical and chemical scarification. Scarano and Crawford (1992) even obtained a germination rate of 80%. All these studies used a similar high number of repetitions and time spans for their experiments. Beside these laboratory tests, germination of *P. pendula* seeds was also analyzed in comparable field studies. Camargo and collaborators (2002) directly sowed the seeds after mechanical scarification at undisturbed forest, secondary vegetation, pasture, and bare soil sites. Germination rate was highest at the bare soil transects (*ca.* 70%), but low at the other three sites (*ca.* 15%, 5%, 0%, respectively). Germination experiments by Schulze (2003) in logging gaps and neighboring forests revealed an "overall extremely low germination rate for *P. pendula*" of 4.6%. Furthermore, he found no significant difference in germination rates between untreated and manually scarified seeds.

In relation to growth and survival, Knowles and Parrotta (1995) recorded a vigorous shoot growth and survival rate greater than 75% during the first two years after planting seedlings of *P. pendula* at an open reforestation site. On the contrary, only *ca.* 25% of the *P. pendula* seedlings on bare soil sites survived the first year whereas the seedlings at forest and secondary forest sites died within this period (Camargo *et al.* 2002).

Forest edges are known to have an enormous influence on the seed production of *P. pendula* trees (Piechowski 2007b) as well as on the secondary dispersal of their seeds by ants (Piechowski 2007b). These two processes in a plant's "seed dispersal cycle" (Wang and Smith 2002) are crucial for the following processes of germination and recruitment and therefore seedling distribution (Wang and Smith 2002). These edge effects on *P. pendula* could sustain from the pre-germination level to the next levels up to population structure. Furthermore, beside these edge effects, germination and recruitment itself are known to be influenced by factors that are altered by forest edges, like the quantity and quality of irradiance, soil moisture, litterfall, and pathogen damage (Sizer and Tanner 1999; Bloor and Grubb 2003; Pearson *et al.* 2003; Asbjornsen *et al.* 2004; Benítez-Malvido and Lemus-Albor 2005; López-Barrera and Newton 2005).

The goal of this study was to determine possible differences in germination, seedling establishment, and population structure of *P. pendula* between locations in the forest interior and in the forest edge zone in an Atlantic Forest fragment in Northeast Brazil.

MATERIALS AND METHODS

Study area

The study was carried out in the 306 ha sized forest fragment *Piedade* (7°49′12.66″-7°50′55.43″S, 35°0′35.92″-34°59′21.29″W), property of the Usina São José, municipality of Igarassu, Pernam-

Received: 23 April, 2008. Accepted: 30 June, 2008.

buco State, Northeast Brazil. The matrix surrounding this fragment consists of sugarcane fields. The climate of this region is characterized by a rainy season from April to August (CPRH 2003). The annual precipitation is 1,520 mm but shows strong inter-annual and spatial variations (Schessl *et al.* 2008). The temperature is relatively constant along the year at *ca*. 25 °C (Schessl *et al.* 2008). An analysis of a time series of aerial photographs and satellite images revealed that the creation of the *Piedade* fragment out of continuous forest is relatively old since the shape and size of this fragment has not changed within the last 30 years. This remnant is believed to be much older although precise data are lacking (Schessl *et al.* 2008). An inclusion of further forest fragments in this study was logistically impossible.

Studied species

Parkia pendula (Willd.) Walp. (Fabaceae, Mimosoideae) is the most widely distributed Neotropical *Parkia* species, occurring in lowland terra-firme forests from Honduras in Central America southwards to the Atlantic Forest of the Brazilian state of Espírito Santo (Hopkins 1986). The adult trees are easily recognizable by their very distinctive flattened crown (Ribeiro *et al.* 1999). Its density in Northeast Brazil is much higher than in the Amazonian forests (Peres 2000; M.J.G. Hopkins, pers. comm.). This species is known to be pollinated by bats (Carvalho 1961; Hopkins 1984) and primarily dispersed by primates and parrots (Peres 2000). In the study area, eight mammalian species from five orders were observed to feed on *P. pendula* buds, nectar, and seedpod gum (Piechowski 2007a, 2007b). Trees in the forest edge zone at the *Piedade* fragment produce significantly more seeds than trees in the forest interior (Piechowski 2007b) and secondary seed dispersal by ants is much higher in the forest interior (Piechowski 2007b).

Germination and seedling establishment

In early February 2004, one month after seedpod opening, 32 circular plots (diameter: 6 m; area: 28.27 m²) were installed underneath the crowns of fruit-bearing *P. pendula* trees in the edge zone and the interior of the forest (14 and 18 trees respectively). All *P. pendula* seedlings (**Fig. 1**) within the plots were marked individually with colored wooden spikes. Monthly, the number of leaves per seedling and the total number of seedlings per plot were counted and new sprouted seedlings were marked. The last counting was in December 2004, right before the release of new seeds.

All variables were calculated for a standard area of 100 m^2 per tree and were set into relation to the number of produced seeds per 100 m^2 crown area (Piechowski 2007b) to calculate a comparable germination rate per tree. Therefore, the 'germination rate' term adopted here is the percentage of germinated seeds underneath the mother-tree per produced seeds, calculated for equal areas. This calculation of germination rate ignores primary as well as secondary seed dispersal and predation and is therefore somehow simplified.

Fig. 1 ***P. pendula*** **seedling.** Illustration by J. Piechowski after a photograph.

Since the data were not normally distributed (Shapiro-Wilk-test of normality), the non-parametrical Mann-Whitney U test was used to detect differences between the two habitats using the software-package SPSS for Windows 11.0 (SPSS Inc. 2001). The seedling survival time was calculated using the Kaplan-Meier survival analysis. The survival time was set to a half month for seedlings, which were not detected the month after their first registration, since a zero is interpreted as missing data by the software. Fisher's exact test was used to analyze the leaf growth between the habitats. The Kaplan-Meier survival analysis and Fisher's exact test were performed using SigmaStat 3.5 (Systat Software Inc. 2006).

Population structure

Ten 20 m × 50 m plots were installed each in the forest edge zone and in the forest interior of the *Piedade* fragment in March 2005. All plots were subdivided in ten 10 m × 10 m sub-plots. The plots were located parallel to the forest edge. The diameter at breast height (dbh) of all *P. pendula* individuals > 2 m in height was calculated after measuring the circumference at breast height following Condit (1998); the tree height was estimated. The root collar diameter (rcd) and height of all *P. pendula* individuals < 2 m in height were measured in four randomly chosen sub-plots per plot. Because many seedlings and saplings were < 15 cm in height, the rcd was measured at soil level with a caliper. Tree position was recorded per sub-plot. An individual was classified as 'seedling' if the simplified prophyll was still attached; all individuals that already had lost their prophyll and were < 2 m in height were classified as 'saplings'; individuals > 2 m in height and a dbh < 19.5 cm were classified as 'juveniles'; all larger individuals were classified as 'adults'. The dbh threshold between juvenile and adult trees was chosen since it was the dbh of the smallest flowering *P. pendula* tree observed within the *Piedade* fragment.

RESULTS

Germination and seedling establishment

In total, 1,465 *P. pendula* seedlings were monitored, 750 of them in the edge zone and 715 in the forest interior. The median number of *P. pendula* seedlings underneath the adult tree crowns in the edge zone (180.5) was significantly higher than in the forest interior (76.1) (Mann-Whitney U: 70.5; p = 0.034). This higher number arose from the significantly higher number of newly germinated seedlings in February (54.9 vs. 21.2; Mann-Whitney U: 63.5; p = 0.016), one month after pod opening. The number of new seedlings did not differ between environments during the remaining year (**Fig. 2**).

This relation changes dramatically after considering the seed production per tree in the two environments (Piechow-

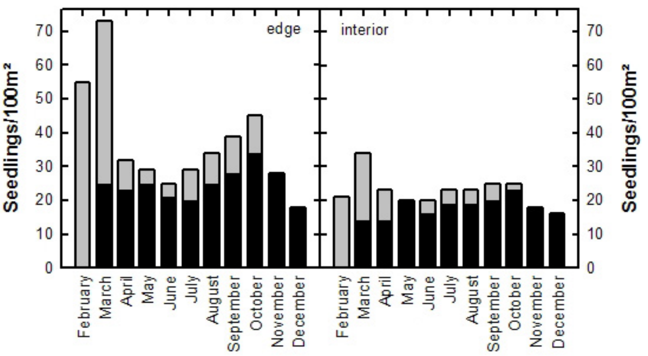

Fig. 2 Median number of ***P. pendula*** **seedlings per 100 m² in the edge zone and forest interior of the** ***Piedade*** **fragment, municipality of Igarassu, NE Brazil.** Gray bars: newly germinated seedlings; black bars: old seedlings.

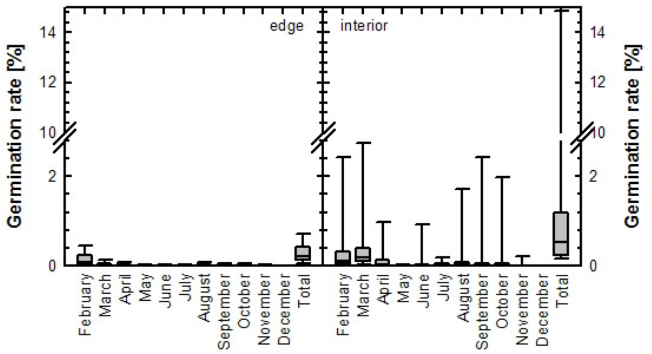

Fig. 3 Monthly and total germination rate [%] underneath *P. pendula* trees in the edge zone and forest interior of the *Piedade* fragment, municipality of Igarassu, NE Brazil.

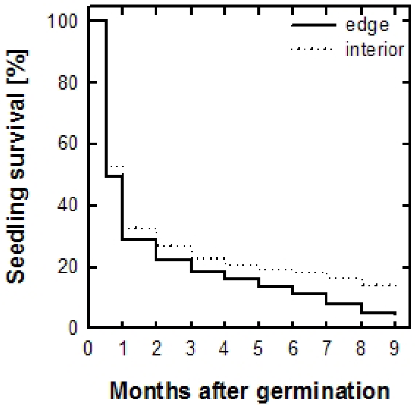

Fig. 4 Seedling survival rate [%] underneath *P. pendula* trees in the edge zone and forest interior of the *Piedade* fragment, municipality of Igarassu, NE Brazil.

Table 1 Median survival times of *P. pendula* seedlings underneath the mother trees in the edge zone and forest interior of the *Piedade* fragment, municipality of Igarassu, NE Brazil.

	n	Median (month)	25/75 percentile (month)	Log-Rank statistic	p
edge	750	<1	<1/2	11.949	<0.001
interior	715	1	<1/3		

ski 2007b). In median, 0.21% of the produced seeds germinated underneath the mother trees in the forest edge zone. The median germination rate underneath trees in the forest interior was 0.52%, which was significantly higher (Mann-Whitney U: 52.0; p = 0.004). The monthly germination rates showed a clear tendency towards a germination of *P. pendula* seeds during the first two months after seedpod opening. Furthermore, the ability of a several months lasting germination delay was also obvious, especially in the forest interior (**Fig. 3**).

Beside the median number of seedlings per tree and their germination rate, the seedlings' median survival time differed significantly between the two environments. The median survival time was one month in the forest interior and less than one month in the forest edge zone (**Table 1**). The probability to survive the first nine months after germination was three times higher in the forest interior compared with the forest edge zone (13.2% and 4.3%, respectively; **Fig. 4**).

The higher number of germinated seedlings underneath the mother trees in the forest edge zone (**Fig. 2**) and the higher germination rate in the forest interior (**Fig. 3**) in combination with the higher survival probability (**Fig. 4**) led to an equal seedling density in the two environments at the end of the observation in December 2004 (**Fig. 2**).

In the forest edge zone, 89% of the seedlings that germinated in February and survived until December had more leaves than their prophyll. This rate was 82% in the forest interior, which is not significantly different (Fisher's exact test: p = 1.0).

The median number of leaves differed significantly only in March, when the seedlings in the forest edge zone had 0.07 leaves additional to their prophyll and the seedlings in the forest interior had none (Mann-Whitney U: 63.0; p = 0.016). Although not significantly different, there was a trend towards more leaves per seedling in the forest interior later on. In December, the median number of additional leaves was 0.85 in the forest interior and 0.28 in the forest edge zone (Mann-Whitney U: 88.5; p = 0.156).

Population structure

Saplings were found to dominate the size-class distribution of *P. pendula* in the forest edge zone as well as in the forest interior, with 335 and 407.5 individuals per ha respectively (**Fig. 5**). Three adult trees per ha were found in the forest edge zone, two in the forest interior (**Fig. 5**). The densities of both size-classes did not differ between the environments (**Table 2**). The densities of the remaining two size-classes differed significantly between the two environments (**Table 2**); the seedling density was higher in the forest interior (27.5/ha vs. 5/ha) whereas the density of juvenile trees was higher in the forest edge zone (99/ha vs. 29/ha; **Fig. 5**).

Besides differences in densities between the two environments, the mean diameter and height were significantly different for saplings and juveniles. Saplings were higher and their rcd was thicker in the forest edge zone (**Table 3**). In opposition, the fewer juvenile trees in the forest interior (**Table 2**) were higher and thicker than the juvenile trees in the forest edge zone (**Table 3**). No differences were detec-

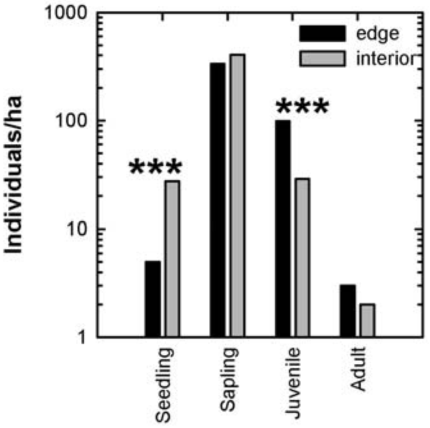

Fig. 5 Seedlings, saplings, juvenile, and adult *P. pendula* individuals per hectare in the edge zone and forest interior of the *Piedade* fragment, municipality of Igarassu, NE Brazil. Asterisks represent highly significant (p<0.001) differences.

Table 2 Number of seedlings, saplings, juvenile, and adult trees of *P. pendula* per hectare, minimum and maximum per 100 m² plot, and their p-values in the edge zone and forest interior of the *Piedade* fragment, municipality of Igarassu, NE Brazil.

		n/ha	Min-Max/ 100 m² plot	U	p
seedling	edge	5.0	0 – 0.5	3,450.0	< 0.001
	interior	27.5	0 – 1.3		
	total	16.3	0 – 1.3		
sapling	edge	335	0 – 8.3	4,900.0	0.806
	interior	407.5	0 – 17.5		
	total	371.3	0 – 17.5		
juvenile	edge	99.0	0 – 10.0	3,626.0	< 0.001
	interior	29.0	0 – 5.0		
	total	64.0	0 – 10.0		
adult	edge	3.0	0 – 1.0	4,950.0	0.651
	interior	2.0	0 – 1.0		
	total	3.0	0 – 1.0		

Table 3 Mean diameter and height of saplings and juvenile *P. pendula* individuals in the edge zone and forest interior of the *Piedade* fragment, municipality of Igarassu, NE Brazil.

			Mean ± SD	**Min – Max**	**U**	**p**
saplings	rcd [cm]	edge	0.6 ± 0.5	0.1 – 2.8	8,480.0	0.001
		interior	0.4 ± 0.5	0.1 – 4.4		
		total	0.5 ± 0.5	0.1 – 4.4		
	height [cm]	edge	37.8 ± 30.3	11 – 171	8,534.0	0.001
		interior	27.9 ± 20.1	3 – 140		
		total	32.4 ± 25.6	3 – 171		
juvenile	dbh [cm]	edge	4.2 ± 2.9	1.0 – 13.9	1,007.5	0.015
		interior	6.4 ± 4.5	0.7 – 18.6		
		total	4.7 ± 3.5	0.7 – 18.6		
	height [m]	edge	5.3 ± 2.6	2 – 11	943.5	0.005
		interior	7.1 ± 3.0	2 – 12		
		total	5.7 ± 2.8	2 – 12		

ted for these parameters in seedlings between the environments. The mean parameters for height and dbh were not calculated for the adult tree class due to their low number of individuals.

DISCUSSION

Germination and seedling establishment

The calculated germination rates can only hardly be compared with experimentally gained germination rates. The germination rates presented here were computed by the number of seedlings underneath the adult tree crowns divided by the extrapolated number of produced seeds (Piechowski 2007b) and therefore disregard primary and secondary seed dispersal, on-site predation as well as the problem of germination underneath the mother tree (Janzen 1971). However, primary dispersal of *P. pendula* seeds was rather uncommon in the study area, since this forest fragment does not host any population of larger primates and large parrots are rare (Piechowski, pers. obs.). Secondary dispersal of *P. pendula* seeds was very frequent (Piechowski 2007b) but even the largest dispersing ant, *Pachycondyla crassinoda*, moved the seeds probably seldom farther than a few meters only (compare seed transport distances of *Pachycondyla harpax* and *P. apicalis* in Horvitz and Schemske 1986). Therefore, secondary dispersed seeds were most likely mainly deposited still within the circular plots. On-site predation rate was the same in both environments (Piechowski 2007b) and therefore lowered the calculated germination rate equally. Furthermore, density-depending effects (pathogens, predators, parental and sibling competition) are quite unlikely because the seedling density was far below the seedling densities where these effects were proved (Gilbert *et al.* 2001). Therefore, the rates presented here might be regarded as a rough picture of a more precisely gained experimental germination rate.

The overall calculated germination rate was very low, even lower than the germination rates in the other two studies under field conditions that had *ca.* 15% (Camargo *et al.* 2002) and 4.6% (Schulze 2003) in forests. The higher rate by Camargo *et al.* (2002) might be related to their use of scarified seeds, which has an experimentally shown effect on germination (Barbosa *et al.* 1984; Scarano and Crawford 1992) although Schulze (2003) did not find any significant difference between scarified and non-scarified seeds under field conditions. Another reason for the lower median germination rate is certainly the way of calculating this rate in the present study excluding all possible interactions with animals and pathogens. Nevertheless, all three studies show quite low germination rates of *P. pendula* in forests compared with laboratory studies (Alencar and Magalhães 1979; Barbosa *et al.* 1984; Scarano and Crawford 1992) as well as with habitats with higher irradiance, like pasture and bare soil (Camargo *et al.* 2002). This might be an indication of a germination threshold in light quality (r:fr) or daily temperature fluctuation as it was shown for some Neotropical pioneer species (Pearson *et al.* 2002, 2003). The significant decrease in germination rate of *P. pendula* in the forest edge zone might be an additional cue for positive photoblastic seeds in this species. The leaf litterfall is significantly higher in the forest edge zone of the studied *Piedade* fragment (11.01 ± 1.91 vs. 8.55 ± 1.46 t/ha/y; Schessl *et al.* 2008) and dead leaves on the forest floor decrease the r:fr ratio beneath them and inhibit germination of seeds (Vázques-Yanes *et al.* 1990; Vázquez-Yanes and Orozco-Segovia 1993). Similar results were obtained by Bruna (1999) who showed that the impact of leaf litter on seed germination of the herb *Heliconia acuminata* is larger near forest edges. This effect could also be the reason for the germination delay of *P. pendula* seeds, which was observed in the recent study as well as in prior ones (Alencar and Magalhães 1979; Schulze 2003).

Beside possible impacts of the highest litterfall values reported for the Atlantic Forest (Schessl *et al.* 2008) on germination rate and germination delay, this higher litterfall might also be a reason for the higher seedling mortality in the edge zone. Personal observations show that a single larger leaf may act as a physical barrier for the delicate seedlings of *P. pendula*, which often led to the seedlings' death. High seedling mortality due to leaf litterfall was already confirmed experimentally on community level at *La Selva* (Clark and Clark 1989).

Another factor known to decrease germination rates and increase mortality rates is soil moisture (Gilbert *et al.* 2001; McLaren and McDonald 2003; Bunker and Carson 2005). Soil (litter) moisture is known to be lower at open forest edges (Kapos *et al.* 1997; Didham and Lawton 1999). Nevertheless, soil moisture is not suspected to be a major cause for the observed edge effects on germination and survival of *P. pendula* seedlings since the observation year was a very wet one (nearly double the average annual rainfall; Schessl *et al.* 2008). Furthermore, germination rate of *P. pendula* seeds was highest on bare soil and *ca.* 25% of the seedlings survived the first year at this dry site, whereas germination was much lower in the wetter forest where none of the seedlings survived (Camargo *et al.* 2002).

Population structure

Several factors might be the reason for the overall very low seedling density in the sampled sub-plots. The first obvious reason is the low number of fruiting *P. pendula* trees in 2004/05 in the edge zone and the lack of trees with fruits in the forest interior (Piechowski 2007b). All counted seedlings within the sub-plots are therefore most probably 'old' ones from the 2003/04 fruiting season; i.e., they were up to one year old. Therefore, only the small percentage of seedlings that survived the first months after germination were counted. Secondly, many individuals of this 2003/04 cohort may have already lost their prophyll and were therefore included in the sapling group due to the strict group definitions. If all individuals < 20 cm – the maximum height of 1 year old *P. pendula* seedlings (Piechowski, pers. obs.) –

were classified as seedlings, the densities were 85 and 187.5 per ha (edge zone and interior, respectively). However, even with this wider definition, the seedling density was significantly lower in the forest edge zone (Mann-Whitney U: 3,550.0; $p < 0.001$). Therefore, the difference in seedling density was not caused by class definition. A third important reason for the overall low number of seedlings remote from adult trees is the lack of primary dispersers.

The lower seedling density in the forest edge zone sub-plots can be explained by the processes, which were studied in this survey. The lower germination rate and higher seedling mortality but also higher absolute number of seeds in the edge zone led to an equivalent seedling density underneath the mother trees in both environments almost one year after seed dispersion. The result of a higher seedling density in the forest interior sub-plots was recorded three months later than underneath the adult trees (March 2005) and remote from them. This density is most probably the result of the ongoing trend of a higher mortality at the edge and better growth conditions in the forest interior. Furthermore, the higher secondary seed dispersal rate by ants (Piechowski 2007b) is surely also an important reason for the higher seedling density remote from adult trees in the forest interior. These processes apparently overcompensated for the lower seed production in 2003/04 and even the absence of seeds in the flowering season 2004/05 in the forest interior.

The distribution patterns of the later size classes (saplings, juveniles, and adults) did not follow the seedling pattern of a higher density in the forest interior. The pattern seems to obvert instead, namely similar densities of saplings and even a higher juvenile tree density in the forest edge zone. Survivorship of the larger size classes was therefore obviously positively affected by the forest edge. Nevertheless, this is somehow contradicted by the taller and thicker juvenile trees in the forest interior. A clear, monotonically edge effect on the population structure of *P. pendula* is therefore not detectable. But these simple effects are "unrealistic to expect" (Murcia 1995) since different effects are likely to interact with each other or processes at one level could obscure or neutralize edge effects at a different level (Murcia 1995). This is especially true if patterns of long-living and immobile organisms (like trees) are the focus of research with the immense number of possible processes affecting their distribution (establishment I and II in Wang and Smith 2002).

The seedling density therefore is a bad prediction for the patterns of size classes of saplings, juveniles, and adult trees because the older size-classes were influenced by further factors that were altered by the forest edge. A re-census after a time-span of some years might be the appropriate method to analyze the differences in saplings and juveniles. High-resolution satellite images (< 1 m × 1 m) could enlarge the observation area for the adult size class, since the flat but large crowns of *P. pendula* trees should be easily distinguishable. Furthermore, a re-census will reveal better predictions for the future population structure in the two environments than the static size class distribution (Condit *et al.* 1998).

Summarizing it can be stated, that forest edges affected some stages in the life cycle of *P. pendula* positively (seed production, survivorship of later size classes) while other stages were negatively affected (germination rate, seedling survivorship). However, positive and negative edge effects seem to equate each other, wherefore the overall, long-term distribution of this tree species should not be affected by edge effects in the northeastern Atlantic Forest of Brazil.

ACKNOWLEDGEMENTS

Contribution of the project "Sustainability of remnants of the Atlantic rainforest in Pernambuco and its implications for conservation and local development", a Brazilian-German scientific cooperation within the program "Science and Technology for the Atlantic Rainforest" funded by CNPq (590039/2006-7) and BMBF (01 LB 0203 A1). The Usina São José S.A./Grupo Cavalcanti Petribú kindly allowed access to their properties and supported fieldwork logistically.

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