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Experimental assessment of *Heliconia acuminata* growth in a fragmented Amazonian landscape

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Summary

1 Fragmentation severely alters physical conditions in forest understories, but few studies have connected these changes to demographic impacts on forest species using detailed experimental examination at the individual and population levels.
2 Using a 32-month, reciprocal-transplant experiment, we show that individuals of the Amazonian understory herb *Heliconia acuminata* transplanted into forest fragments lost over 20% of their vegetative shoots, while those transplanted to continuous forest showed a slight gain. The leaf area of plants in fragments also increased at half the rate it did in continuous forest sites.
3 It appears that the normal dry season stresses to which forest understorey plants are exposed are greatly exacerbated in fragments, causing plants to shed shoots and leaves.
4 The observed shifts in size could help explain why populations in fragments are more skewed towards smaller demographic stage classes than those in continuous forest. These shifts in size structure could also result in reduced abundances of flowering plants, as reproduction in *H. acuminata* is positively correlated with shoot number.
5 Fragmentation-related changes in growth rates resulting from abiotic stress may have significant demographic consequences.

Key-words: forest fragmentation, growth rates, Heliconiaceae, root : shoot ratio, understorey plants, water stress

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Introduction

The fragmentation of once-continuous habitats is a globally pervasive phenomenon, and understanding how communities respond to fragmentation remains a central area of research in ecology (reviewed in Laurance & Bierregaard 1997; Harrison & Bruna 1999). One of its most consistently documented consequences is the dramatic alteration of abiotic conditions in fragments, particularly in forest ecosystems (Kapos 1989; Chen *et al*. 1992; Gehlhausen *et al*. 2000). Fragments of rain forest, for example, often have increased air and soil temperatures, reduced relative humidity and reduced soil moisture levels (Kapos 1989; Didham & Lawton 1999). These changes are thought to drive many of the negative effects of fragmentation, including the local extinction of plants and animals (Leach & Givnish 1996; Didham *et al*. 1998; Carvalho & Vasconcelos 1999).

Altered environmental conditions could also affect the individuals that survive in fragmented landscapes by influencing their physiological condition (Weishampel *et al*. 1997; Berwaerts *et al*. 1998; Sumner *et al*. 1999; Stratford & Stouffer 2001). For instance, lizards in Australian rain forest fragments were found to be smaller than those in continuous forest, which was hypothesized to result from increased thermal variance during gestation or perhaps the reduced abundance of temperature-sensitive prey items (Sumner *et al*. 1999). Similarly, temperature-related reductions in the abundance of insects could account for the lower feather growth rates of insectivorous birds in Amazonian forest fragments although higher evaporative water loss might also be responsible (Stratford & Stouffer 2001). As no studies have used manipulative experiments to investigate such fragmentation-related differences, it is difficult to determine whether they actually followed fragmentation or merely reflect pre-isolation variation.

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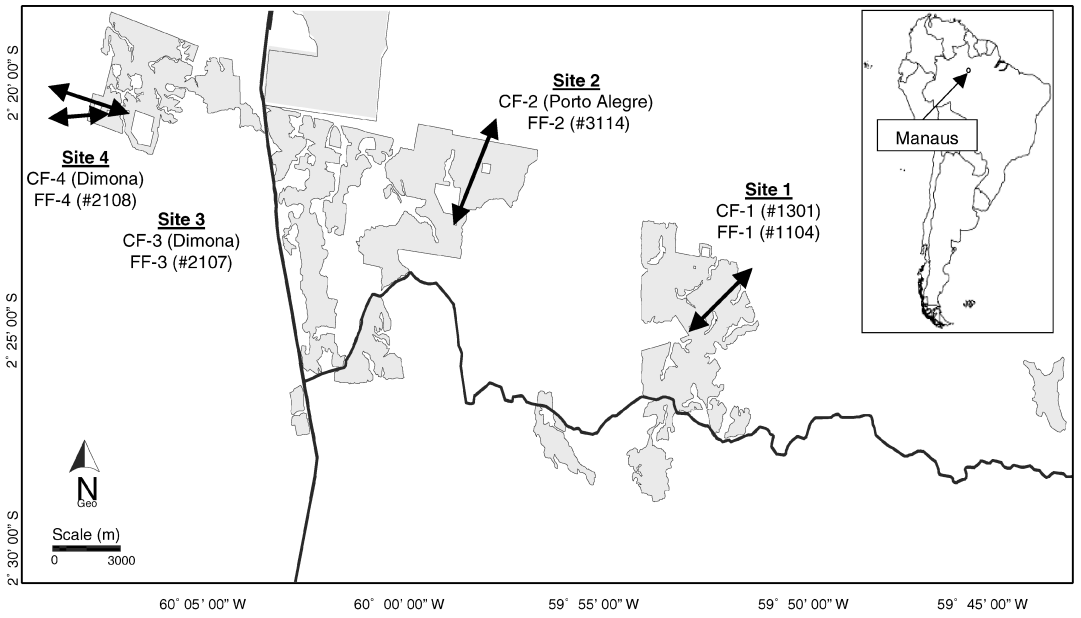

Fig. 1 Map of the Biological Dynamics of Forest Fragments Project, indicating sites used in this study. Arrows represent fragments and continuous forest areas between which plants were reciprocally transplanted. Continuous forest areas are white, secondary forest and pastures are grey, dark lines represent roads. Reserve numbers are given in parentheses (Lovejoy *et al*. 1986), except for continuous forest sites with no BDFFP number, which are referred to by the name of the ranch in which they are located. FF = forest fragment, CF = continuous forest.

Furthermore, the long-term demographic consequences of these changes are usually unknown, as the link between the characters measured and individual fitness is unclear.

Understorey plants are ideal systems for experimental investigation of the consequences of fragmentation for individual growth. First, they grow in a layer of the forest characterized by low air and soil temperatures, high relative humidity and limited light, all of which are dramatically altered in tropical forest fragments (Kapos 1989; Camargo & Kapos 1995; Didham & Lawton 1999). Secondly, they are readily amenable to landscape-scale experimental manipulations, whereas animals or woody plants frequently are not. Finally, critical life-history transitions in plants, such as survivorship and reproduction, are often size-dependent (Harper 1977; Horvitz & Schemske 1995), making it possible to infer the demographic consequences of changes in plant size.

Heliconia acuminata is an understorey herb native to central Amazonia and the Guyanas (Berry & Kress 1991). At Brazil's Biological Dynamics of Forest Fragments Project, where *H. acuminata* is the subject of an ongoing demographic study, populations in small forest fragments are skewed towards smaller size classes than those in continuous forest (Bruna & Kress 2002). Here we use a 32-month reciprocal transplant experiment to evaluate the prediction that this pattern is due in part to reduced plant growth rates in fragments. We then use the relationship between *H. acuminata* size and reproduction (Bruna 2001; Bruna & Kress 2002) to infer the demographic consequences of changes in plant size.

Materials and methods

STUDY SITE AND SPECIES

This study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), located 70 km north of Manaus, Brazil (2°30′ S, 60° W, Fig. 1). The habitat at the BDFFP is non-flooded lowland rain forest with undulating topography that ranges from 50 to 150 m in elevation. Mean annual temperature is 26 °C (range 19–39 °C), and annual rainfall ranges from 1900 to 3500 mm. There is a pronounced dry season from June to November

The BDFFP is surrounded by forest that extends for over 200 km to the north, east and west. In addition to large continuous forest reserves embedded in this expanse, the BDFFP also has several forest fragment reserves isolated in the early 1980s by the creation of cattle pastures (Lovejoy *et al*. 1986). Fragments are separated from regenerating secondary growth by a 100-m buffer strip that is repeatedly cleared (BDFFP Records).

Heliconia acuminata (Heliconiaceae) is an understorey perennial monocot found in both the fragment and continuous forest reserves at the BDFFP (Bruna & Kress 2002). It produces vegetative shoots from a basal rhizome, and each shoot has several large, broad leaves (Berry & Kress 1991). Reproductive plants also have one or more flowering shoots, each of which has a single infloresence with 20–25 flowers (Bruna & Kress 2002). Plants usually begin flowering at the start of the rainy season and continue until March; clonal reproduction via underground runners is very limited (E. M. Bruna, personal observation).

A key advantage of the *H. acuminata* system is the lack of major foliar herbivores. Throughout the Neotropics the primary herbivores of *Heliconia* are Hispine beetles, which cause leaf scarring and readily identifiable perforations but remove little foliar tissue (Strong 1977). In our study sites Hispines primarily feed on inflorescences and developing fruits, and the patterns of herbivory are similar in continuous forest and fragments (E. M. Bruna, unpublished data). Changes in shoot number and leaf area observed during the experiment are therefore not attributable to fragmentation-related differences in herbivore density.

EXPERIMENTAL DESIGN

We began by choosing 40 *H. acuminata* individuals in each of four 1-ha fragment reserves and four continuous forest sites (Fig. 1). Most plants initially had two to five vegetative shoots (mean = 3.38 ± 0.04 SE); these size classes represent 65–67% of the plants found in permanent demographic plots (Bruna 2001). Half of the selected individuals in each site were chosen at random and immediately transplanted to a paired site of the opposite habitat type (i.e. 'experimental' plants). The other half were removed from the ground and replanted in the same fragment or forest site after an equal amount of time to serve as controls for the effects of travel, transplanting and the possibility of adaptation to local site conditions (i.e. 'control' plants).

Four edge-to-interior transects were established in each fragment, each with an experimental and a control plant transferred to the fragment edge, and at 5, 10, 20 and 40 m from the edge. Pairs of control and experimental plants had the same number of shoots whenever possible. After transplanting, some of the plants at 40 m were found to be closer to other edges than the one from which their transect originated. We calculated the distance from these plants to the nearest fragment edge and analyses were conducted using these adjusted distances. In continuous forest, sites were 500–2000 m from the nearest primary forest/secondary forest border and transplants were arrayed along four 40 m transects.

Transplantation occurred during the early part of the 1999 rainy season (7–28 February 1999), at which time we counted the number of vegetative shoots on each plant and calculated its total leaf area using the regression equation:

$$\sqrt{\text{Leaf Area (cm}^2\text{)}} = 1.72 + 0.35 \times \text{leaf length (cm)}$$

($R^2 = 0.959$, $P < 0.0001$, based on $n = 144$ leaf tracings measured with a LI-COR Model 3000 A Leaf Area Meter). Both characters are important indicators of overall plant condition in *H. acuminata*: total leaf area plays an important role in photosynthesis and the regulation of water loss in many tropical understorey species (Begg 1980), while the number of vegetative shoots is strongly positively correlated with the probability the species will flower (Fig. 2).

We re-measured 7 months after transplanting (18 October to 9 November 1999, following the completion of one rainy and one dry season), 14 months after transplanting (19 April to 14 May 2000, at the end of a second rainy season) and 32 months after transplanting (22–29 October 2001, following three rainy and three dry seasons). All plants were harvested immediately after the final measurement and above- and below-ground portions separated, dried and weighed to the nearest 0.01 g. We used these data to calculate the ratio of root biomass to shoot biomass (R : S ratio) for each plant.

STATISTICAL ANALYSES: GROWTH RATES AND BIOMASS ALLOCATION

Because shoot number and leaf area are significantly positively correlated in *H. acuminata* ($n = 320$, $\rho = 0.402$, $P < 0.0001$), we used multivariate analysis of covariance (MANCOVA) to compare changes in plant size in forest fragments and continuous forest. The dependent variables were the proportional change in leaf area (Δ_{la}) and shoots (Δ_{shoots}) 32 months after transplanting, calculated as:

$$\text{proportional change in size } (\Delta) = \frac{\text{final size} - \text{initial size}}{\text{initial size}}$$

Proportional change of both shoots and leaf area were square-root-transformed to meet the assumptions of parametric statistics. Source and destination habitat (fragment or continuous forest) and site (1–4) were independent variables, and initial plant size (one to three shoots or four to six shoots) was included as a covariate. Note that while we made repeated measurements of plant size, our experiment was not designed to assess interseason variation in plant growth rates. Therefore although we present data from earlier census dates, only overall growth rates are compared statistically. Analyses were conducted on proportional changes in plant size, but are presented as percentages.

We compared overall Δ_{la} and Δ_{shoots} in forest fragments at four distances from the fragment edge (0, 5, 10 and ≥ 20 m) using multivariate analysis of variance (MANOVA) with site and source habitat type as independent variables. Tukey posthoc tests were used to compare individual means at different distances.

We compared the final R : S ratio of plants in continuous forest and forest fragments using analysis of covariance (ANCOVA). The R : S ratio at the time of harvesting (log-transformed to correct for non-normality) was used as the dependent variable, with source and destination habitat type and site, as independent variables. As R : S ratio in herbaceous plants tends to decrease with increasing plant size (McConnaughay & Coleman 1999), we included final plant biomass (also log-transformed) as a covariate after confirming

the negative correlation between ln(R : S ratio) and ln(biomass) for *H. acuminata* ($n = 300$, $\rho = -0.410$, $P < 0.0001$).

We also used ANCOVA to test for an effect of increasing edge proximity on biomass allocation, as for Δ_{la} and Δ_{shoots}, but comparing the final R : S ratio and with ln(biomass) as the covariate.

SOIL CHEMISTRY

To determine if differences in soil nutrients or chemistry could be contributing to the observed results we collected four soil cores from a 5 × 5 m area adjacent to a randomly selected point along each transect. These cores were of the uppermost 10 cm of soil, where the roots of *H. acuminata* are generally found (E.M. Bruna and O. Nardy, personal observation). The four subsamples were then homogenized and bulked into a single sample per transect, yielding a total of four soil samples from each forest fragment or continuous forest site. Total P, K^+, Ca^{2+}, Mg^{2+}, Al^{3+}, total C, total organic material, Cu, Fe, Zn^+, Mn^{2+} and pH in water were analysed by the Soil Chemistry Laboratory at the Brazilian Agricultural Research Centre in Manaus using standard protocols (EMBRAPA 1997). The average value for the four transects from each site was calculated and median values from continuous forest and forest fragments were compared using Bonferroni-corrected Mann–Whitney *U*-tests.

PREDICTED CHANGES IN FLOWERING PLANT ABUNDANCE

Finally, we used survey data (Bruna 2001) to determine the average values for probability of flowering at a given size (Fig. 2). This, together with the size distributions of experimental plants at the time of transplanting and at the end of the experiment, was used to calculate how many flowering plants would be expected in fragments and continuous forest before and after fragmentation.

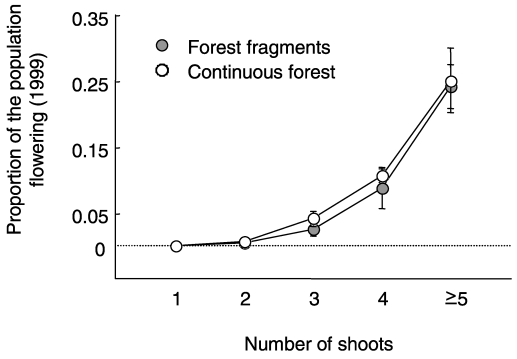

Fig. 2 The mean proportion (± 1 SE) of flowering *Heliconia acuminata* for a given number of shoots. Individuals in four permanent demographic plots in 1-ha fragments (filled circles) and six plots in continuous forest (open circles) were surveyed in 1999 (Bruna 2001). The proportion flowering is significantly positively correlated with shoot number in both habitat types (FF: $n = 796$, $\rho = 0.864$, $P < 0.0002$; CF: $n = 2384$, $\rho = 0.904$, $P < 0.0001$).

We tested for shifts in the initial and final predicted numbers with a χ^2 test, in which the predicted numbers in each habitat type at the start of the experiment were used as the expected values and the predicted numbers 32 months later were used as the observed values.

All statistical analyses were conducted with Statview 5.0.1. We present back-transformed values when transformations were necessary.

Results

There was a significant difference in the growth of *H. acuminata* transplanted to forest fragments and continuous forest ($P = 0.021$, Table 1). After 32 months plants in fragments had 21.5% (± 4.6 SE) fewer shoots than when the experiment began, whereas those in continuous forest were slightly larger (+1.2% ± 4.5 SE) than when originally transplanted (Fig. 3c). Leaf area increased more than twice as much in continuous forest as in forest fragments (Δ_{la}: 12.3% ± 7.6 SE vs. 5.5% ± 12

Table 1 Results of a multivariate analysis of covariance on the proportional change in leaf area and shoot number 32 months after reciprocal transplants between forest fragments and continuous forest

Source of variation	Wilks' Λ	d.f.	*F*	*P*
Destination habitat	0.973	2, 284	3.923	0.021
Site	0.831	6, 568	9.198	< 0.0001
Source habitat	0.999	2, 284	0.171	0.843
Initial shoot number	0.953	2, 284	6.971	0.001
Destination habitat × Site	0.898	6, 568	5.251	< 0.0001
Destination habitat × Source habitat	0.993	2, 284	1.003	0.368
Destination × Initial shoot number	0.995	2, 284	0.760	0.469
Site × Source habitat	0.982	6, 568	0.860	0.525
Site × Initial shoot number	0.969	6, 568	1.511	0.172
Source habitat type × Initial shoot number	0.986	2, 284	2.082	0.127
Destination habitat × Site × Source habitat	0.986	6, 568	0.693	0.656
Destination habitat × Site × Initial shoot number	0.984	6, 568	0.757	0.604
Source habitat × Source × Initial shoot number	0.992	6, 568	0.377	0.894
Destination × Source × Initial shoot number	0.998	2, 284	0.335	0.715
Destination habitat × Site × Source habitat × Initial shoot number	0.987	6, 568	0.623	0.712

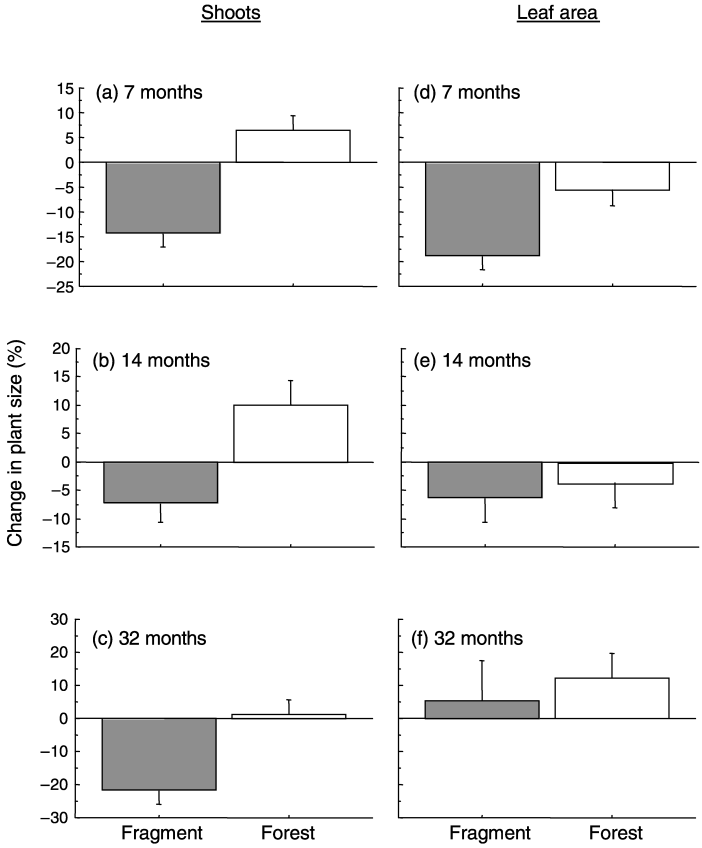

Fig. 3 Mean change in leaf area and shoots (± 1 SE) 7, 14 and 32 months after transplanting to continuous forest (open bars) and forest fragments (filled bars).

Table 2 Results of a multivariate analysis of variance on the proportional change in leaf area and shoot number 32 months after transplanting at increasing distances from fragment edges

Source of variation	Wilks' Λ	d.f.	*F*	*P*
Distance from edge	0.873	6, 250	2.926	0.009
Source habitat	0.989	2, 125	0.690	0.503
Site	0.892	6, 250	2.447	0.026
Site × Source habitat	0.943	6, 250	1.249	0.282
Site × Distance from edge	0.919	18, 254	0.919	0.556
Source habitat × Distance from edge	0.967	6, 254	0.703	0.647
Distance from edge × Site × Source habitat	0.898	18, 254	0.765	0.740

SE, Fig. 3f). While the strength of these responses varied across sites ($P < 0.0001$), the source habitat did not significantly affect growth rates, either as a main effect or in any interaction terms (Table 1).

Thirty-two months after transplanting there were significant differences between the growth rates of plants at different distances from fragment edges ($P = 0.009$, Table 2). Plants on edges were significantly larger than plants at almost all other distances and, on average, these were the only plants in fragments that increased in size (Fig. 4c,f). Growth rates were not, however, consistent among fragments (site main effect, $P = 0.026$, Table 2) and, although there was no significant site–distance interaction, growth rates were positive on the edges of two of the fragments (FF-3 and FF-4) and negative on the borders of the other two (FF-1 and FF-2).

Final *H. acuminata* root biomass ranged from 0.01 to 24.06 g in continuous forest (mean = 5.75 ± 0.34 SE) and from 0.12 to 76.92 g in forest fragments (mean = 8.35 ± 0.88 SE). There was a significant main effect of destination habitat on final R : S ratio ($F_{1,268} = 4.251$, $P = 0.04$), with a mean final R : S ratio of 1.57 ± 0.16 SE for plants transplanted to forest fragments vs. 1.19 ± 0.11 SE for those transplanted to continuous forest. There was no significant main effect of source habitat or site, although there was a significant site × ln(final biomass) interaction (Table 3). Results of Tukey tests indicated that plants at site 2 had significantly higher R : S ratios than plants at the other

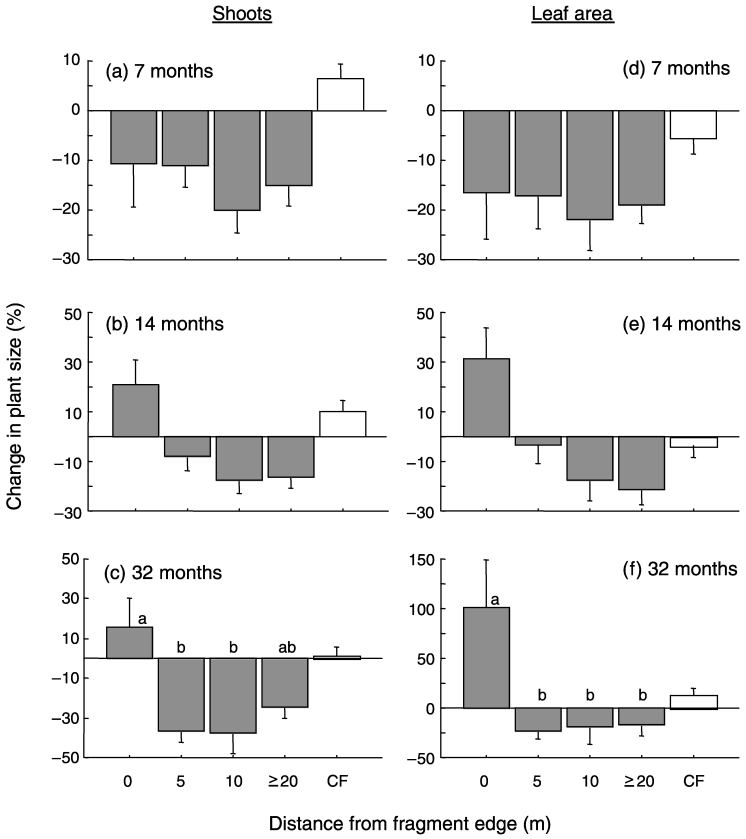

Fig. 4 Mean change in leaf area and shoots (± 1 SE) 7, 14 and 32 months after transplanting at increasing distances from fragment edges. For overall values, different letters indicate significant differences ($P < 0.05$) between means on the basis of Tukey posthoc tests. The mean change for plants in continuous forest (CF) is shown for comparison but was not included in statistical analyses. Note the different scales in 4c and 4f.

Table 3 Results of an analysis of covariance on the ratio of root biomass to shoot biomass 32 months after reciprocally transplanting *H. acuminata* individuals between continuous forest and forest fragments

Source of variation	d.f.	SS	*F* ratio	*P*
Destination habitat type	1	1.979	4.251	0.040
Site	3	2.348	1.682	0.171
Source habitat type	1	0.129	0.278	0.600
Ln(final biomass)	1	9.359	20.108	< 0.0001
Destination habitat × Site	3	1.523	1.091	0.353
Destination habitat × Source habitat	1	0.211	0.453	0.501
Destination × Ln(final biomass)	1	1.517	3.260	0.072
Site × Source habitat	3	2.492	1.785	0.150
Site × Ln(final biomass)	3	6.779	4.855	0.003
Source habitat type × Ln(final biomass)	1	0.172	0.369	0.544
Destination habitat × Site × Source habitat	3	2.513	1.8	0.148
Destination habitat × Site × Ln(final biomass)	3	0.56	0.401	0.752
Source habitat × Source × Ln(final biomass)	3	1.586	1.136	0.335
Destination × Source × Ln(final biomass)	1	0.009	0.02	0.888
Destination × Site × Source × Ln(final biomass)	3	2.934	2.101	0.100
Residual	268	124.733		

three sites, despite having the lowest biomass of all locations.

In forest fragments the R : S ratios varied significantly with edge proximity ($P = 0.015$), although not with site or source habitat (Table 4). Tukey tests were unable to detect differences in mean R : S ratio between any pairs of edge distances, possibly due to the lower power of multiple-comparison tests relative to ANOVA (Zar 1999). However, visual inspection indicates that R : S ratios were lower 5 m from the edges than at other distances (Fig. 5).

The soils in the BDFFP study area are generally poor, with high levels of aluminium, a paucity of organic material, limited macro- and micronutrients,

Table 4 Results of an analysis of covariance on the ratio of root biomass to shoot biomass 32 months after transplanting *H. acuminata* individuals at increasing distances from fragment edges

Source of variation	d.f.	SS	*F* ratio	*P*
Distance from the edge	3	4.848	3.663	0.015
Site	3	1.493	1.128	0.342
Source habitat type	1	0.087	0.196	0.659
Ln(final biomass)	1	8.0858	18.263	< 0.0001
Distance from the edge × Site	9	5.468	0.608	0.211
Distance from the edge × Source habitat	3	0.283	0.214	0.887
Distance from the edge × Ln(final biomass)	3	3.526	2.664	0.053
Site × Source habitat	3	1.099	0.830	0.481
Site × Ln(final biomass)	3	1.672	1.263	0.292
Source habitat type × Ln(final biomass)	1	0.145	0.328	0.569
Distance from the edge × Site × Source habitat	9	3.171	0.799	0.619
Distance from edge × Site × Ln(final biomass)	9	4.843	1.220	0.294
Source habitat × Source × Ln(final biomass)	3	0.851	0.643	0.589
Distance from edge × Source × Ln(final biomass)	3	0.400	0.302	0.824
Distance × Site × Source × Ln(final biomass)	9	2.749	0.692	0.714
Residual	87	38.384		

Table 5 Soil chemistry parameters in continuous forest and forest fragments, and results of Mann–Whitney *U*-test comparisons (Bonferroni adjusted α value required for significance, $P = 0.004$)

Variable	Continuous forest (Mean ± SE)	Forest fragments (Mean ± SE)	*U*	*P*-value
pH in water	3.78 ± 0.105	3.68 ± 0.034	8.0	0.48
Ca^{2+} (m.e. 100 g^{-1} dry soils)	0.076 ± 0.024	0.086 ± 0.017	6.0	0.99
Cu (mg kg^{-1})	0.135 ± 0.028	0.146 ± 0.025	7.0	0.72
Fe (mg kg^{-1})	254.017 ± 15.058	218.095 ± 23.409	10.0	0.16
Mn^{2+} (mg kg^{-1})	1.727 ± 0.812	1.878 ± 0.352	7.0	0.72
Zn^{+} (mg kg^{-1})	0.544 ± 0.085	0.721 ± 0.09	10.0	0.16
Mg^{2+} (m.e. 100 g^{-1} dry soils)	0.1 ± 0.034	0.139 ± 0.031	7.0	0.72
K^{+} (mg kg^{-1})	18.794 ± 2.807	24.067 ± 3.241	8.0	0.48
Al^{3+} (m.e. 100 g^{-1} dry soils)	1.728 ± 0.263	1.929 ± 0.095	7.0	0.72
Total P (mg kg^{-1})	1.067 ± 0.067	1.278 ± 0.137	9.0	0.27
C (g kg^{-1})	19.63 ± 4.097	24.652 ± 2.246	10.0	0.16
Total org. material (g kg^{-1})	33.763 ± 7.048	42.401 ± 3.863	10.0	0.16

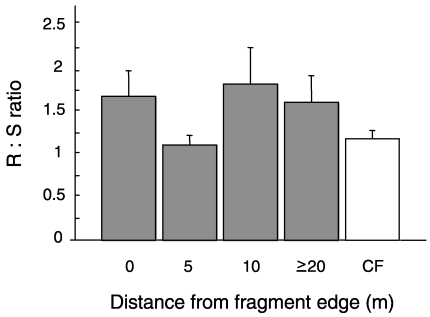

Fig. 5 The mean ratio of root biomass to shoot biomass (R : S ratio ± 1 SE) 32 months after plants were transplanted to continuous forest (open bars) or fragments (filled bars). The CF value is included only for comparison.

and extremely low pH (Table 5). No significant differences were found, however, between continuous forest and fragments for any of the 12 soil attributes measured (Table 5).

The number of plants predicted to flower in continuous forest increased from 15 to 17 (+ 13%), while the number in fragments decreased from 11 to 7 (–36%). This difference was marginally significant ($\chi^2 = 3.61$, $\chi^2_{0.05,1} = 3.841$, $0.10 < P < 0.05$).

Discussion

The shedding of shoots and leaves, which limits water loss by reducing surface area (Begg 1980), is a common response by many tropical plants to water and temperature stress (Wright 1996; Rundel *et al.* 1998). By the end of the 2001 dry season, plants transplanted to forest fragments had lost 20% of their vegetative shoots, while those in continuous forest had grown slightly (Fig. 3c). Plants in continuous forest also increased in leaf area twice as much as plants in forest fragments (Fig. 3f). These long-term results are consistent with patterns observed during earlier measurements. Although there was considerable growth by plants in both fragments and continuous forest during the second rainy season (Fig. 3b,e), plants in fragments never recovered from initial dry season losses of leaf

area and shoots (Fig. 3a,d). The asymmetrical losses of leaf area and shoots during the dry seasons, as well as final differences in growth rates, suggest that the normal abiotic stresses to which these understorey plants are exposed are greatly exacerbated in forest fragments.

Previous studies conducted in the BDFFP reserves – including the reserves used in this study – have demonstrated that fragments are hotter and drier than continuous forest. Ambient temperatures in fragments and forest edges, for example, can be up to 8 °C higher than in forest interiors (Kapos 1989; Didham & Lawton 1999). Fragments are also exposed to increased wind turbulence (Miller *et al*. 1991; Laurance *et al*. 1998), which, in combination with elevated temperatures, accelerates rates of evaporative water loss (Didham & Lawton 1999) and reduces relative humidity. While the precise physiological mechanism responsible for leaf shedding by *H. acuminata* is unclear, it is likely that both higher temperatures and reduced humidity contribute to the disparities in growth rates. Both can cause increased evapotranspiration, reductions in turgor pressure, and leaf wilt (Dias-Filho & Dawson 1995). We often found dried leaves attached to plants in fragments a full 32 months after the transplants were conducted.

A recent study comparing patterns of wet- and dry-season vegetative growth in *Heliconia* and other understorey monocots indicates they are relatively intolerant of dry-season water stress (Skillman *et al*. 1999). Fragmentation-related differences in soil moisture may therefore be an additional mechanism responsible for reduced growth in fragments. Soil moisture in the BDFFP fragments is lower than in control areas (Kapos 1989; Kapos *et al*. 1997), and it can be substantially depleted at distances up to 20–40 m from a fragment edge (Kapos 1989; Kapos *et al*. 1997). Furthermore the soils in our study sites are heavily weathered ferralsols, which in addition to being acidic and bereft of nutrients have poor water-retention capacity (Chauvel *et al*. 1987; Laurance *et al*. 1999). As understorey *Heliconia* have very shallow root systems (Skillman *et al*. 1999, E. M. Bruna, personal observation), it is likely that water stress in fragments is particularly acute (Wright *et al*. 1992).

In addition to the overall negative effect of fragmentation on *H. acuminata* growth, the significant effect of 'site' indicates there was considerable heterogeneity in growth rates among fragments (Tables 1 and 2). Inter-site variability in demographic parameters is not unexpected, particularly in tropical systems (e.g. Horvitz & Schemske 1995). In addition to variability in soil chemistry (Laurance *et al*. 1999; this study) and initial forest structure (Rankin-de Mérona *et al*. 1992), each fragment has also had a unique isolation history (BDFFP records). Furthermore, the landscape in which fragments are embedded contains several different kinds of regenerating forest (Mesquita *et al*. 2001), and the structure of this regrowth has previously been shown to influence plants surviving in fragments (Mesquita *et al*. 1999). All of these factors could potentially be driving the observed interfragment differences in growth rates. However, it is worth noting that no logging or other form of anthropogenic disturbance that might increase canopy openness, and therefore exacerbate abiotic changes, is permitted in the BDFFP fragments. This suggests that the reductions in plant growth we describe might actually be highly conservative when compared with those of plants in 'natural' forest fragments.

Plants can be phenotypically plastic in their responses to stress and acclimate physiologically to altered environmental conditions over time (Turner & Kramer 1980). However, the lack of any significant effects of source habitat on growth rates (Tables 1 and 2) might indicate that there was no pre-transplant response to conditions in forest fragments. Alternatively, optimality theory predicts that, when exposed to more xeric conditions, plants should shift resources from above-ground tissue to the production of roots in rhizomes in order to enhance the uptake of water from the soil (Struik & Bray 1970; Bloom *et al*. 1985). Plants in high light environments would be expected to respond similarly, as light is no longer limiting carbon fixation (McConnaughay & Coleman 1999). Given the reduced soil moisture and increased sunlight in fragments, one might predict that *H. acuminata* transplanted to fragments should have higher R : S ratios than those transplanted to continuous forest.

The results of our experiment are consistent with this prediction, as both below-ground biomass and R : S ratios are higher in forest fragments. However, several caveats require that these results be interpreted cautiously. First, the proportion of below-ground biomass could have increased in part because above-ground tissue was lost. This would give the appearance of active shifts in resource allocation, without actually resulting from a change in allocation strategy. Secondly, R : S ratios are negatively correlated with plant size (McConnaughay & Coleman 1999) and, as plants in continuous forest grew more than those in forest fragments, they might *a priori* be expected to have lower R : S ratios. Thirdly, plants on the borders of fragments should have the largest R : S ratios of all, as edges have the highest levels of solar radiation and lowest soil moisture levels. This is not the case, however, with R: S ratios similar on fragment borders and in fragment interiors (Fig. 5). Finally, if plants in fragments are in fact reallocating resources in response to abiotic conditions, then those individuals collected and replanted in the same forest fragments should have already shifted biomass prior to the start of the experiment. The lack of any significant main or interaction effects of 'source habitat', however, strongly suggests there had been no local pre-transplant response by plants. Careful experiments are needed to discriminate among these hypotheses; nevertheless, our results provide tantalizing evidence that plants in forest fragments may shift biomass to below-ground storage structures in response to altered abiotic conditions. Because root size and thus the ability to extract water from drying

soil can influence survival after rain forest disturbance (Lovelock *et al*. 1994), this could be an important mechanism promoting plant persistence in habitat fragments.

Perhaps the most unexpected result of our study was the rapid and substantial growth by plants on fragment edges. While initial dry-season losses in these locations were comparable with those at other distances from the edge (Fig. 4a,d), these plants rebounded extremely quickly during the following rainy season (Fig. 4b,e). By 32 months after transplanting their rate of growth far outpaced not only that of other plants in fragments, but also that of plants in continuous forest sites (Fig. 4c,f). These results were not consistent across locations, however. Plants on the edges of two fragments responded favourably to edge proximity (FF-3, FF-4), while those on the edges of the other two responded negatively (FF-1, FF-2). The mechanisms responsible for these idiosyncratic growth rates on edges are unclear. Increased solar radiation on edges is one likely causal factor, but, as plants regenerated quickly on the edges of only two fragments, it is probably only partially responsible. Microscale variation in soil chemistry, which was not significantly different among sites at the coarse scale at which we measured it, is probably also playing a role. It is worth noting that the newly flushed leaves of plants on fragment edges, including rapidly growing ones, had the characteristic yellowing indicative in *Heliconia* of solar damage to the photosynthetic system (He *et al*. 1996). In shade-tolerant species photoinhibition can increase susceptibility to drought and other forms of stress, and it may ultimately promote leaf death and abscission (Gamon & Pearcy 1990; Lovelock *et al*. 1994; Lovelock *et al*. 1998). As such, the increases in leaf area and shoot numbers seen in some 'edge' plants may not correspond to increases in photosynthetic capacity or overall plant health.

Changes in shoot number may be particularly critical demographically (Bruna 2001). Plants in fragments failed to recuperate fully from initial dry season losses before the onset of subsequent dry season (Fig. 3b), and these losses continued during the following year of the experiment (Fig. 3c). The compounding loss of shoots over the course of multiple dry seasons could explain why the *H. acuminata* populations in habitat fragments are more skewed towards smaller demographic size classes than those in continuous forest (Bruna & Kress 2002). Furthermore, while the predicted shifts in the abundance of flowering *H. acuminata* in fragments and continuous forest were only marginally significant, they closely mirror the disparities documented in permanent demographic plots (Bruna & Kress 2002). Previous efforts to quantify the consequences of fragmentation for plant reproduction have focused almost entirely on changes in plant–animal interactions, particularly pollination and seed predation (Aizen & Feinsinger 1994; Jules & Rathcke 1999; Cunningham 2000; Dick 2001). Our results suggest a new way that plant fitness can be reduced in fragments: indirectly, via environmentally induced changes in plant size and population structure.

We took a novel, experimental approach to show that organismal growth rates can be altered in habitat fragments. As suggested by a number of previous correlative studies, these physiological changes are probably the result of the striking changes in abiotic conditions associated with the fragment isolation and edge creation. We suggest that fragmentation-related reductions in growth rates could have important demographic consequences for understorey plants, as they could drive alterations in population structures and the reduced abundance of reproductive plants. If severe enough, environmentally induced changes in plant size may help explain why populations of plants in habitat fragments often fail to persist over the long-term (Turner *et al*. 1994; Jules 1998), particularly if reductions in flowering act in concert with fragmentation-related changes in other stages of plant reproduction (Aizen & Feinsinger 1994; Bruna 1999; Jules & Rathcke 1999; Ortiz-Pulido *et al*. 2000). Finally, the results of this study provide additional evidence that even geographically widespread or abundant species can be detrimentally affected by the environmental changes associated with fragmentation (Stratford & Stouffer 2001; Bruna & Kress 2002). This further underscores the importance of implementing conservation strategies that reduce abiotic edge effects, such as the use of buffer zones and the active management of habitat surrounding fragments (Gascon *et al*. 2000), as edge effects may substantially influence the growth and reproduction of remnant populations in previously unexpected ways.

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