

SHORT COMMUNICATION

Regeneration and population structure of *Heliconia acuminata* in Amazonian secondary forests with contrasting land-use histories

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(Accepted 21 May 2004)

Key Words: *Cecropia*, dispersal limitation, edge effects, forest regeneration, Heliconiaceae, population structure, seed germination, *Vismia*

An estimated 154 million ha of tropical forest are cleared each year by human activities such as cattle ranching and agriculture (Whitmore 1997). When the economic return of these sites declines, they are often abandoned and allowed to regenerate. As a result, ‘secondary’ or ‘regenerating’ forests are becoming an increasingly common feature in tropical landscapes (Guariguata & Ostertag 2001). Unlike treefall gaps and other ‘naturally’ disturbed areas, the regeneration of secondary forests on anthropogenically disturbed lands does not always follow a predictable pathway (reviewed in Guariguata & Ostertag 2001). Instead, the type and intensity of post-clearing land use has major implications for the trajectory along which succession proceeds (Guariguata & Ostertag 2001, Mesquita *et al.* 2001, Uhl *et al.* 1988).

In the central Amazon, regenerating forests follow well-defined successional trajectories based on land-use history (reviewed in Mesquita *et al.* 2001). Areas that are clear-cut and burned to create cattle pastures are soon dominated by pioneer trees from the genus *Vismia* (Clusiaceae), while stands on sites that are cleared but abandoned without burning are dominated by pioneer trees from the genus *Cecropia* (Cecropiaceae). Species richness in *Cecropia* stands is higher than in *Vismia* stands, and *Cecropia* stands have a significantly higher density of trees. Furthermore, the density of plants decreases with increasing distance from the edge of primary forest in both types of secondary forest, as does the density of seedlings and saplings.

Studies investigating how land-use influences succession have, by definition, focused on elucidating community-level patterns of diversity and abundance (Aide *et al.* 2000, Finegan & Delgado 2000, Uhl *et al.* 1988). We therefore have a limited understanding of the population-level variation exhibited by individual species found in different secondary forests. Given the species richness in tropical forests, a population-level assessment of all species in a community is rarely feasible. However, by studying focal species representing key taxonomic or functional groups we may gain insights that allow us to predict the responses of ecologically similar species. When combined with experimental manipulations, these observations can also help disentangle the mechanisms influencing regeneration on degraded lands (Holl 1999, Pinard *et al.* 1996).

The objective of this study was to compare the abundance, population structure, and recruitment of a focal understorey herb (*Heliconia acuminata* L. C. Rich., Heliconiaceae) in central Amazonian secondary forests undergoing contrasting successional trajectories. We asked the following questions: (1) Does *H. acuminata* density and demographic structure differ between secondary forests dominated by *Vismia* and *Cecropia*? (2) Do patterns of seedling recruitment differ with secondary forest type?

This study was conducted in three cattle ranches that are home to Brazil’s Biological Dynamics of Forest Fragments Project (BDFFP, Bierregaard *et al.* 2002). The four secondary forest sites used in this study were cleared in 1980–1984; two sites were burned after clearing while the other two sites were not. Throughout the paper we refer to these stands by the dominant vegetation

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type and the name of ranch in which they are located: *Vismia*-Dimona, *Vismia*-Colosso, *Cecropia*-Porto Alegre, and *Cecropia*-Colosso.

From May–June 2002 we established five transects separated by 60 m in each of the four stands. Each transect began at the border of primary and secondary forest, and extended 150 m into the secondary forest. All four stands were bordered by continuous forest on only one side. Along each transect we placed five 10 × 10-m quadrats at random distances from the forest edge. We counted all *H. acuminata* individuals in these quadrats and marked them with a numbered stake. Plants were measured by counting the number of vegetative shoots they had. We compared *H. acuminata* density in the stands using Kruskal–Wallis tests, since the data could not be transformed to meet the assumptions of parametric statistics necessary to analyse by forest type. Spearman rank correlations were used to test for decreasing density with increasing distance from the forest edge. To compare the demographic structure of the populations, all plants in a stand were pooled and assigned to size categories based on shoot number. We used G-tests to compare the proportion of individuals in each size class.

We quantified seedling establishment using two complementary methods: a survey of naturally emerging seedlings and an experimental test of germination success. To survey natural regeneration in each stand, we randomly selected 12 of the 25 quadrats in which we recorded *H. acuminata* density. We then returned to these sites in May 2003 and surveyed them for new seedlings. Prior work indicated this interval was sufficient to ensure all naturally dispersed seeds from the 2002 cohort that were going to germinate had probably done so (Bruna 1999, 2002). We compared the density of newly emerged seedlings using a Kruskal–Wallis test. We also tested for an association between the distance from the forest edge and the seedling density using Spearman rank correlations, with each stand again tested separately.

To assess the effect of post-clearing land use on germination success, we sowed known quantities of seeds in each stand. In June 2002, we established 10 × 10-m quadrats adjacent to the ones selected for seedling surveys. In each quadrat we arranged 20 round plastic containers (15 cm diameter) in a grid. Containers were half-filled with local soil and buried so that the level of the soil matched that of the surrounding ground. We then added a single *H. acuminata* seed to each container. Previous work has shown leaf-litter can significantly reduce seedling establishment (Bruna 2002), therefore we randomly selected half of the containers in each quadrat and covered them with plastic mesh. A total of 960 seeds were used for the experiment (20 seeds per quadrat × 12 quadrats per forest × 4 forests). These seeds were collected in April–May 2002 in two continuous forest reserves and a 100-ha fragment (BDFFP reserves #1301, #1501 and #3304)

and stored using previously published protocols (Bruna 2002). We distributed seeds from each collection site equally among the stands, then randomly assigned seeds to each quadrat and container (Bruna 1999, 2002).

We returned to survey these seeds in January and May 2003. We used Wilcoxon signed rank tests to compare the proportion of seeds establishing as seedlings in the protected and exposed treatments (each stand analysed separately), and then used Kruskal–Wallis tests to compare seedling establishment across sites. Since the differences between protected and unprotected treatments were significant or marginally significant for two sites, we compared the treatments separately. A Kruskal–Wallis test was also used to compare inter-site differences in seedling mortality between the two sampling dates.

Heliconia acuminata density was significantly different among the four secondary forests ($H = 25.3$, $P < 0.0001$, Figure 1a). Density was highest in Colosso's *Vismia* forest (mean = 5.44 ± 1.08 SE plants per quadrat; median = 4 plants per quadrat) and was lowest in Porto Alegre's *Cecropia* forest (mean = 0.88 ± 0.23 SE plants per quadrat; median = 1 plant per quadrat). There was no relationship between density and distance from the forest edge in any of the four sites (results not shown). There was also no significant difference between locations in the number of plants per size class ($G^2 = 9.27$, $df = 12$, $P = 0.68$, Figure 1b).

The density of naturally emerging *H. acuminata* seedlings ranged from 0–6 seedlings per quadrat (mean = 0.46 ± 0.16 SE; median = 0), and there was a highly significant difference among the four stands ($H = 23.7$, $P < 0.0001$). These differences appear to be independent of the dominant vegetation type – no new seedlings were recorded in Porto Alegre's *Cecropia* forest, while Colosso's *Cecropia* forest had a mean of 0.5 ± 0.26 SE seedlings per plot. The density of newly emerging seedlings in *Vismia*-dominated forests was comparable or slightly higher to that in Colosso's *Cecropia* forest (Colosso-*Vismia*: 0.42 ± 0.15 SE, median = 0; Dimona-*Vismia*: 0.92 ± 0.54 SE, median = 0). Seedling abundance was not correlated with distance from the edge of continuous forest in any site (results not shown).

Protecting seeds from litter resulted in significantly greater germination in *Vismia* but not *Cecropia* stands (Colosso-*Cecropia*: $Z = -1.0$, $P = 0.32$; Porto Alegre-*Cecropia*: $Z = -0.45$, $P = 0.65$; Colosso-*Vismia*: $Z = -2.72$, $P = 0.007$; Dimona-*Vismia*: $Z = -1.85$, $P = 0.07$, Figure 2). For both treatments, the proportion of seeds establishing as seedlings was significantly different between stands (protected: $H' = 25.5$, $P < 0.0001$; unprotected: $H' = 9.5$, $P = 0.03$). Seedling establishment was much lower in *Cecropia* forests (proportion germinating per plot = 0.067–0.29 in *Vismia* vs. 0.017–0.067 in *Cecropia*, Figure 2). Seedlings were equally likely

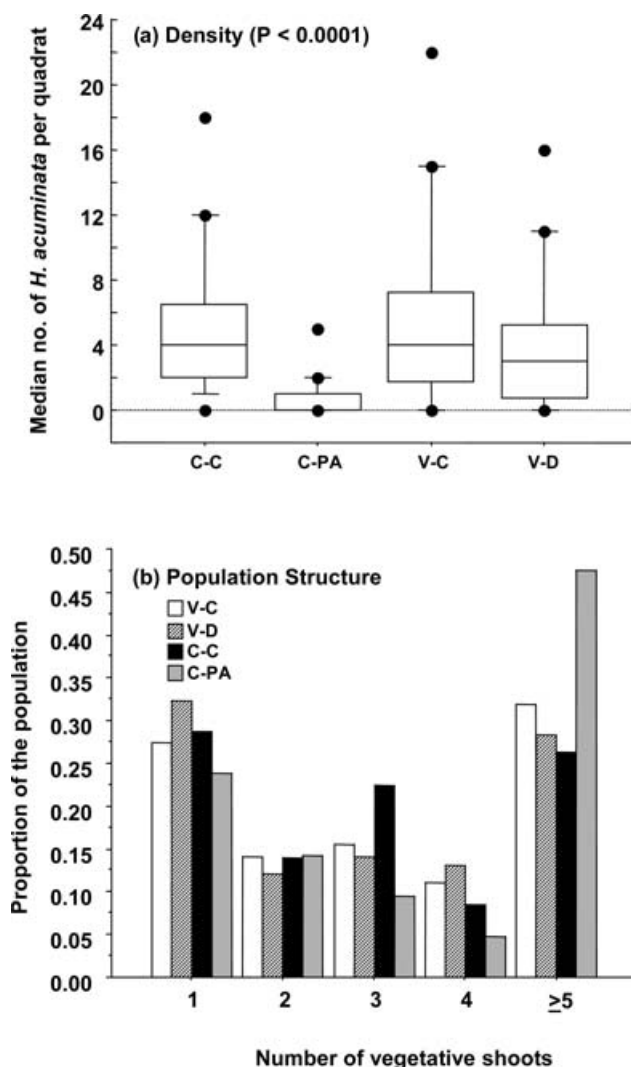


Figure 1. The (a) density and (b) population structure of *Heliconia acuminata* in four secondary forests undergoing different regeneration trajectories. Abbreviations: C-C = *Cecropia-Colosso*, C-PA = *Cecropia-Porto Alegre*, V-C = *Vismia-Colosso*, V-D = *Vismia-Dimona*. The upper and lower limits of the box plots in 1a represent the 75th and 25th percentiles (respectively); the line through the box is the median value. Marks beyond the error bars represent outliers lower or greater than the 10th and 90th percentiles. The median value for C-PA is 0. Each quadrat is 10 × 10 m.

to survive until May in all sites ($H' = 4.32$, $P = 0.23$; survivorship across all sites = $82.6\% \pm 5.7\%$ SE).

Our results suggest that secondary forest type may be a poor predictor of *H. acuminata* density or population structure. However, we found striking differences between forest types in *H. acuminata* seed germination and seedling establishment. Experimentally sown seeds were up to 17-fold more likely to germinate and become established seedlings if dispersed to sites dominated by *Vismia* instead of those dominated by *Cecropia*. Previous seed-sowing experiments, including

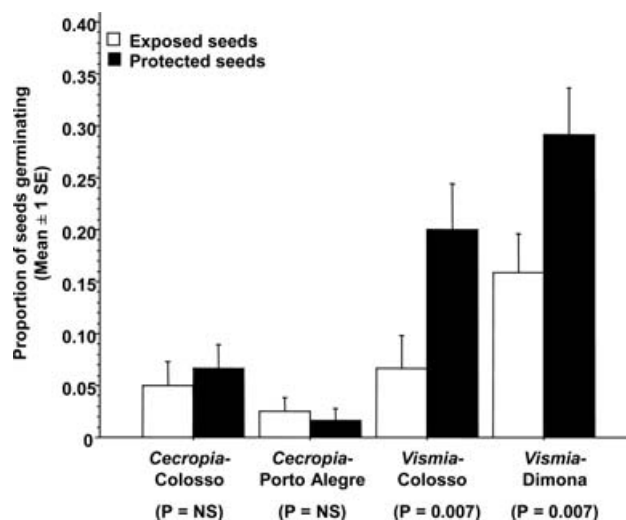


Figure 2. The proportion of *Heliconia acuminata* seeds germinating in secondary forest stands dominated by *Cecropia* or *Vismia*. Seeds were planted in two treatments: exposed (open bars) or protected with mesh from leaf-litter accumulation and predators (closed bars).

several comprehensive ones conducted in nearby sites (Camargo *et al.* 2002, Ganade & Brown 2002), have compared seedling establishment in broad categories such as ‘forest’, ‘pasture’, and ‘regenerating forest’. Our results suggest that for some species, not all ‘regenerating forests’ will be equivalent in terms of seedling establishment. Restoration strategies that utilize seed sowing techniques (Guariguata 2000, Parrotta & Knowles 1999) but ignore these differences may therefore have only limited success.

Secondary forests dominated by *Cecropia* have much higher humidity, lower temperatures and limited penetration of photosynthetically active radiation to the forest floor (Mesquita 2000). All of these abiotic variables can be important cues used by seeds to initiate germination (Baskin & Baskin 1998), and are probably at least partly responsible for the observed differences in germination rates. However, while previous work in both primary forest and forest fragments has found protecting *H. acuminata* seeds from leaf-litter accumulation can increase germination success (Bruna 2002), we found this was only true in *Vismia* stands. We hypothesize that the high humidity in *Cecropia* stands has elevated the probability of attack by fungal pathogens or microbial agents of seed mortality (Vázquez-Yanes & Orozco-Segovia 1993), irrespective of whether they are protected from litter. Although the role that pathogens play in influencing patterns of seedling growth and survival in disturbed habitats is well documented (García-Guzmán & Benítez-Malvido 2003), few empirical studies have evaluated how soil bacteria and fungi influence seed survival and germination (Baskin & Baskin 1998).

Despite higher rates of germination in *Vismia* stands, seedling density appears independent of regeneration

pathway. The local abundance of seedlings depends on myriad factors that influence both seed availability and seedling survivorship, including the efficacy of dispersers, the presence of seed predators, and site-specific biotic and abiotic idiosyncrasies (Holl *et al.* 2000, Pinard *et al.* 1996, Wenny 2000). To date, few studies have explicitly compared how any of these vary between different types of regenerating forests. The complete absence of seedlings in one of our sites suggests dispersal limitation may be important, and Mesquita *et al.* (2001) argue that the preference of animals for secondary forests dominated by different tree species may lead to contrasting patterns of regeneration. However, the disparity in *H. acuminata* seedling abundance between stands dominated by the same pioneer species suggests that a preference by avian dispersers of *Heliconia* for certain forest types is at most only partially responsible for the patterns of abundance. Furthermore, these disparities are probably not the result of pathway-specific differences in seed predation. The predation of *H. acuminata* seeds in continuous forest and forest fragments is minimal, and seed banks are probably uncommon (Bruna 2002). Work in other systems suggests that local differences in soil chemistry, the density and identity of competitors, disturbance and light levels are also important predictors of seedling abundance (Augspurger & Kelly 1984, Ceccon *et al.* 2003, Kennard *et al.* 2002); ongoing work with other herbaceous genera in these sites may help clarify if these mechanisms are also important here (M. B. Nogueira Ribeiro, *unpubl. data*).

Mesquita *et al.* (2001) found strong edge-related declines in community-wide abundance and recruitment. We found no evidence for such declines, however, perhaps because these effects have dissipated in the 20 y since the sites were cleared (Mesquita *et al.* 2001). We also did not find evidence for inter-site differences in population structure (Figure 1b). The general decrease in proportional abundance from size classes 1–4 suggests plant growth and survivorship is similar in different forest types. Furthermore, the large proportion of the populations with ≥ 5 shoots is also consistent with the hypothesis that some plants survive the process of forest clearing (Bruna *et al.* 2002). The pre-clearing density of plants in a site may therefore help present day differences in density. *Heliconia acuminata* abundance in nearby continuous forest ranges from 250–1800 individuals per hectare (Bruna & Kress 2002, E. M. Bruna *unpubl. data*); it is probable that density was initially variable between these stands as well.

Our results indicate that some components of plant population structure, such as seed germination, may vary consistently with land-use history (Mesquita *et al.* 2001). However, other factors that contribute to population density and structure may be driven primarily by local site characteristics, irrespective of the regeneration pathway

along which a secondary forest stand is proceeding (Pinard *et al.* 1996). Our results therefore support the conclusion that while the regenerative capability of tropical forest is extremely high (reviewed in Guariguata & Ostertag 2001), predicting successional trajectories for individual species is extremely difficult due to the dynamic interplay between site-specific biophysical properties and land-use history.

ACKNOWLEDGEMENTS

We thank O. F. da Silva for assistance in the field and E. Venticinqui, P. Delamônica, A. Jerozolinski, and J. L. Camargo for helpful discussions. This work was supported by the University of Florida and the National Science Foundation. This is publication number 433 in the BDFFP technical series and number R-10045 in the Florida Agricultural Experiment Station Journal Series.

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