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Variation on fruit production of *Nectandra megapotamica* (Lauraceae) trees on the edge and interior of a semideciduous forest – a case study

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Abstract

Disturbance is a key factor determining the patterns of occurrence and reproduction of plant species on forests. We compared the edge and the forest interior of a 400 ha remnant and those with the edges and forest interior of a 35 ha forest remnant of semideciduous forest on South Brazil (Santa Maria County, Rio Grande do Sul) regarding the fruit production (number and size of fruits) of trees of *Nectandra megapotamica* (Lauraceae) as a case study to test if edge affects the phenology of a canopy tree. We discussed the results taking into account the light incidence and the density of trees in the edge and forest interior. Trees on the edge of the 400 ha remnant produced more fruits than those in the interior, and a significantly higher number of fruits than those in the interior of the 35 ha remnant. Trees in the interior of the 400 ha remnant occurred in higher density and, even receiving less incident light, produced more fruits than those in the interior of the 35 ha remnant. In the forest remnants studied, light may affect fruit production although not in the direct proportion of the amount of light available, which was corroborated by the fact that we not have found *Nectandra* trees on the edges of the 35ha remnant. The tree density appears as an important variable influencing the fruit production mainly on the interior of the better preserved forest remnant, outperforming the advantage attained by the higher light incidence observed in the edge.

Key words: ligh incidence, urban forest, fruit production, tree density, phenology

INTRODUCTION

The anthropogenic disturbance in the tropical forests has caused great concern, mainly because of interrelated effects such as the alteration of light and temperature conditions in forest edges when compared to the forest interior (Chazdon & Fetcher, 1984, Somanathan & Borges, 2000, Siqueira *et al*. 2004), which influences the plant phenology and visitation pattern of organisms depending on plants (Murcia, 1995, Restrepo *et al.* 1999). These alterations can modify the dynamics of resource distribution in the forest, producing impacts on the plant and animal populations (see Lamont *et al.* 1993, Murcia, 1995, Gazhoul *et al.* 1998, Somanathan & Borges, 2000, Gazhoul & McLeish, 2001).

There is a lot of uncertainty regarding the influence of edges in the phenological activity of plant species. As a consequence of different anthropogenic disturbances, edges generally have greater light incidence than forest interior, and can also have greater fruit production (Chazdon & Fetcher, 1984, Hernandes *et al.* 2004). Murcia (1996) observed a low number of significant alterations in the phenology of plants exposed to the lighter edges. In contrast, a general increase in the production of flowers and fruits has been observed in plants found on edges, clearings and trails when compared with forest interior (Dahlem & Boerner 1987, Johns 1988, Restrepo *et al.* 1999, Costa & Magnusson, 2003, Wheelwright & Logan, 2004, Ramos & Santos, 2005, Alberti & Morellato, 2008). For instance, Smith-Ramirez *et al.* (2003) observed an increase in flowering but a decreasing in fruiting of *Embothrium coccineum* trees in forests with high proportion of edge. On the other hand the probability of conversion of flower to fruit is greater on forest interior on the works of Gazhoul *et al.* (1998) and Quesada *et al.* (2004) and D'eça Neves & Morellato (2010) observed less flowers and fruits of *Persea venosa* (Lauraceae) at the edge when compared with the forest interior.

Recently, the density of individuals has been used as a promising variable in the characterization of habitats favorable for the conservation of plant species (e.g. Lamont *et al.* 1993, Ghazoul *et al.* 1998, Restrepo *et al.* 1999). The species population that are dense and more aggregated may present greater reproductive success, as it is easier for them to exchange pollen or attract pollinators than very small populations or isolated individuals (Murcia 1993, Ghazoul *et al.* 1998, Restrepo *et al.* 1999).

In all the studies conducted the results varied considerably, and there is little information regarding the spatial pattern and reproductive output of plants, particularly trees (Aguirre & Dirzo, 2008). Henceforth, it is imperative to conduct as many studies as possible on the infuence of edge in tree phenology (see Gazhoul *et al.* 1998, Restrepo *et al.* 1999, Somanathan & Borges, 2000, Dick, 2001).

Fruiting is a crucial stage of plant life cycle, and the process of seed dispersal has a profound effect on vegetation structure and diversity in tropical forests (Dennis & Westcott, 2006). To compare the number of fruits produced by individuals inhabiting the forest edge and interior is important for pointing out species that are particularly sensitive to habitat disturbance. These species can be used as bio-indicators to understand changes in the resources availability for fauna on lighter environments such as edges, anthropogenic clearings and forest gaps, a key condition for the preservation of the species (Smith-Ramirez & Armesto, 2003, Wheelwright & Logan, 2004), and the maintenance and creation of reserves (Viana & Pinheiro, 1998).

Nectandra megapotamica (Sprengel) Mez (Lauraceae), the "canela-preta" or "laurel negro", is a canopy tree up to 25 m high, very important on Brazilian seasonal semideciduous forests. Its range of occurrence covers forests from Amazon to South Brazil (Reitz *et al.* 1988, Longhi, 1995), regenerating and growing better in forest interior of preserved forests (Tonini *et al.* 2003 Della-Flora *et al.* 2004). The

Nectandra megapotamica of South Brazilian semideciduous forests flowers from June to November (Alberti *et al.* 2010), and the small, sessile, white cream, bisexual flowers are pollinated mainly by small bees and wasps (Wanderley *et al*. 2003). The ellipsoid, oil-rich fruits are dark purple when ripening, from December to February, and consumed by more than 18 species of birds, half of them migratory (Krügel *et al.* 2006).

The present study aim to test if the number and size of fruits produced by trees of *Nectandra megapotamica,* (hereafter referred to by genus only), change among forest edge and interior differing in the amount of light incidence across two forest remnants. The complex role of solar radiation in fruiting can be summarized as follows: trees in lighter habitats generally produce more and larger fruits than shadowed trees, due to large photossynthetic rates and carbon assimilation in lighter conditions (Begon *et al.* 2006). Considering that light is an important factor in the reproductive activity of the plants (Niesenbaum, 1993, Murcia, 1995, Hernandes *et al.* 2004, Wheelwright & Logan, 2004, Burgess *et al*. 2006), we expect that edge *Nectandra* trees will produce more and larger fruits when compared to those on forest interior. We have discussed the results taking also into account the density and spatial distribution of trees in the forest edge and interior.

METHODS

Study area and sampled habitats - The study was conducted in 2003 in two semideciduous forest remnants at Santa Maria municipality, Rio Grande do Sul State, South Brasil. Both remnants have a matrix composed of urban areas and open fields and suffered selective wood extraction between 1949 and 1960 (P.F. dos S. Machado, A. Muller, personal communication, 2000, 2003). The 400 ha remnant, located at 29º40'S and 53º43'W, and 458 m a.s.l., is the better preserved remnant. The 35 ha remnant is located at 29º42'S and 53º47'W, has an altitude of 246 m a.s.l. The vegetation in the study areas is a seasonal semideciduous forest (Veloso *et al.* 1991), growing mainly on cambisols (Streck *et al.* 2002). The region has a subtropical climate of the Cfa type according to the classification of Köppen (1948). The mean annual temperature is 19.2°C, and the mean annual rainfall is 1823 mm (meteorological station of the Universidade Federal de Santa Maria, 1980-2003). We sampled for *Nectandra* trees in forest edge and interior at a 400 and 35 ha forest remnant, which are similar regarding soil types, vegetation, etc.

400 ha remnant.

Edge400 - Comprises an abrupt transition between open fields and forest interior, and trees were sampled in a trail of 500 x 10 m at 29°40'43.58"S and 53°43'22.45"W, at 177 m a.s.l., with additional sample points located on forest clearings, located mainly at 29°40'38.80"S and 53°42'59.18"W. Satellite images of the habitats can be seen downloading the software Google Earth at <http://earth.google.com/intl/pt/>. The sample points were selected according to the ease of access since the area explored in 1960 became secondary growth forests (capoeirão) in 2003, which makes it difficult to access the remnant as well as finding the transition between fields or clearing and forest.

Interior400 - It comprises the dark interior of the forest and is located at 29°40'25.24"S and 53°43'07.02"W at 229 m a.s.l. and trees were sampled at least 20 m from the closest forest edge, near a trail, about 500 m long and 3 m wide.

35 ha remnant.

Edges 35A and 35B - The edge35A is located at 29°40'01.00"S and 53°47'15.48"W at 182 m a.s.l. The edge35B is located at 29°42'40.16"S and 53°47'54.01"W at 146 m a.s.l. We searched for *Nectandra* trees at least 10 m from the 35A and 35B edge but we did not find any tree.

Interior35A - The trees were sampled near a trail about 700 m long and 5 m wide (29°42'03.01"S and 53°47'08.30"W) and at least 15 m from the edge. It was originated from a road used for wood felling (A. Muller, personal communication, 2003), and ranges from the base of the hill (locally named Cerrito) until about 100 meters from its crest at 246 m a.s.l.

Interior35B - The trees were sampled near a trail at 29°42'43.16"S and 53°47'42.44"W at least 15 m from the closest edge and about 3 m wide and 500 m long and that ranges from the base to the crest of the hill (locally named Tabor), at 244 m a.s.l.

We sampled all individuals of *Nectandra* with a CBH greater than 31.4 cm found 10 m from the center of the trails. The CBH was chosen to include just reproductive trees, reducing the frequency of zeros for reproductive variables and increasing the confidence of results and statistical analyses. The sampled individuals provided the density of individuals of *Nectandra* in each habitat (see Table 1) and were conditionally chosen for fruit collection, excluding the trees with difficult access or crown overlapping between neighbors, which could affect the number of fruits estimated**.** For each individual, the trunk was used as a reference for installing a sampling unit of 5x5 m on the ground. In each sampling unit, the mature fruits not shrunken or rot were collected during a 20-minute search. These fruit collections were performed in three days in January 2003. The fruits were counted and measured. The number of fruits is giving by 25 m^2 of tree crown projection (Table 1). The total amount of fruit produced in all sample units with 25 m^2 was converted to number of fruits by hectare (ha) and provided the total number of fruits produced by habitat, considering just the conditionally chosen trees (Table 1). Several studies confirm the consistency of counting fruits found on the ground or in fruit collectors for estimating fruit abundance (see Barlow & Peres 2006 and references therein).

Light measures - The incident light was measured along the edge400 with one LI-210 *Photometric Sensor* at 1.3 m above the ground, during four 20-second stops, between 13:30h and 15:30h. Light was not measured in the edges 35A and 35B. Light radiation is hard to be described at the microsite scale (Ramos & Santos, 2006, Alberti & Morellato, 2008), not always providing substantial information, what justifies in part our choice for a general description of light. To cover the heterogeneity of vegetation in the forest interior (Ramos & Santos, 2005), the incident light was measured in the interior400, interior35A and interior35B trails during at least 1100 five second stops. The light measurements were repeated for each season of the year.

Statistical analysis - The edge and the interior400 and the interiors 35A and 35B were compared regarding light incidence, fruit number and size using the Dunn test for post hoc multiple comparison of the Kruskal-Wallis test.

Spatial distribution of trees - The sampled area in the interior400, interior35A and interior35B trails was subdivided into 20x10 m plots and the number of individuals of *Nectandra* in each plot was recorded and used to calculate the pattern of spatial distribution of the individuals in each trail. We applied the Standardized Morisita Index (*Ip*), which vary from -1 to +1 with confidence limits of 95% to *Ip* <-0,5 and >+0,5, and recognizes three spatial distribution patterns: clumped, when *Ip*>0, random, *Ip*≈0 and uniform, *Ip*<0 (Krebs, 1989). To improve the discussion we verified whether the order of the habitats according to density of individuals and *Ip*, was similar to that observed for number and size of fruits.

RESULTS

The four habitats differed significantly regarding light incidence (H= 727.8, df 3, n= 3992, $p<1 \times 10^{-4}$, Dunn test $p<1 \times 10^{-4}$ for all the post hoc comparison between habitats). The trees on the edge400 received significantly more light than trees from the other three habitats that were ordered from higher to small light incidences as follows: interior35B, interior35A and interior400 (see Table 1, Figure 1 for details), thereby confirming the existence of a gradient of light incidence among the four habitats.

The number of fruits produced by individuals of *Nectandra* differed among habitats (H= 11.96, df= 3, n= 35, p<0.007, (Table 1, Figure 2A). The trees on the forest edge400 did not differ significantly from the interior400 trees regarding fruit number. However, due to a single tree, the total number of fruits produced on the edge trees was twice the amount produced by trees in the interior. The number of fruits produced by individuals of *Nectandra* on the edge400 was significantly greater than the number produced by individuals in the interior35A (Dunn test p<0.02).

The individuals of the forest interior400 produced more fruits than those in the interior 35A and 35B (Dunn test p=0.06 and p=0.3, respectively), although the values did not differ significantly. The fruit size differed among habitats (H= 12.22, df = 3, n = 29, p<0.006) and was significantly smaller in individuals of the interior35B than those located in the edge400 (Dunn test $p<6 \times 10^{-3}$) but the remaining habitats did not differ among themselves (Figure 2B). The density of individuals was higher in the interior400 than in the other habitats studied (Table 1). *Nectandra* individuals had a random distribution pattern in interior400 and interior35A and a significantly aggregated pattern in the interior35B (Table 1). The increasing order in the number of fruits produced corresponded to the increasing order of magnitude of light incidence, with the exception of the interior400, the better preserved habitat, Table 1). The order for fruit size did not have a clear tendency. There is also a better reproductive performance on the trees located at the 400 ha remnant when compared with the 35 ha ones (Table 1).

Table 1. Characteristics of the edge400, interior400, interior35A and interior35B, and characteristics of the populations of *Nectandra megapotamica* studied in two remnants of semideciduous forest, South Brazil.

	Habitats			
Characteristics	**Edge400**	**Interior400**	**Interior35A**	**Interior35B**
Habitat area (ha)	0.84#	400	35	35
Tree density (individuals/ha)	24	76	16	50
Annual incident light (lm/m^2)				
Median (1st-3th quartile)	37.800 (30.000-47.000)	300 (200-700)	400 (200-1.000)	1.000 (400-480)
number of samples	52	1435	1318	1187
date of light sampling	10.2.2002, 12.23.2002, 3.21.2003, 8.6.2003	Same as edge400	10.1.2002, 12.27.2002, 3.22.2003, 8.8.2003	9.28.2002, 12.26.2002, 3.23.2003, 8.7.2003
Number of fruits/25 m^2				
Median (1st-3th quartile)	16(8-65)	17(9-42)	3(0-6)	1(0-18)
number of trees sampled	9	10	7	9
Total number of fruits produced (ha)	456	224	24	75
Size of fruits (cm)				
Median (1st-3th quartile)	1.0 (0.9-1.1)	0.81 (0.79-0.88)	0.94 (0.8-1.0)	0.82 (0.75-0.87)
number of individuals sampled	9	9	5	4
number of fruits sampled	327	210	24	76
Tree CBH (cm)				
Median (1st-3th quartile)	87 (65-117)	87.5 (62.2-194)	46 (43-84)	82 (59-107)
number of individuals sampled	9	10	7	9
Standardized Morisita Index	-	0.07	0.09	0.5*
number of plots		19	18	17
Spatial pattern	-	random	random	aggregated

\# Area of the 10 x 500 m trail plus area of clearings.
* Significantly at $p<0.05$ of error.

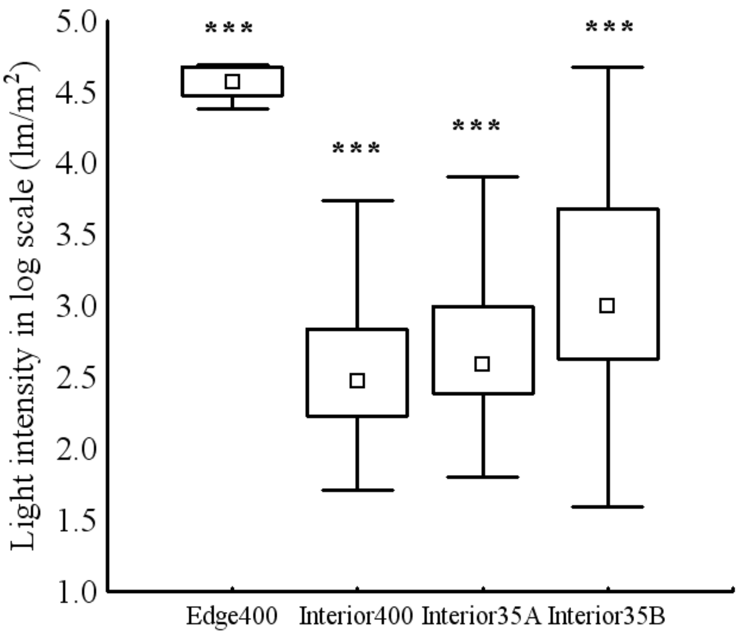

Figure 1. Light incidence on log scale in the four habitats of the semideciduous forest remnants, South Brazil. Legend: median (□), the box is determined by 25th and 75th percentiles and the minimum and maximum values are displayed by the whiskers. Box-plots with *** indicates significant differences (p<0.01) between habitats according to the Dunn test for post hoc multiple comparison of the Kruskal-Wallis test.

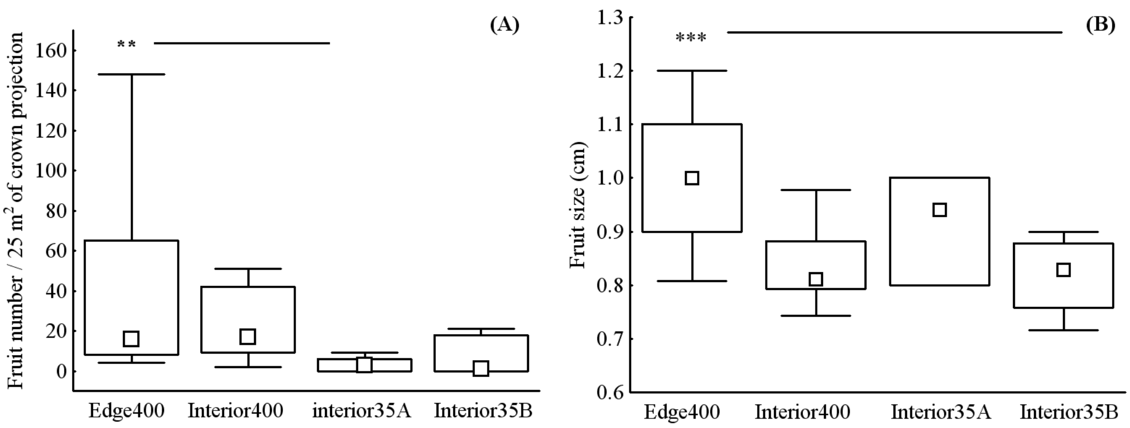

Figure 2. Number of fruits (A) and size of fruits (B), produced by *Nectandra megapotamica* trees in the four habitats of the urban semideciduous forest remnants, South Brazil. Legend: median (□), the box is determined by 25th and 75th percentiles and the minimum and maximum values are displayed by the whiskers. Box-plots with *** or with ** and linked by lines indicates significant differences (p<0.01 and p<0.05, respectively) between habitats according to the Dunn test for post hoc multiple comparison of the Kruskal-Wallis test.

DISCUSSION

The comparison of the four habitats showed that in the forest remnants studied, light may affect fruit production although not in the direct proportion of the amount of light available in each habitat. The tree density appears as an important variable influencing fruit production mainly on the interior of the better preserved forest remnant, outperforming the advantage attained by the significantly higher light incidence on the edge. The fact that the trees on the edge400 did not differ significantly from the interior400 trees with regard to the fruit number, even though they produced double the amount of fruits, was related to their uneven fruit production, meaning that some of the trees in the edge were excellent fruit producers. This lack of a greater difference favoring edge400 in relation to interior400 regarding fruit number may be due to photoinhibition (Begon *et al.* 2006) on the edge400 tree canopies, since the light incidence on the edge is extremely high (see table 1). Since the seed dispersers generally prefer individuals producing more fruits (Blake & Loisele, 1991), the concentrated fruit production of trees found on the edge may have important consequences for the dispersion of seeds and *Nectandra* gene flow (Aldrich & Hamrick, 1998).

Similarly, the quantity of fruits produced by individuals of *Nectandra* in the interior400, although not significant, was more than the double of the amount observed in the interior35A and interior35B that received on average two to five times more light than the interior400. Therefore, considering the total number of fruits produced, the individuals of *Nectandra* located inside the 35 ha remnant did not respond as expected to the greatest amount of light available (Wheelwright & Logan, 2004).

Moreover, since the interior400 trees were located in the remnant with the largest area and density of individuals of *Nectandra*, we can assume that the diminished or more isolated population of *Nectandra* in the interior of the 35 ha remnant was not sufficient for sustaining the production of fruits at a level comparable with that of the 400 ha remnant, even with more available light. The absence of *N. megapotamica* individuals in the edges of the 35 ha remnant suggest that some edges can be harshy habitats limiting flower and fruit production (D'eça Neves & Morellato, 2010), tree regeneration and even adult survivorship (Müller *et al.* 2007) of the climax Lauraceae tree species (Tonini *et al.* 2003, Della-Flora *et al.* 2004, Wheelwright & Logan (2004).

Therefore, it seems that, in the present work, the influence of the state of preservation allied to the density of individuals in the production of fruits was important as the intensity of light itself. The occurrence of the smallest median of fruit production on the interior35B, which exhibited the more aggregated distribution of trees, did not support the idea that larger fruit productions are necessarily associated with more aggregated populations (Ghazoul *et al.* 1998). In fact, the trees of the dark interior400 are randomically distributed in space, suggesting no environmental barrier in their distribution. Recent studies have shown that significant spatial aggregation in *Ocotea tenera* (Lauracea) can be a consequence of high mortality and low fecundity of trees due to high levels of stress (Wheelwright & Logan, 2004 and references therein). Fruit size was significantly smaller in forest interior35B, suggesting again a low reproductive performance of *Nectandra* in that remnant.

A small remnant may have a large population whose reproductive success is not compromised (Tomimatsu & Ohara, 2002). Instead, in the present study the 35 ha remnant included one small population of *Nectandra*, which affected the production of fruits, supporting the suggestion by Lamont *et al.* (1993) and Aizen & Feinsinger (1994) that small populations do not favor plant reproduction. The interior400 had lower incident light but the larger population size, and produced more and larger fruits. The production of more fruits in the forest interior at the 400 ha remnant when compared to the two other habitats at the 35 ha remnant, even with less incident light at the 400 ha remnant, suggests that in the small remnant the reproductive activity of *Nectandra* trees was not limited by light, but perhaps by the quality of pollination, as the small populations of *Nectandra* in this remnant would not be attractive enough (Murcia, 1993). We didn't make detailed observations on pollination activity, but we observed more pollinators in the interior400 than in interior35A and 35B (L.F. Alberti, personal observation, 2003). Additionally, the distance from pollination sources could explain the better reproductive performance of trees on the 400 ha remnant in relation to those in the 35 ha remnant (Murcia, 1993, Gazhoul *et al.* 1998 but see Tonhasca *et al.* 2002). Somanathan & Borges (2000) observed that in a disturbed forest the production of fruits was smaller than in a preserved forest, due to limited pollination related to isolation and small population density of plants.

Therefore, the population size is an important variable to take into account when evaluating habitats regarding tree phenology (Somanathan & Borges, 2000). The high fruit production on the edge400, the large, more preserved remnant, suggests that the greater amount of light favored fruit production in the *Nectandra megapotamica*, as observed in well iluminated sites on preserved forests (Wheelwright & Logan, 2004). Recent studies shows a tendency of higher flower and fruit production on lighter habitats (Fuchs *et al.* 2001, Rocha & Aguilar, 2001, Wheelwright & Logan, 2004, Ramos & Santos, 2005, Burgess *et al.* 2006, but see D'eça Neves & Morellato, 2010), as long as there is not a limitation in pollination (Niesenbaum, 1993). The edge400 appears once again as an important source of flowers and fruits, possibly affecting the patterns of resource utilization by fauna in forest remnants. Nevertheless, the advantages of the edge400 regarding the number of fruits produced by *Nectandra* trees are apparently lost under conditions of reduced density in the 35 ha remnant.

The conclusions of the present study are limited by the small number of habitats sampled and the lack of a more detailed description of light variation at the forest canopy. However, data collected on fruiting of *Sorocea bomplandii* (Moraceae, Alberti, unpublished data, 2008) corroborated the general trends of results here presented, suggesting that such trends are not mere due to chance and only applied to *Nectandra megapotamica*.

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