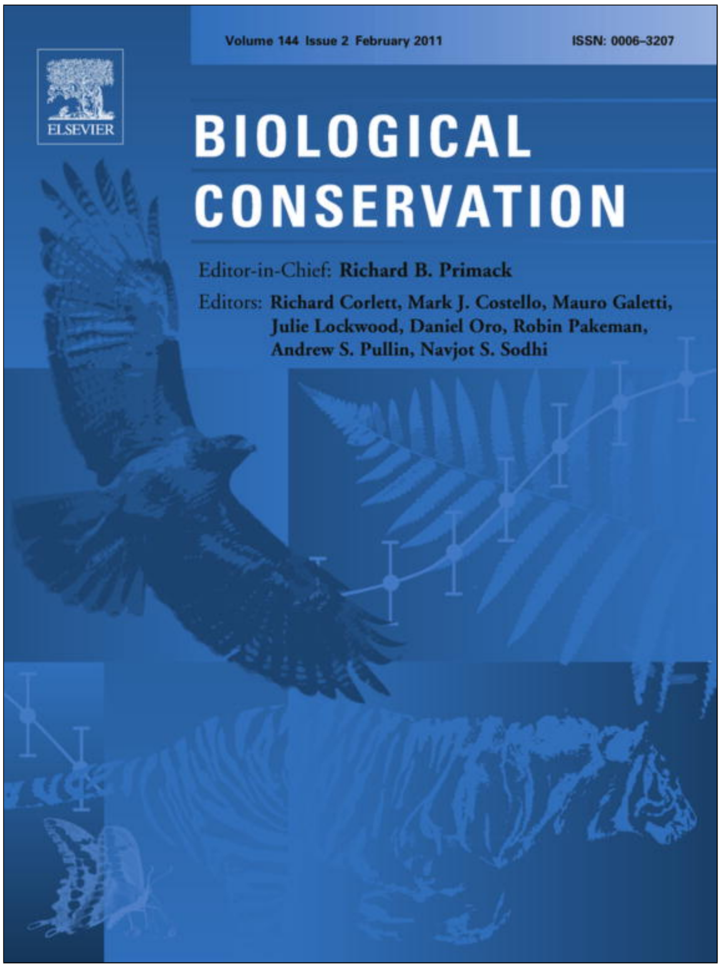
Volume 144 Issue 2 February 2011
ISSN: 0006-3207
ELSEVIER
BIOLOGICAL CONSERVATION
Editor-in-Chief: Richard B. Primack
Editors: Richard Corlett, Mark J. Costello, Mauro Galetti, Julie Lockwood, Daniel Oro, Robin Pakeman, Andrew S. Pullin, Navjot S. Sodhi

Biological Conservation 144 (2011) 830–835

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Growth of an understory herb is chronically reduced in Amazonian forest fragments

Paul R. Gagnon[a,b,*], Emilio M. Bruna[a,b,c], Paulo Rubim[c], Maria Rosa Darrigo[c], Ramon C. Littell[d], Maria Uriarte[c,e], W. John Kress[f]

[a] *Dept. of Wildlife Ecology & Conservation, University of Florida, PO Box 110430, Gainesville, FL 32611-0430, USA*
[b] *Biological Dynamics of Forest Fragments Project, INPA-PDBFF, CP 478, Manaus, AM 69011-970, Brazil*
[c] *Center for Latin American Studies, University of Florida, PO Box 115530, Gainesville, FL 32611-5530, USA*
[d] *Dept. of Statistics, University of Florida, PO Box 118545, Gainesville, FL 32611, USA*
[e] *Dept. of Ecology, Evolution, and Environmental Biology, Columbia University, 10th Floor Schermerhorn Extension, 1200 Amsterdam Avenue, New York, NY 10027, USA*
[f] *NMNH – Dept. of Botany, Smithsonian Institution, PO Box 37012, Washington, DC 20013-7012, USA*

ARTICLE INFO

Article history:
Received 24 August 2010
Received in revised form 7 November 2010
Accepted 21 November 2010
Available online 13 December 2010

Keywords:
Habitat fragmentation
Heliconia acuminata
Plant demography
Relative growth rate
Reproductive output
Vital rates

ABSTRACT

The biotic and abiotic changes associated with habitat fragmentation have been shown to have major consequences for plant recruitment and survivorship. However, few studies have quantified the growth of plants that persist in fragments. Over the course of a decade, we measured annual growth of 5200 individuals of the common understory herb *Heliconia acuminata* (Heliconiaceae) in an experimentally fragmented Amazonian forest. We tested (A) whether annual growth rates were lower in fragments than in continuous forest, and (B) whether cumulative growth rates of plants that survived the entire period were lower in fragments. While mean annual growth rates were often lower in fragments, differences were not significant in any year. After 10 years, however, the cumulative effect was that plants in fragments were significantly smaller. This had a clear demographic consequence – plants in fragments produced fewer inflorescences than plants in continuous forest. Our results demonstrate that chronic reduced individual growth may be an important mechanism contributing to reduced population viability in fragmented forests, and that negative demographic consequences of fragmentation for plants can take years to manifest themselves.

1. Introduction

Habitat fragmentation is a globally pervasive form of environmental change. One widespread consequence of fragmentation is the decline of isolated plant populations that may ultimately precede their local extinction (Kolb and Diekmann, 2005; Sutton and Morgan, 2009; Turner et al., 1995). Because population decline is a demographic process, considerable effort has gone into documenting how components of plant demography are altered in fragmented landscapes (Bruna, 2003; Laurance et al., 1998b; Lopez-Gallego, 2008; Tomimatsu and Ohara, 2010; Zartman and Shaw, 2006). Researchers have paid particular attention to plant reproduction and seedling establishment, in part because of the direct link between recruitment and population persistence (reviewed in Bruna et al. (2009) and Hobbs and Yates (2003)). Indeed, recruitment-related processes can be dramatically altered in habitat fragments (e.g., Aizen and Feinsinger, 1994; Bruna, 2002; Cramer et al., 2007; Cunningham, 2000a). However, demographic analyses indicate that growth and survivorship of established individuals have larger influences on population growth rates of perennial plants than those related to recruitment (Bruna et al., 2009; Crone, 2001; Silvertown et al., 1996; Tomimatsu and Ohara, 2010). Nevertheless, surprisingly little is known about the growth of plants in habitat fragments (reviewed in Bruna et al. (2009)).

Understory plants in fragmented landscapes face a battery of biotic and abiotic changes. These include an influx of pioneer species, changes in the density of conspecifics, elevated air temperatures and wind turbulence, reduced relative humidity, and increased light penetration to the forest floor (Chen et al., 1995; Gehlhausen et al., 2000; Laurance and Curran, 2008; Matlack, 1993, 1994). The abiotic changes associated with fragmentation are particularly pronounced in tropical forests (Camargo and Kapos, 1995; Didham and Lawton, 1999; Kapos, 1989; Kapos et al., 1997), where they are thought to be especially important drivers of tree mortality (Laurance et al., 1998a). Abiotic changes have also been hypothesized to reduce the growth rates of understory species, although studies addressing this possibility are few and of brief duration (e.g., Benítez-Malvido, 2001; Bruna, 2002; Sizer and Tanner, 1999). Although the magnitude of abiotic changes decreases with distance from fragment edges (reviewed in Broadbent et al. (2008)), all plants in small fragments are subject to strong

---

* Corresponding author at: Dept. of Wildlife Ecology & Conservation, University of Florida, PO Box 110430, Gainesville, FL 32611-0430, USA. Tel.: +1 352 846 0527; fax: +1 352 392 6984.

E-mail address: pgagnon@ufl.edu (P.R. Gagnon).

0006-3207/$ - see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2010.11.015

edge effects because of high edge:area ratios (Laurance, 1991). Falling trees and limbs, which are more common in fragments because of increased wind turbulence and tree mortality (D'Angelo et al., 2004; Laurance et al., 2002), could also damage plants and thereby cause decreased individual growth rates.

The changes associated with forest fragmentation are not necessarily detrimental to plant growth. Although it is often assumed that increased light levels at forest edges negatively affect forest understory species (e.g., Bruna, 2002: p. 239; Laurance et al., 2002: p. 609), there is evidence that light levels in fragments are well within the range that stimulates plant growth (Bruna and Andrade, *unpubl. manuscript*). Consequently, woody plant species in close proximity to edges can have sharply elevated growth rates (e.g., Sizer and Tanner, 1999). Secondary vegetation rapidly seals fragment edges (Mesquita et al., 1999), which reduces environmental stress for surviving plants. Finally, many shade-tolerant tropical plants can respond to damage with rapid compensatory or even overcompensating growth (Bruna and Ribeiro, 2005). Consequently, plant growth in fragments may be comparable to or even higher than in continuous forest.

Several key factors limit our ability to elucidate the consequences for plant growth of changes in environment conditions associated with fragmentation. First, different life-history stages can respond in different ways to altered environmental conditions (Horvitz and Schemske, 1995; Morris and Doak, 2005). While several studies have addressed growth of seedlings in fragments (Benitez-Malvido et al., 2005; Sizer and Tanner, 1999), we are aware of only two studies to date that have evaluated individual growth rates across a plant's entire life cycle in a fragmented tropical landscape (Bruna, 2003; Portela et al., 2010; see also Tomimatsu and Ohara (2010) for a similar study in a temperate forest). Furthermore, most studies of plant responses to fragmentation have been brief (i.e., <3 years; Hobbs and Yates, 2003) despite that many tropical plants can live for decades. This limits both our ability to assess inter-annual variation in growth and our understanding of the extent to which short-term patterns reflect long-term trends. Finally, it is difficult to find fragmented landscapes with fragments whose histories are well-documented and with nearby areas of continuous forest for comparison.

We tested the hypothesis that plant growth rates are lower in forest fragments than in continuous forest in an experimentally fragmented landscape in central Amazonia. To do so we used a decade of annual measurements of 5200 individuals of the common perennial understory herb *Heliconia acuminata* (Heliconiaceae). We analyzed (1) the annual growth of all plants in the dataset, and (2) the cumulative growth of those plants marked in the original census that survived the entire decade. We then compared inflorescence production of plants of varying sizes in both forest fragments and continuous forest. Because individuals in our study populations span the continuum of *H. acuminata* life-history, our dataset provides an excellent opportunity to elucidate how different life-history stages respond to the same environmental disturbance.

2. Methods

2.1. Study site and system

We conducted the study at the Biological Dynamics of Forest Fragments Project (BDFFP), located 70 km north of Manaus, Brazil (2°30′S, 60°W). Mean annual temperature in the region is 26 °C (range 19–39 °C); annual rainfall ranges from 1900 to 3500 mm with a pronounced dry season from June to November. The BDFFP maintains reserves in primary lowland forest as well as in forest fragments isolated in the early 1980s by the creation of cattle pastures. In years since the fragments were created, secondary growth surrounding them has been regularly cleared to maintain their isolation. Consequently, fragments are continuously subjected to edge effects ranging from increased light and air temperature (Camargo and Kapos, 1995; Kapos, 1989; Sizer and Tanner, 1999) to elevated rates of tree mortality and uprooting (D'Angelo et al., 2004; Laurance et al., 1998a). Although the intensity of these effects can decline with increasing distance from the forest edge, the small size of the BDFFP's 1-ha fragments means the entire fragment is dominated by many of these altered environmental conditions (Laurance et al., 2002). For a detailed description of the BDFFP reserves see Bierregaard et al. (2002).

In January 1998, two of us (EMB and WJK) initiated a long-term study at the BDFFP investigating the demographic consequences of fragmentation for tropical understory plants. The focal species for this study was *H. acuminata* L.C. Rich. (Heliconiaceae), a self-incompatible perennial herb native to central Amazonia and the Guyanas (Berry and Kress, 1991). This species is one of a suite in the genus *Heliconia* found primarily in forest understory rather than in gaps or disturbed areas (Berry and Kress, 1991), and it is the numerically dominant understory herb in the BDFFP's forests (Ribeiro et al., 2010). *H. acuminata* produces aboveground stems from a rhizome and does not divide clonally (Bruna, 2003). It is largely self-incompatible and reproduces only via seed; the mean life expectancy for *H. acuminata* of different sizes ranges from 17 to 30 years, though some individuals are capable of living for decades longer (Gagnon and Bruna, *unpubl. data*).

We established permanent 50 m × 100 m plots in several BDFFP reserves in which to monitor *H. acuminata* populations; in this study we focus on populations located in continuous forest ($N = 6$ plots) and in 1-ha forest fragments ($N = 4$ plots). Plots in 1-ha fragments were located on one randomly selected half of the fragment; plots in continuous forest were located 500–4000 m from the primary forest borders (see Bruna, 2003; Bruna and Kress, 2002 for a complete description of how plots were established and maps of the sites). We marked and mapped all *H. acuminata* in the plots, and measured plants by counting their number of vegetative stems. Stem number was positively correlated with other measures of plant size (e.g., leaf area, height) and with probability of surviving and reproducing (Bruna, 2003; Bruna and Kress, 2002). We subsequently surveyed all plots annually to record plant growth, mortality, and recruitment of new seedlings. The analyses we present here were based on the first 10 years of surveys (1998–2007); during this time period in these sites we followed $N = 5200$ plants ($N = 30{,}342$ observations). Mean sample size was $N = 846 \pm 34$ SD plants in 1-ha fragments and $N = 2977 \pm 292$ SD plants in forest plots.

2.2. Quantifying and analyzing plant growth and reproductive output

We compared inter-annual growth rates of plants growing in fragments and continuous forest using mixed 3-way analysis of variance. We first calculated growth as the proportional change in the number of live stems a plant had from one census (time t) to the next (time $t + 1$) as $G = N_{t+1}/N_t$ [hereafter G; (Gagnon and Platt, 2008)]. Values of $G > 1$ indicate plants grew from 1 year to the next; values of $G = 1$ indicate plants stayed the same size; values of $G < 1$ indicate plants shrank. While the maximum number of stems we recorded on a plant was 24, the large majority had far fewer (median = 2 stems plant^{-1}; mean = 2.81 ± 1.81 SD stems plant^{-1}; $N = 30{,}342$). At the start of each time interval we assigned plants to one of six size classes (1, 2, 3, 4, 5, or $\geqslant 6$ stems). Because we were explicitly interested in how forest fragmentation might differentially affect the growth of plants of different sizes, we included plant size class as a fixed effect in our models. Our 3-way ANOVAs therefore included transition (1–9), habitat type (forest fragment or continuous forest) and size class as three fixed effects, with plot as random effect. We opted against a repeated measures framework because such a framework is used to account for individual-level differences as reflected by covariance structure (Littell et al., 2006), and preliminary analyses indicated almost no measurable covariance in our dataset. We square-root transformed values of G to improve normality; we determined that heterogeneous variance models were unnecessary by comparing variances among the different fixed-effects groups. We used Kenward–Roger approximations to address lack of balance (Littell et al., 2006) and the Mixed procedure in SAS version 9.2 in Windows (copyright 2002–2007) for all mixed model statistical analyses.

We also compared the long-term patterns of growth of the $N = 400$ plants in fragments and the $N = 1339$ plants in continuous forest that were present at the first census and survived the entire 10-year study interval. We used the same approach as for annual growth to calculate decadal growth (i.e., N_t/N_{t+10}; plants in 6 size classes), then used ordered logistic regression to compare growth rates in the two habitat types. Ending size class was the multinomial response variable, and habitat-type and initial size class were our two predictor variables; a habitat-type by size-class interaction was not significant ($P = 0.308$), so we report results from our model that included only main effects (Stokes et al., 1995). We used the Logistic procedure in SAS version 9.2 to perform the analysis.

To elucidate the consequence of altered plant growth for reproduction, we quantified the relationship between plant size and reproductive output. We used inflorescence production as our metric of reproduction because previous work in this system found that the number of flowers per inflorescence (20–25 flowers), the proportion of flowers developing into fruits, and seed set per fruit were similar in fragments and continuous forest (Bruna and Kress, 2002). We examined the effects of fragmentation on reproduction in three ways. First, we calculated mean number of inflorescences produced annually by plants of each size class in both habitat types. Second, we used plants that survived the entire 10 year study period to compare mean total inflorescences produced per plant in both habitat types over the course of the decade using a t-test on rank-transformed data (as per Conover and Iman, 1981). Third, we compared the proportion of the population in both habitat types that produced 0, 1, 2, 3, or $\geqslant 4$ inflorescences over the course of the decade using a Chi-square test. Because the number of flowering plants in fragments is extremely low (Bruna and Kress, 2002), we pooled data from plots in each habitat class for these analyses. We used the t.test and chisq.test functions in R version 2.9.0 for the latter two analyses.

3. Results

3.1. Inter-annual variation in plant growth rates

There was no main effect of habitat on annual plant growth ($F_{1,8.79} = 0.65$, $P = 0.441$) even though mean growth rates were lower in forest fragments in 7 of 9 transition years. Plant growth rates did vary by year ($F_{8,164} = 37.74$, $P < 0.001$); on average, plants grew during transitions beginning in 2001 and 2003, retrogressed during transitions beginning in 2002, 2004 and 2006, and stayed the same size during the transitions beginning in 1998, 1999, 2000 and 2005. There was also an effect of plant size on growth rates ($F_{5,164} = 712.55$, $P < 0.001$), with a clear inverse relationship between the two. For plants that survived given transition periods, small plants with 1 or 2 stems most often grew into larger size classes (1 stem: $G = 1.42$, 95% CI = 1.38, 1.47; 2 stems: $G = 1.09$, 95% CI = 1.05, 1.13), while mid-sized plants with 3 stems on balance stayed the same size ($G = 1.00$, 95% CI = 0.96, 1.04). Large plants with 4, 5 and 6 or more stems regressed on average into smaller size classes (4 stems: $G = 0.92$, 95% CI = 0.86, 0.96; 5 stems: $G = 0.88$, 95% CI = 0.84, 0.92; $\geqslant 6$ stems: $G = 0.81$, 95% CI = 0.77, 0.86).

All two-way interactions between the three fixed effects were significant. The size class by year interaction indicates that the inverse relationship between plant size and growth rate varied in magnitude from year-to-year ($F_{40,164} = 2.50$, $P < 0.001$; Fig. 1A), while the habitat by year interaction indicates that estimated plant growth was greater in continuous forest in some years but greater in 1-ha fragments in others ($F_{8,164} = 2.57$, $P = 0.009$). For example, during the first 5 years of the study, plants had higher estimated mean growth in continuous forest than in 1-ha fragments, but this disparity reversed in two later years (Fig. 1B). This general pattern wherein plants growing in continuous forest outperformed those in fragments was also reflected in mean growth rates of several individual size classes. A habitat by size-class interaction indicated that although size class and growth were inversely related in both habitats, the degree of that inverse relationship varied by habitats ($F_{5,164} = 4.25$, $P < 0.001$). For example, while the smallest size class of plants in fragments had a slightly higher estimated growth rate when compared to plants in continuous forest ($G_{\text{fragments}} = 1.43$, 95% CI = 1.36, 1.50; $G_{\text{forest}} = 1.41$, 95% CI = 1.35, 1.47), plants in the larger size classes had lower estimated growth rates (4 stems: $G_{\text{fragments}} = 0.91$, 95% CI = 0.85, 0.97; $G_{\text{forest}} = 0.94$: 95% CI = 0.89, 0.98; 5 stems: $G_{\text{fragments}} = 0.87$: 95% CI = 0.81, 0.94 and $G_{\text{forest}} = 0.89$: 95% CI = 0.84, 0.94; $\geqslant 6$ stems: $G_{\text{fragments}} = 0.80$: 95% CI = 0.72, 0.88 and $G_{\text{forest}} = 0.83$: 95% CI = 0.79, 0.88). There was no three-way interaction between size class, year and habitat ($F_{40,164} = 1.09$, $P = 0.317$).

3.2. Cumulative effects of forest fragmentation on plant growth

In contrast to results of annual rates of plant growth, by study end growth of plants that persisted for 10 years was reduced in fragments compared to continuous forest ($\chi^2 = 7.233$, DF = 1, $P = 0.007$). Specifically, the odds of plants ending in smaller size classes were lower in continuous forest than in 1-ha fragments (odds ratio of continuous forests vs. fragment habitats = 0.756; 95% CI = 0.617, 0.927). Initial plant size influenced cumulative growth ($\chi^2 = 134.620$, DF = 1, $P < 0.001$), with the odds of plants ending in larger size classes decreasing as initial plant size increased (odds ratio of starting size class = 0.679, 95% CI = 0.635, 0.724).

3.3. Implications of the different growth rates for reproductive output

Whether in fragments or in continuous forest, plants possessing a particular number of stems produced similar numbers of inflorescences in any given year (Fig. 2A). However, because populations in fragments had proportionally fewer large plants, these populations produced fewer inflorescences per plant than populations in continuous forest. At the individual level, plants in fragments produced on average one third fewer inflorescences than plants in continuous forest over the course of a decade (mean = 0.565 vs. 0.858 inflorescences per plant in fragments vs. continuous forest; $t = -4.983$, DF = 738, $P < 0.001$). Stated differently, populations in fragments had proportionally more individuals that failed to reproduce at all, and fewer that produced 1, 2, 3, and $\geqslant 4$ inflorescences during the 10 years ($\chi^2 = 27.9$, DF = 4, $P < 0.001$; Fig. 2B).

4. Discussion

Using a decade of annual measurements on over 5000 *H. acuminata* plants, we showed that individuals that persist in

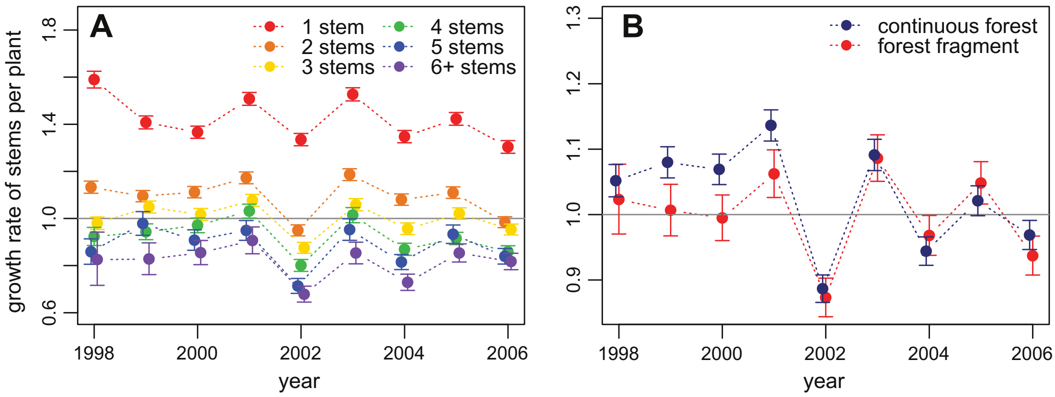

Fig. 1. Growth rate of stems per plant ($G = N_{t+1}/N_t$, defined as proportional change in the number of live stems [N] of a plant from one annual census [time t] to the next [time $t + 1$]) over 9 annual transition periods for *Heliconia acuminata* growing in the central Amazon. Panel A shows growth rates of plants in six different size classes; panel B shows growth of plants in forest fragments versus continuous forest (back-transformed least-squares means ± back-transformed SE). Values >1 indicate growth; values <1 indicate decline; note the different scales on the two *Y*-axes.

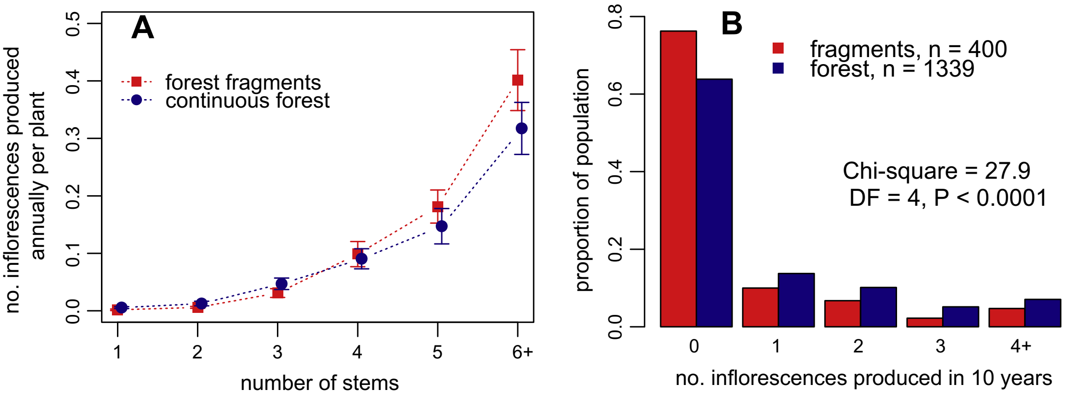

Fig. 2. (A) Average annual inflorescence production of *H. acuminata* in the central Amazon over the course of 10 years (1998–2007) in continuous forest and 1-ha fragments (mean ± SE) as a function of the number of stems a plant has. (B) The proportion of individuals surviving the entire 10-year study interval that produced different numbers of inflorescences over the 10 years.

forest fragments have significantly altered rates of growth and reproduction over the long-term. Annual reductions were small but had a large cumulative effect – after a decade, plants in fragments were significantly smaller than those in continuous forest. Smaller plants in turn produced fewer inflorescences than their larger counterparts in continuous forest. Our results emphasize the importance of long-term datasets for elucidating human-generated impacts on perennial plants, and the importance of evaluating these impacts at multiple temporal scales.

The reduced rate of growth means it will take longer for *H. acuminata* individuals in forest fragments to reach large size classes, and that fewer individuals will eventually do so. This reduced growth has important consequences for plant fertility. As in most plants (Harper, 1977; Horvitz and Schemske, 1995), reproduction in *H. acuminata* is size dependent, and plants with four or more stems are responsible for most of the reproduction (Fig. 2A; Bruna, 2003; Bruna and Kress, 2002). However, there are fewer large, flowering plants in fragments in both absolute and proportional terms (Bruna and Kress, 2002). Slower growth of plants in fragments appears to explain this disparity – every additional stem a plant has doubles its probability of flowering (Fig 2A). Precise mechanisms underlying reduced plant growth in BDFFP fragments undoubtedly vary among sites (Laurance et al., 2007) and microsites (Benitez-Malvido et al., 2005). Nevertheless, we suggest that two putative causal agents ubiquitous across sites are of primary importance in explaining altered growth rates in forest fragments. First, BDFFP fragments are susceptible to more frequent branch- and treefalls (D'Angelo et al., 2004), which can destroy stems of *H. acuminata* and hence cause negative growth (Bruna and Ribeiro, 2005). Second, fragments generally have warmer and drier air and soil (Camargo and Kapos, 1995; Sizer and Tanner, 1999), which can cause *H. acuminata* to shed leaves and stems (Bruna et al., 2002). Regardless of the specific mechanisms, it is important to note that plant fertility in the central Amazon is extremely low when compared with that of other tropical forests, probably due to the extremely poor soils in the region (Gentry and Emmons, 1987). Although altered plant reproduction has been documented in other fragmented tropical forests (e.g., Cascante et al., 2002; Cunningham, 2000b), only two studies to date have investigated whether low fertility in the central Amazon is exacerbated in fragments. While Laurance et al. (2003) showed edge effects had only a limited influence on tree reproduction, Bruna and Kress (2002) found a trend towards proportionately fewer reproductive plants in fragments. Both studies were based on 2 years of phenological data; with this decadal dataset we not only document lower per-individual reproductive rates but also provide strong evidence for the demographic mechanism underlying these reductions.

Another important result of our study was the marked inter-annual variation in growth rates. That the patterns of growth in fragments and continuous forest oscillate in a similar fashion suggests this variation is driven by a larger-scale, regional driver (e.g., climate). However, we were unable to detect a link between

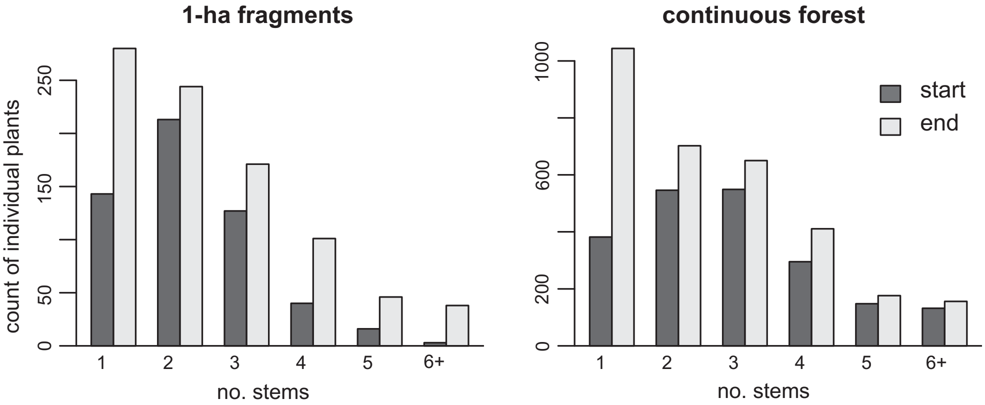

Fig. A1. Number of *H. acuminata* plants in each size class at the start (1998) and end (2007) of the study for both 1-ha fragment and continuous forest plots in the central Amazon. Note the different scales on the *Y*-axes. Figure includes all plants present in the dataset at the start and end of the study, respectively, including those that died during the study as well as those that recruited after the study began (which is different than the subset of plants present for the entire 10 year study used in our ordered logistic regression analysis described in Sections 2 and 3.).

growth rate and annual, seasonal or monthly precipitation in the study area (Gagnon et al., *unpubl. data*). Interestingly, the large drop in growth rates in the 2002–2003 transition year coincides with drought conditions in the region resulting from the 2002 El Niño Southern Oscillation (ENSO) event. Studies investigating the effects of ENSO events on herbaceous species with which we can compare our results are virtually nonexistent (Wright, 2005); still, our results are consistent with those of a prior study documenting a 1 year spike in tree mortality at the BDFFP during the 1997 ENSO (Williamson et al., 2000). Williamson et al. (2000) also observed a rapid return to pre-drought patterns of plant condition; this appears to be the case with *H. acuminata* as well and may result from the species' capacity to compensate for tissue loss with rapid growth (Bruna and Ribeiro, 2005). Regardless, pronounced inter-annual variation underscores the year-to-year dynamism of this system and emphasizes the need for long-term datasets to fragmentation's consequences (Laurance et al., 2002). Because the magnitude of inter-annual variation depends on whether plants are growing in fragments or in continuous forest, our results also support the hypothesis that populations in continuous forest are better buffered against environmental perturbations than those in fragments (Laurance, 2002).

Finally, most previous studies investigating the influence of environmental changes associated with fragmentation on plants have focused on a single stage or size class, particularly on seedlings (reviewed in Bruna et al. (2009) and Hobbs and Yates (2003)). Our results emphasize the importance of evaluating a range of life-history stages when elucidating the effects of fragmentation on plants – plant size was an important determinant of *H. acuminata* growth rate. We found that, on average, small plants grew larger while large plants shrank; had we focused exclusively on either small or large individuals we would have reached contradictory conclusions. The focus on a limited suite of demographic stages may help explain why previous reviews conclude that fragmentation's impacts on plants are idiosyncratic (Hobbs and Yates, 2003); additional research simultaneously comparing juveniles and adults would greatly advance our understanding of plant responses to environmental change in fragments (Bruna et al. (2009)).

5. Conclusion

Plant growth is a fundamental component of demography that exerts a major influence on population dynamics (Harper, 1977; Salguero-Gomez and Casper, 2010; Silvertown et al., 1993). However, how plant growth rates change in fragments has been inexplicably overlooked by ecologists in favor of studying survival- and reproduction-related processes (Bruna et al., 2009). We have shown that beyond widely documented increases in plant mortality in fragments (e.g., see Laurance et al., 2002 and references therein), plants surviving in fragments can also have altered growth rates across the range of life-history stages. Because of the demographic feedback between growth, survival, and reproduction in *H. acuminata* (e.g., Bruna, 2002, 2003; Bruna and Oli, 2005), reduced rates of individual growth may be an important indirect mechanism contributing to reduced population viability in fragments; we are currently testing this hypothesis using matrix models (sensu Morris and Doak, 2002). If growth responses of other understory or herbaceous species are comparable to those observed in our study system, reduced growth could also help explain their decline in habitat fragments.

Acknowledgements

We thank Kathleen Kiernan for suggestions with analyses and Heather Passmore and three anonymous reviewers for comments on the manuscript. We also thank the many technicians and students who helped conduct the censuses and the logistical support of the BDFFP and its staff. Financial support was provided by the US National Science Foundation (awards DEB-0614149, DEB-0614339, DEB-0309819, DBI-0109226, and INT 98-06351) and the University of Florida. This is publication number 566 in the BDFFP Technical Series.

Appendix A

See Fig. A1.

References

Aizen, M.A., Feinsinger, P., 1994. Forest fragmentation, pollination, and plant reproduction in a chaco dry forest, Argentina. Ecology 75, 330–351.

Benítez-Malvido, J., 2001. Regeneration in tropical rain forest fragments. In: Bierregaard, R.O., Lovejoy, T.E., Mesquita, R. (Eds.), Lessons from Amazonia: The Ecology and Management of a Fragmented Forest. Yale University Press, New York, pp. 136–145.

Benitez-Malvido, J., Martinez-Ramos, M.M., Camargo, J.L.C., Ferraz, I.D.K., 2005. Responses of seedling transplants to environmental variations in contrasting habitats of Central Amazonia. Journal of Tropical Ecology 21, 397–406.

Berry, F., Kress, W.J., 1991. *Heliconia*: An Identification Guide. Smithsonian Institution Press, Washington, DC, USA.

Bierregaard, R.O., Gascon, C., Lovejoy, T.E., Mesquita, R. (Eds.), 2002. Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest. Yale University Press, New Haven.

Broadbent, E.N., Asner, G.P., Keller, M., Knapp, D.E., Oliveira, P.J.C., Silva, J.N., 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biological Conservation 141, 1745–1757.

Bruna, E.M., 2002. Effects of forest fragmentation on *Heliconia acuminata* seedling recruitment in central Amazonia. Oecologia 132, 235–243.

Bruna, E.M., 2003. Are plant populations in fragmented habitats recruitment limited? Tests with an Amazonian herb. Ecology 84, 932–947.

Bruna, E.M., Kress, W.J., 2002. Habitat fragmentation and the demographic structure of an Amazonian understory herb (*Heliconia acuminata*). Conservation Biology 16, 1256–1266.

Bruna, E.M., Oli, M.K., 2005. Demographic effects of habitat fragmentation on a tropical herb: life-table response experiments. Ecology 86, 1816–1824.

Bruna, E.M., Ribeiro, M.B.N., 2005. The compensatory responses of an understory herb to experimental damage are habitat-dependent. American Journal of Botany 92, 2101–2210.

Bruna, E.M., Nardy, O., Strauss, S.Y., Harrison, S.P., 2002. Experimental assessment of *Heliconia acuminata* growth in a fragmented Amazonian landscape. Journal of Ecology 90, 639–649.

Bruna, E.M., Fiske, I.J., Trager, M.D., 2009. Habitat fragmentation and plant populations: is what we know demographically irrelevant? Journal of Vegetation Science 20, 569–576.

Camargo, J.L.C., Kapos, V., 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. Journal of Tropical Ecology 11, 205–221.

Cascante, A., Quesada, M., Lobo, J.J., Fuchs, E.A., 2002. Effects of dry tropical forest fragmentation on the reproductive success and genetic structure of the tree *Samanea saman*. Conservation Biology 16, 137–147.

Chen, J.Q., Franklin, J.F., Spies, T.A., 1995. Growing-season microclimatic gradients from clear-cut edges into old-growth Douglas-Fir forests. Ecological Applications 5, 74–86.

Conover, W.J., Iman, R.L., 1981. Rank transformations as a bridge between parametric and nonparametric statistics. The American Statistician 35, 124–129.

Cramer, J.M., Mesquita, R.C.G., Bentos, T.V., Moser, B., Williamson, G.B., 2007. Forest fragmentation reduces seed dispersal of Duckeodendron cestroides, a central amazon endemic. Biotropica 39, 709–718.

Crone, E.E., 2001. Is survivorship a better fitness surrogate than fecundity? Evolution 55, 2611–2614.

Cunningham, S.A., 2000a. Depressed pollination in habitat fragments causes low fruit set. Proceedings of the Royal Society Biological Sciences Series B 267, 1149–1152.

Cunningham, S.A., 2000b. Effects of habitat fragmentation on the reproductive ecology of four plant species in mallee woodland. Conservation Biology 14, 758–768.

D'Angelo, S.A., Andrade, A.C.S., Laurance, S.G., Laurance, W.F., Mesquita, R.C.G., 2004. Inferred causes of tree mortality in fragmented and intact Amazonian forests. Journal of Tropical Ecology 20, 243–246.

Didham, R.K., Lawton, J.H., 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. Biotropica 31, 17–30.

Gagnon, P.R., Platt, W.J., 2008. Multiple disturbances accelerate clonal growth in a potentially monodominant bamboo. Ecology 89, 612–618.

Gehlhausen, S.M., Schwartz, M.W., Augspurger, C.K., 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. Plant Ecology 147, 21–35.

Gentry, A.H., Emmons, L.H., 1987. Geographical variation in fertility, phenology and composition of the understory of neotropical forests. Biotropica 19, 216–217.

Harper, J.L., 1977. Population Biology of Plants. Academic Press, London, UK.

Hobbs, R.J., Yates, C.J., 2003. Impacts of ecosystem fragmentation on plant populations: generalising the idiosyncratic. Australian Journal of Botany 51, 471–488.

Horvitz, C.C., Schemske, D.W., 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb – projection matrix analysis. Ecological Monographs 65, 155–192.

Kapos, V., 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. Journal of Tropical Ecology 5, 173–185.

Kapos, V., Wandelli, E., Camargo, J.L., Ganade, G., 1997. Edge-related changes in environment and plant responses due to forest fragmentation in Central Amazonia. In: Laurance, W.F., Bierregaard, R.O., Jr. (Eds.), Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, Chicago, IL, USA.

Kolb, A., Diekmann, M., 2005. Effects of life-history traits on responses of plant species to forest fragmentation. Conservation Biology 19, 929–938.

Laurance, W.F., 1991. Edge effects in tropical forest fragments: application of a model for the design of nature reserves. Biological Conservation 57, 205–220.

Laurance, W.F., 2002. Hyperdynamism in fragmented habitats. Journal of Vegetation Science 13, 595–602.

Laurance, W.F., Curran, T.J., 2008. Impacts of wind disturbance on fragmented tropical forests: a review and synthesis. Austral Ecology 33, 399–408.

Laurance, W.F., Ferreira, L.V., Rankin de Merona, J.M., Laurance, S.G., 1998a. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology 79, 2032–2040.

Laurance, W.F., Ferreira, L.V., Rankin de Merona, J.M., Laurance, S.G., Hutchings, R.W., Lovejoy, T.E., 1998b. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. Conservation Biology 12, 460–464.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G., Sampaio, E., 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conservation Biology 16, 605–618.

Laurance, W.F., Merona, J.M.R.D., Andrade, A., Laurance, S.G., D'Angelo, S., Lovejoy, T.E., Vasconcelos, H.L., 2003. Rain-forest fragmentation and the phenology of Amazonian tree communities. Journal of Tropical Ecology 19, 343–347.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ewers, R.M., Harms, K.E., Luizao, R.C.C., Ribeiro, J.E., 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. PLoS One 2.

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., Schabenberger, O., 2006. SAS for Mixed Models, 2nd ed. SAS Institute Inc., Carey, North Carolina, USA.

Lopez-Gallego, C., 2008. Demographic variation in cycad populations inhabiting contrasting forest fragments. Biodiversity and Conservation 17, 1213–1225.

Matlack, G.R., 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation 66, 185–194.

Matlack, G.R., 1994. Vegetation dynamics of the forest edge: trends in-space and successional time. Journal of Ecology 82, 113–123.

Mesquita, R., Delamonica, P., Laurance, W.F., 1999. Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. Biological Conservation 91, 129–134.

Morris, W.F., Doak, D.F., 2002. Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis. Sinauer Associates Inc., Sunderland, MA, USA.

Morris, W.F., Doak, D.F., 2005. How general are the determinants of the stochastic population growth rate across nearby sites? Ecological Monographs 75, 119–137.

Portela, R.D.Q., Bruna, E.M., dos Santos, F.A.M., 2010. Demography of palm species in Brazil's Atlantic forest: a comparison of harvested and unharvested species using matrix models. Biodiversity and Conservation 19, 2389–2403.

Ribeiro, M.B.N., Bruna, E.M., Mantovani, W., 2010. Influence of post-clearing treatment on the recovery of herbaceous plant communities in Amazonian secondary forests. Restoration Ecology 18, 50–58.

Salguero-Gomez, R., Casper, B.B., 2010. Keeping plant shrinkage in the demographic loop. Journal of Ecology 98, 312–323.

Silvertown, J., Franco, M., Pisanty, I., Mendoza, A., 1993. Comparative plant demography – relative importance of life cycle components to the finite rate of increase in woody and herbaceous perennials. Journal of Ecology 81, 465–476.

Silvertown, J., Franco, M., Menges, E., 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. Conservation Biology 10, 591–597.

Sizer, N., Tanner, E.V.J., 1999. Responses of woody plant seedlings to edge formation in a lowland tropical rainforest, Amazonia. Biological Conservation 91, 135–142.

Stokes, M.E., Davis, C.S., Koch., G.G., 1995. Categorical Data Analysis Using the SAS System. SAS Institute, Inc., Cary, NC, USA.

Sutton, F.M., Morgan, J.W., 2009. Functional traits and prior abundance explain native plant extirpation in a fragmented woodland landscape. Journal of Ecology 97, 718–727.

Tomimatsu, H., Ohara, M., 2010. Demographic response of plant populations to habitat fragmentation and temporal environmental variability. Oecologia 162, 903–911.

Turner, I.M., Chua, K.S., Ong, J.S.Y., Soong, B.C., Tan, H.T.W., 1995. A century of plant species loss from an isolated fragment of lowland tropical rain forest. Conservation Biology 10, 1229–1244.

Williamson, G.B., Laurance, W.F., Oliveira, A.A., Delamonica, P., Gascon, C., Lovejoy, T.E., Pohl, L., 2000. Amazonian tree mortality during the 1997 El Nino drought. Conservation Biology 14, 1538–1542.

Wright, S.J., 2005. The El Nino Southern Oscillation influences tree performance in tropical rainforests. University of Chicago Press, Chicago.

Zartman, C.E., Shaw, A.J., 2006. Metapopulation extinction thresholds in rain forest remnants. American Naturalist 167, 177–189.