Oecologia (2010) 162:923–934
DOI 10.1007/s00442-009-1524-5

POPULATION ECOLOGY - ORIGINAL PAPER

Altered resource availability and the population dynamics of tree species in Amazonian secondary forests

**Lucas Berio Fortini · Emilio M. Bruna ·
Daniel J. Zarin · Steel S. Vasconcelos ·
Izildinha S. Miranda**

Received: 19 March 2009 / Accepted: 18 November 2009 / Published online: 9 December 2009

Abstract Despite research demonstrating that water and nutrient availability exert strong effects on multiple ecosystem processes in tropical forests, little is known about the effect of these factors on the demography and population dynamics of tropical trees. Over the course of 5 years, we monitored two common Amazonian secondary forest species—*Lacistema pubescens* and *Myrcia sylvatica*—in dry-season irrigation, litter-removal and control plots. We then evaluated the effects of altered water and nutrient availability on population demography and dynamics using matrix models and life table response experiments. Our results show that despite prolonged experimental manipulation of water and nutrient availability, there were nearly no consistent and unidirectional treatment effects on the demography of either species. The patterns and significance of observed treatment effects were largely dependent on cross-year variability not related to rainfall patterns, and disappeared once we pooled data across years. Furthermore, most of these transient treatment effects had little effect on population growth rates. Our results suggest that despite major experimental manipulations of water and nutrient availability—factors considered critical to the ecology of tropical pioneer tree species—autogenic light limitation appears to be the primary regulator of tree demography at early/mid successional stages. Indeed, the effects of light availability may completely override those of other factors thought to influence the successional development of Amazonian secondary forests.

Keywords Amazonia · Regrowth forests · Succession · Water stress · Nutrient limitation

Introduction

Water and nutrient availability influence multiple ecosystem processes in tropical forests. For instance, limited water availability can increase rates of tree mortality (Condit 1998; Chazdon et al. 2005; Nepstad et al. 2007), reduce photosynthesis (Nepstad et al. 2002; Fortini et al. 2003; Aragão et al. 2005), change leaf and reproductive phenology (Kitajima et al. 1997; Malhi et al. 1998), and increase the susceptibility of forests to fire (Nepstad et al. 2004). Similarly, observational and manipulative studies have shown that nutrient availability alters patterns of tree growth (Davidson et al. 2004), fine litterfall production (Mirmanto et al. 1999), above-ground biomass (Laurance et al. 1999), and resource allocation to below-ground structures (Gower 1987; Giardina et al. 2004). Despite considerable work investigating the individual- or ecosystem-level consequences of nutrient and water availability for tropical forests, however, little has been done to explore

Communicated by Peter Clarke.

L. B. Fortini (✉) · D. J. Zarin
School of Forest Resources and Conservation, University of Florida, P.O. Box 110760, Gainesville, FL 32611-0760, USA
e-mail: lfortini@ufl.edu

E. M. Bruna
Department of Wildlife Ecology and Conservation and Center for Latin American Studies, University of Florida, PO Box 110430, Gainesville, FL 32611-0430, USA

S. S. Vasconcelos
Laboratório de Ecofisiologia e Propagação de Plantas, Embrapa Amazônia Oriental, Belém, PA 66095-100, Brazil

I. S. Miranda
Universidade Federal Rural da Amazônia, CP 917,
Belém, PA 66077-530, Brazil

how these factors influence the population dynamics of tropical trees. Elucidating these relationships is critical, since population dynamics link individual responses to abiotic constraints with patterns of community composition and ecosystem processes.

"Secondary" or "regenerating" forests account for more than 40% of tropical forest worldwide (Brown and Lugo 1990) and play a critical role in regional C dynamics, the maintenance of biodiversity, and income generation (Chazdon and Coe 1999; Hughes et al. 1999; Aide et al. 2000; de Jong et al. 2001; Smith et al. 2003; Gavin 2004; Olschewski and Benitez 2005). There are many models of succession that attempt to explain how secondary forest composition and structure change over time (Clements 1916; Yarranton and Morrison 1974; Pickett 1976; Noble and Slatyer 1980). A commonality of these models is that populations of species reach peak abundances at different stages of succession, resulting in easily recognizable species turnover. While light availability is a key driver of these successional dynamics (Huston and Smith 1987), tree populations may also be particularly susceptible to changes in water and nutrient availability. For instance, some secondary forest species may be very susceptible to drought because they allocate more fine roots to shallower soil, while others may face nutrient limitation due to depletion from past anthropogenic activities (Juo and Manu 1996; Hopkins et al. 1996; Ayuba et al. 2000; Pavlis and Jenik 2000; McGrath et al. 2001). However, it is unclear how the rate and magnitude of changes in abundance during succession are altered by the availability of water and nutrients.

Unfortunately, the high cost and logistical issues associated with establishing experiments at suitable spatial scales, along with the need to monitor permanent forest plots for multiple years, have resulted in few studies that rigorously test the effects of water and nutrient availability on the population dynamics of trees in tropical secondary forests. Descriptions and comparisons of stands, chronosequences, and observational longitudinal studies provide limited inference regarding mechanisms underlying complex forest dynamics and their potential abiotic constraints. However, when long-term data are available, life table response experiments (LTREs) provide a powerful approach to disentangle how experimental factors influence the growth and demography of populations (Burns 2008). These analyses allow for the decomposition of each experimental treatment's effects on the growth rates of populations (i.e., λ); specifically, they measure the contributions to the differences in λ between treatments arising from changes in size-class specific vital rates (Caswell 2001). Because even similar population growth rates can result from very different demographic mechanisms (e.g., Bruna and Oli 2005), LTREs can elucidate the responses of populations to environmental variability in ways that simply comparing the sizes, structures, or growth rates of populations cannot (e.g., Bruna and Oli 2005).

In this study we used LTRE to investigate how a long-term, stand-level experimental manipulation of nutrient availability (via litter removal) and water availability (via irrigation) conducted in an Amazonian secondary forest influenced the demography and population growth of two common tree species. These experimental manipulations have been shown at our site and elsewhere to significantly alter ecosystem-level (Vasconcelos et al. 2004, 2007, 2008; Vasconcelos 2006; Veluci-Marlow 2007) and individual-level processes (Fortini et al. 2003; Aragão et al. 2005). We monitored the demography of two early short-lived pioneer species past their peak abundance and under decline, *Lacistema pubescens* (Lacistemataceae) and *Myrcia sylvatica* (Myrtaceae), in dry-season irrigation, litter-removal and control plots for a 5-year period. We then used these demographic data to estimate λ using matrix models and applied two-way LTREs to evaluate whether changes in nutrient and water availability alter the rate of population decline.

Materials and methods

Site description

The experimental site is located at the research station of the Universidade Federal Rural da Amazônia (UFRA), located near the city of Castanhal, Pará, Brazil. Annual precipitation in the region is 2,000–2,500 mm, with a rainy season that extends from December to May. Mean daily temperatures fluctuate between 24 and 27°C. Soils in the site are classified as dystrophic yellow latosols, stony phase I (concretionary, lateritic) in the Brazilian soil classification system, which corresponds to Sombriustox in US soil taxonomy (Tenório et al. 1999). At a 0–10 cm depth, soil pH is 5.0, total N is 0.15%, and Mehlich-1 extractable P is 1.58 mg kg^{-1} (Rangel-Vasconcelos et al. 2005). The landscape surrounding the field station is characterized by secondary forests, annual crops, and active and degraded pastures.

Our experiment was initiated in 2001 in a 2-ha patch of secondary forest that had been fallow for 14 years. Prior to being abandoned, the site had undergone multiple cycles of shifting cultivation that began about 60 years ago when the old-growth forest was first cleared. Each cycle included cultivation of corn, manioc, and beans for 1–2 years, followed by a fallow stage. Interviews with local residents and field station personnel suggest typical shifting cultivation cycles lasted 7–10 years (G. Silva e Souza and O. L. Oliveira, personal communication).

In 2001 stand basal area was 16.7 m^2 ha^{-1}, average stand density was 208 (±33 SE) individuals >1 cm diameter at breast height (DBH), and average species richness was 24 (±1 SE) species 100 m^{-2} (Araújo et al. 2005).

Study species

Lacistema pubescens Mart. and *Myrcia sylvatica* (G. Mey.) DC. are early short-lived pioneer species prevalent in secondary forest stands across the eastern Amazon. *L. pubescens* is one of the earliest tree species to establish in fallows; it typically has a single upright stem and is shade intolerant. *M. sylvatica* generally appears in fallows after *L. pubescens* and other early pioneer species have become established (Coelho et al. 2004). It is noticeably more shade tolerant than its predecessors and typically has a highly branched architecture. *L. pubescens* and *M. sylvatica* are the most abundant overstory species in our experimental plots accounting for 36 and 22% of all stems >1 cm DBH, respectively (Araújo et al. 2005).

Experimental design

The study was conducted in twelve 20 × 20-m plots separated by 10-m buffer strips. We randomly selected four plots for dry-season irrigation, litter removal, and untreated controls ($n = 12$ plots total). The irrigation treatment consisted of providing the equivalent of 5 mm daily precipitation during rainless dry-season days with an irrigation tape system, corresponding to regional estimates of daily evapotranspiration (Shuttleworth et al. 1984; Lean et al. 1996; Jipp et al. 1998). Irrigation was initiated in July 2001, which corresponded to the start of the dry season. Measurements of gravimetric soil moisture content indicated that during the dry season the irrigated plots had slightly more than double the moisture of control plots (22 vs. 10%). Wet-season gravimetric soil moisture content was 27% for both treatments (Vasconcelos et al. 2002). We established four litter-removal plots in an attempt to break the tight nutrient cycling of our forest and thus decrease nutrient availability experienced by plants within these plots. While we acknowledge that litter-removal treatments may result in several secondary effects (e.g., leaching, changes in soil microbial biomass, soil water content, or soil organic matter), we focused our analyses on the primary effect of reducing nutrient availability as most of the secondary effects also exacerbate nutrient limitation (Sayer 2006). In August 2001, all leaf and branch litter was removed from the litter-removal plots with plastic rakes; this process was subsequently repeated every 2 weeks. Standing litter crop was low, but not entirely absent, in the litter-removal plots. Total new non-woody litterfall removed from August 2001 to December 2005 was 3,568 ± 136 g m^{-2}, leading to changes in soil nutrient status and reductions in litterfall N content (Veluci-Marlow 2007; Vasconcelos et al. 2008).

Nested in the center of each 20 × 20-m plot were 10 × 10-m permanent inventory plots (hereafter referred to as “overstory plots”). Within these plots all tree individuals of the two study species with DBH >1 cm had their height and DBH measured annually between July and August. We randomly located four 1 × 1-m quadrats in each plot to monitor individuals ≥10 cm high and <1 cm DBH (hereafter referred to as “understory plots”). Although we monitored these quadrats every 2 months from 2001 to 2006, for our analyses we used data from the surveys conducted in July–August of each year to best match inventory dates for the individuals >1 cm DBH. Here we report on results from five measurement intervals included in the 2001–2006 yearly inventories.

Matrix model construction

We observed a strong relationship between height and DBH for both species ($r^2 = 0.71$ and 0.73 for *L. pubescens* and *M. sylvatica*, respectively). However, because of the difficulty in obtaining accurate height measurements for some individuals and the die-off of some shoots, we used DBH measurements as the state variable for all individuals with DBH ≥1 cm. Height was the only choice for state variable of all individuals with DBH < 1.0 and height ≥10 cm. Following state variable definition, we created a four life cycle model for *L. pubescens* and a five life cycle model for *M. sylvatica*. We defined the number of stages and their size cut-offs based on patterns of mortality across size, limited reproductive phenology data, height to canopy calculations, field observations, and available number of individuals.

Calculating vital rates

Prior to parameterizing our matrices, we calculated separate estimates of survival, growth, regression and fertility rates for each size class in each species × treatment × year combination. Since understory individuals were often difficult to locate in the field, data for a small number of them were missing in some years. Since the exclusion of these individuals from the calculation of mortality rates for a given transition year would artificially depress survival, we replaced all single-year gaps in data with the average size from adjacent years. However, we did exclude the very small number of individuals with more than 1 year of missing data ($n < 10$) from the calculations of vital rates because of the potentially greater errors that could result from interpolating data for longer time periods.

We calculated survival rates for each matrix using logistic models parameterized with all overstory and understory data. This approach avoided the “over-parsing” of our data (sensu Morris and Doak 2002) and perfect survival in size classes with low sample sizes and high survival rates. A separate logistic fit was used for the understory and overstory data, with resulting size class survival values based on the logistic fit evaluated at median individual size observed within each size class. To avoid poor fits to the data, we used the standard count-based methods of survival calculations when $n < 10$ for either data set.

We calculated growth and regression transition probabilities following standard count-based methods where the probability of growth (regression) of any given size class is the proportion of individuals alive at time t that grew (regressed) to another size class at time $t + 1$. Growth transition probabilities between understory and overstory size classes were based on actual observed recruitment to the overstory size classes at time $t + 1$ divided by the area-scaled number of understory size class individuals present at time t. Seedling recruitment rates were calculated based on the observed number of new individuals from one measurement to the next. Lastly, we used Caswell’s (2001) approach to calculate anonymous fertility rates with equal reproductive weights among overstory size classes.

Analyzing differences among vital rates

To evaluate variability in estimates of vital rate, we performed a bootstrapping procedure on the overstory and understory data sets (1,000 runs). We used the resulting bootstrapped estimates to create 95% confidence intervals for each vital rate for each species, size class, treatment and year.

Creating population matrices

We created a total of 30 matrix models (2 species × 3 treatments × 5 time intervals) based on lower level vital rates (Morris and Doak 2002). To avoid problems associated with reducible matrices (Caswell 2001), we substituted the rare zero values for growth and survival probabilities with the lowest bootstrapped non-zero value of the vital rate for the respective treatment among all measurement years. Fecundity values of zero also yield reducible matrices. Therefore, if fecundity for any matrix was zero we only substituted fecundity from the largest size class with the lowest bootstrapped non-zero fecundity value for the respective treatment among all measurement years. Preliminary comparisons showed that while this ad hoc reducibility fix improved the results of subsequent analysis, it had only minor effects on estimates of population vital rates and population growth.

Demographic analyses

Using our 30 matrices, we calculated λ for each species × year × treatment combination, as well as the sensitivities of population growth to all underlying vital rates. We also bootstrapped our data sets using the reducibility fix described above to estimate bias-corrected 95% confidence intervals for λs per species, year, and treatment. We used the 30 matrices to perform standard two-way full factorial LTRE analyses to determine the effects of the experimental treatments and study year on each species (Caswell 2001, p. 263). Because our experimental design does not consider the interaction between irrigation and litter removal, irrigation and litter-removal effects were evaluated independently through separate LTRE analyses in the following comparisons: control versus irrigation and control versus litter removal. For all tests, we computed the “reference matrices” (sensu Caswell 2001) and related vital rates as the average from control plot data for all measurement intervals. For each factor level for each LTRE, the midpoint matrix used to evaluate the contribution of observed vital rate to λ was computed as the average matrix between the reference matrix and related factor matrix. Lastly, we examined the significance of treatment effects statistically by bootstrap-derived confidence intervals of the difference between treatment and reference vital rate estimates.

Precipitation analysis

To determine whether precipitation patterns influenced species demography or treatment effects, we performed a multiple correlation analysis between precipitation and demographic analysis results. Precipitation variables included dry-season rainfall amount, maximum and median rainless interval durations from current and previous year to account for potential time-lagged responses (Table 1; Vasconcelos 2006). Our demographic variables included demographic rates by species and size class from control plants to evaluate precipitation effect on species demography and the difference between treatment and control demographic rates to evaluate potential links between yearly rainfall patterns and treatment response. Results from the multiple comparisons where evaluated using standard and Bonferroni-corrected α-values.

Results

Species demographic trends

Lacistema pubescens and *Myrcia sylvatica* had contrasting patterns of survivorship for the smallest size classes, but

Table 1 Rainfall patterns for Universidade Federal Rural da Amazônia research station, Castanhal, Pará, Brazil

Year	Season	Total rainfall (mm)	Median rainless period length (days)	Maximum rainless period length (days)
1999	Dry	352	3	10
2000	Wet	1,922.9	1	9
2000	Dry	223.5	4.5	11
2001	Wet	3211	2	7
2001	Dry	438.9	5	32
2002	Wet	1,813.2	2	7
2002	Dry	679.4	5	16
2003	Wet	1,718.6	1	11
2003	Dry	696.8	5	21
2004	Wet	2,881.5	2	11
2004	Dry	444.9	4	25
2005	Wet	2,177.2	2	11
2005	Dry	225.2	9	19
2006	Wet	2,234.9	2	4

similarly high rates of survivorship for overstory size classes. *L. pubescens* survival in the smallest two size classes was low for the entire study period, typically ranging from 0.4 to 0.8 (Fig. 1a). Survival in these size classes only peaked above these low values during the 2002–2003 time interval when both dry seasons showed total rainfall amounts considerably greater than usual. On the other hand, nearly all of the survival rates observed for *M. sylvatica* are above 0.8 and present no large differences among years or size classes (Fig. 1b). The only minor temporal trend observed for *M. sylvatica* suggests that the survival of the largest size class is the most stable across all years.

For both species, the probability of growth from understory to overstory size classes was extremely low and there were no clear differences in growth transition probabilities among overstory size classes (Fig. 1c, d). Allometric height/DBH equations reveal that neither species had understory individuals with heights close to the equivalent to the minimum overstory size cut off (1 cm DBH), lending further evidence to a clear overstory recruitment limitation for both species. For *M. sylvatica* individuals in the understory, large growth transition probabilities from size class 1 and regression probabilities for size class 2 reflect the large variability of measured heights that results from the difficulties in evaluating growth based on height (e.g., shoot die-backs, new leaf flushes, etc.; Fig. 1d, f). However, these rates are exceptionally high for the 2002–2004 period, potentially related to the high dry season rainfall years of 2002 and 2003. All other regression probabilities for both species do not show any clear temporal or size-related patterns, although regression probabilities for overstory size classes of *M. sylvatica* were noticeably higher and more variable than that of *L. pubescens* (Fig. 1e, f).

Both species showed contrasting patterns of recruitment across years. While *L. pubescens* showed constant and very low yearly recruitment below 20 individuals 100 m^{-2}, *M. sylvatica* presented recruitment above 400 individuals 100 m^{-2} in the first time interval (2001–2002). However, *M. sylvatica* recruitment dropped across all years to 25 individuals 100 m^{-2} by the 2005–2006 time interval (Table 2).

Population growth patterns across time and treatments

We found that with one exception—the irrigated *L. pubescens* population in 2003–2004—there was no significant difference in λ among populations of the two study species in different treatments (Fig. 2). Furthermore, we found that only the control *M. sylvatica* population in the 2001–2002 transition year included positive, albeit non-significant, population growth (i.e., $\lambda > 1$). The population growth rate for *L. pubescens* ranged from 0.8909 (population in the irrigation treatment in the 2005–2006 period) to 0.9913 (population in the control treatment in the 2003–2004 period). Results for *M. sylvatica* were similar, with λ ranging from 0.8906 to 1.006 and little difference among treatments and years.

Two-way LTRE results

For both species, treatment differences in vital rates were small and mostly fell within 0.05 of control values. Furthermore, LTRE analysis showed that because of the differential impacts of vital rates on population growth, treatment effects on growth and mortality often did not result in commensurate population growth effects for either of the two studied species (Fig. 3). For both species, the

Fig. 1 Size class (*Sz*) annual rates of survival, growth and regression with 0.975 and 0.025 quantiles of *Lacistema pubescens* (**a, c, e**) and *Myrcia sylvatica* (**b, d, f**). *Hgt* Height, *DBH* diameter at breast height

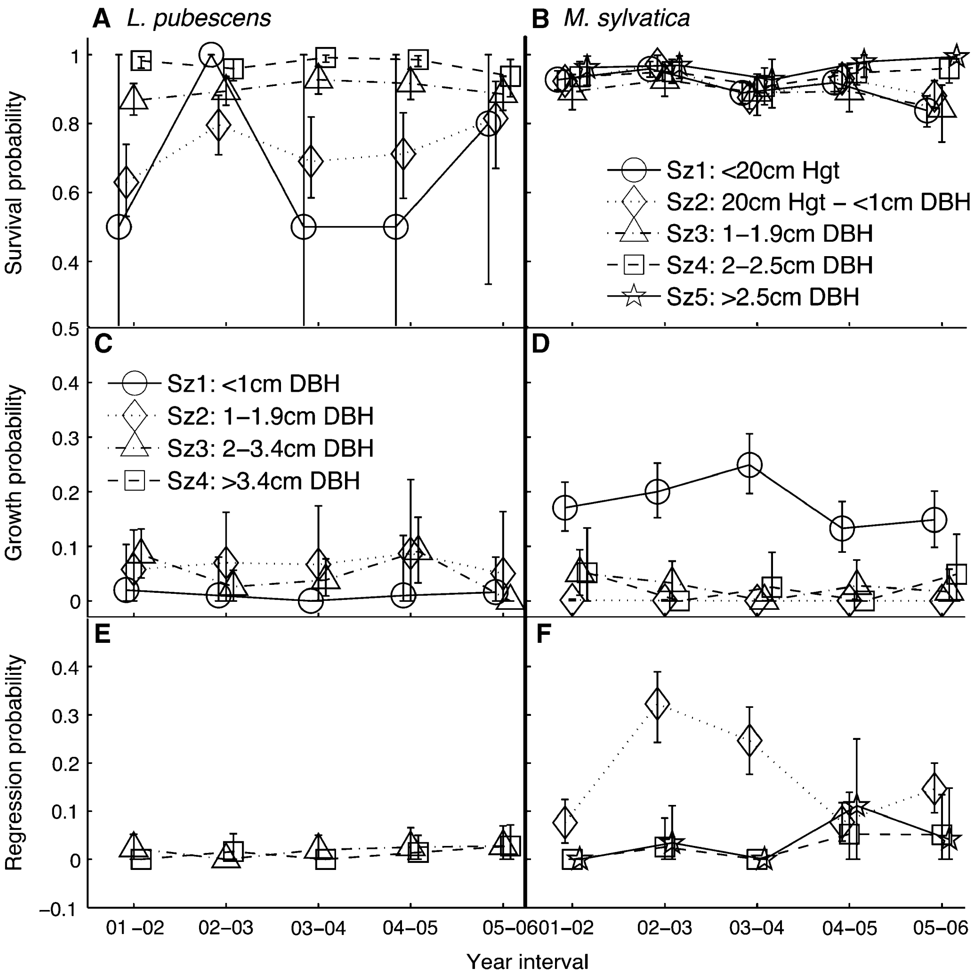


Table 2 Offspring per 100 m^2 for *Lacistema pubescens* and *Myrcia sylvatica* across time intervals. Given no treatment differences, only control data are shown

Year interval	*L. pubescens*	*M. sylvatica*
2001–2002	6.25	406.25
2002–2003	0	181.25
2003–2004	12.5	143.75
2004–2005	18.75	100
2005–2006	6.25	25

survival and regression probabilities make the largest contributions to $\Delta\lambda$ across time and treatments, with transition probabilities describing growth having a relatively smaller impact on population growth. In addition, post hoc bootstrapping of differences in vital rates between the experimental and control treatments indicate that no treatment differences in vital rates were significantly different when averaging data across years. However, the evaluation of the interaction effect between treatment and time suggests significant treatment impacts for specific time intervals (Fig. 4). Of these time-dependent treatment effects, only the irrigation growth of *M. sylvatica*'s seedling size class 1 showed a constant unidirectional response over the course of the experiment.

While vital rates varied considerably from one time interval to the next, we found that—for both species—patterns of "time" effects on vital rates were idiosyncratic. The only consistent temporal pattern observed was a decrease in the survival of all size classes of *M. sylvatica* during the 2003–2004 measurement interval. Surprisingly, inter-annual rainfall patterns were not significantly correlated to size-class specific species and treatment variability of vital rates.

Discussion

To our knowledge, our study is the first large-scale and long-term experimental investigation of how irrigation and litter removal influence the population dynamics of tropical trees. We found that although previous work has documented large ecosystem-level (Vasconcelos et al. 2004, 2007, 2008; Vasconcelos 2006; Veluci-Marlow 2007) and individual-level effects (Fortini et al. 2003; Aragão et al.

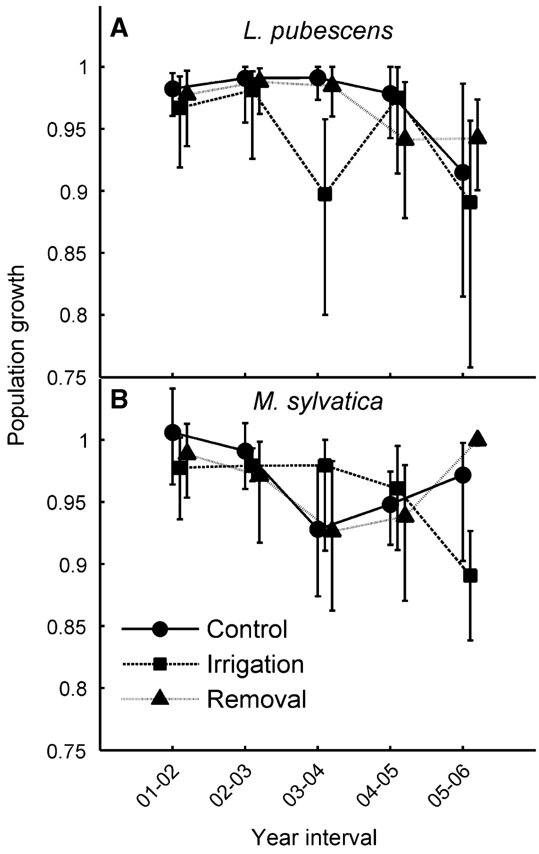


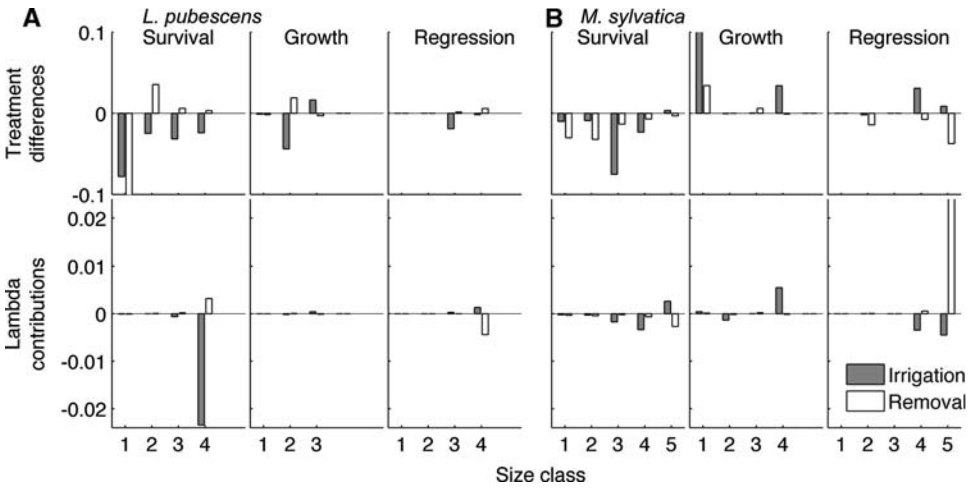
Fig. 2 Population growth rates (λ) of **a** *L. pubescens* and **b** *M. sylvatica* in stands with water addition and litter removal. Values are mean ± 95% confidence interval

2005) of altering dry season water availability and litter abundance in our experimental plots, the patterns and significance of these manipulations on demography over our 5-year experiment were generally negligible. Furthermore, the transient effects of treatment on demography were neither related to inter-annual rainfall patterns nor drove significant changes in population growth.

Our results suggest that the ability to intuit the consequences of environmental change for population dynamics on the basis of short-term experiments is limited. For instance, the high unexplained temporal variability in demographic rates resulted in time-dependent treatment differences; were it not for our long-term and demographic approach we could have easily misinterpreted these differences as persistent and biologically meaningful. Furthermore, the potential disconnect between changes in individual vital rates and actual changes in population dynamics is a cautionary tale for experimental studies that either utilize only a subset of life stages or analyze demographic rate responses separately (see also Halpern and Underwood 2006). Our results also highlight the utility of matrix models, whose integrative nature reveals long-term patterns that would not have been detected by comparison of changes in population size and the distribution or a limited subset of life history stages (Caswell 2007). These models allow us to understand the relative importance to population dynamics of different vital rates; in doing so they link observed shifts in population distribution and abundance to underlying demographic mechanisms. Furthermore, estimates of λ can be interpreted as a measure of relative fitness (McGraw and Caswell 1996), allowing one to better understand successional trends resulting from altered competitive balance between species.

Previous research in tropical forests has shown that there can be major physiological responses to water availability (Engelbrecht and Kursar 2003; Bunker and Carson 2005; Nepstad et al. 2007; Tanner and Barberis 2007; Yavitt and Wright 2008). However, our understanding of how drought impacts tropical tree populations is rudimentary. Nepstad et al. (2007) argue that the effects could be large, in part because large trees are at greater risk due to greater evaporative demand of canopy exposure. This idea is corroborated by their dry season rainfall-exclusion studies conducted in Amazonia, which resulted in substantial

Fig. 3 Impacts of irrigation and litter-removal treatments on survival, growth and regression probabilities on population growth of **a** *L. pubescens* and **b** *M. sylvatica*



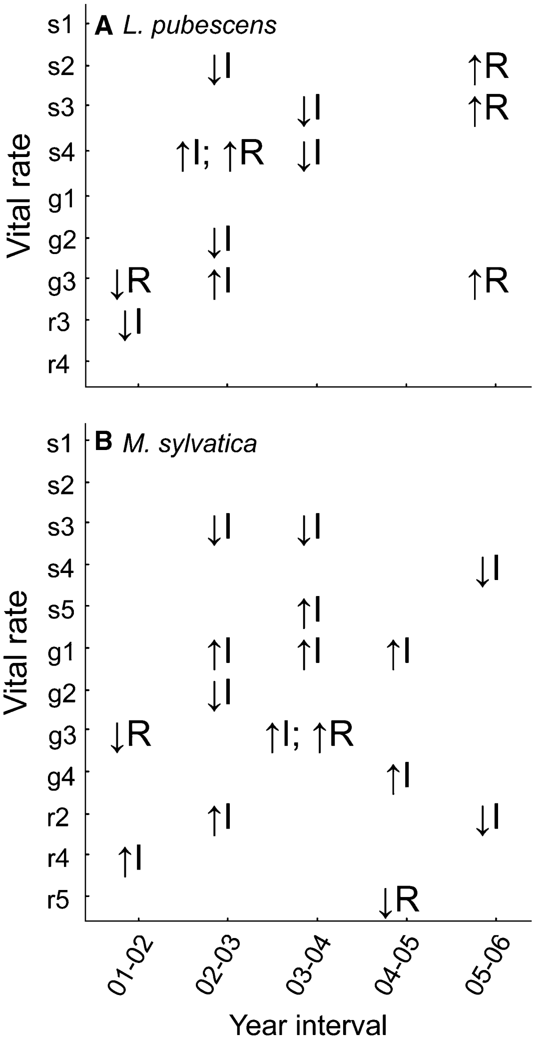


Fig. 4 Statistically significant time × treatment effects on vital rates of **a** *L. pubescens*, **b** *M. sylvatica*. *Up arrow* Increase in vital rate, *down arrow* decrease in vital rate. *s* Survival; *g* growth; *r* regression (vital rate numbers indicate size class, e.g., g3 growth rate of size class 3); *I* significant irrigation effect; *R* significant litter-removal effect

mortality of large trees and canopy-bound lianas (Nepstad et al. 2007). On the other hand, irrigation experiments in Panama and elsewhere have suggested it is actually the seedling stages of tropical trees that are most vulnerable to drought due to their limited root systems (Engelbrecht and Kursar 2003; Yavitt and Wright 2008). If so, the long-term effects of occasional droughts on population dynamics may be limited, owing to the generally low elasticity values of seedling-related vital rates (e.g., Bruna 2003).

Our experimental and demographic design allowed us to explore the responses to drought of stages spanning the seedling-adult continuum. Our results suggest the impacts of drought on tree demography are far more complex than simply influencing primarily seedlings or adults. On the one hand, many of our larger adult trees were exposed to direct sunlight, resulting in increased evaporative demand under drought conditions. They also grew in shallow lateritic soil formations that appear to limit the development of deep root systems. Nevertheless, these conditions did not translate into reduced growth and survivorship. On the other hand, our study shows only limited evidence supporting the notion that seedlings are highly drought sensitive. Only the growth of the smallest *M. sylvatica* seedling size class showed a constant increase in response to irrigation, which probably resulted from large changes in C assimilation (Fortini et al. 2003). However, this effect only lasted for 3 of the 5 years of monitoring and was shown to be inconsequential in terms of contributions to *M. sylvatica* population growth.

Large-scale, long-term natural litter-removal experiments designed to explore the role of nutrient constraints are rare in tropical ecosystems (Sayer 2006). Other research at our study site has found relatively rapid responses of nutrient availability, possibly reflecting the quick and tight cycling of nutrients common in the tropical forests (Vitousek and Sanford 1986; Veluci-Marlow 2007; Vasconcelos et al. 2008). Our analyses suggest secondary forest tree populations are very tolerant to these changes. Although this tolerance is supported by fertilization experiments demonstrating limited effects of reduced nutrient availability on tropical forest vegetation (Mayor and Roda 1994; Pearson and Vitousek 2001), our results are nevertheless at odds with several other studies that have shown clear increases in growth and survival following nutrient addition (Gehring et al. 1999; Lawrence 2001; Ceccon et al. 2003; Davidson et al. 2004; Yavitt and Wright 2008). Indeed, our results are particularly surprising given the relatively low values of soil extractable P present at our site (Rangel-Vasconcelos et al. 2005).

Exploring the limited effects of resource limitation on λ

Our results beget the question of why there were no strong and unidirectional effects on demography and λ in our two focal species. First, it is possible that despite our large experimental manipulations of water and nutrients, the treatments did not result in significant changes in water and nutrient availability. However, recent studies strongly suggest that this is not the case. Past studies from our site have linked changes in water availability to several ecosystem and individual-level responses, including increased above-ground net primary productivity (ANPP; Fortini et al. 2003; Vasconcelos et al. 2004, 2007; Vasconcelos 2006; Veluci-Marlow 2007). Veluci-Marlow (2007) has also demonstrated that our litter-removal treatment resulted in decreased N mineralization, phosphatase activity, and NH_4^+ availability, as well as increased availability of NO_3^-. Furthermore, Vasconcelos et al. (2008) found a

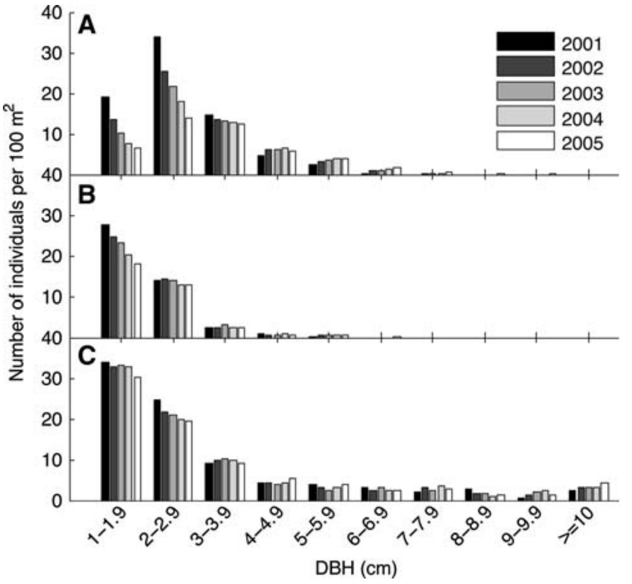


Fig. 5 Changes in the diameter distribution of **a** *L. pubescens*, **b** *M. sylvatica* and **c** all other species from control plots at the 14-year-old secondary forest in Apeú, Pará, Brazil. Irrigation and litter-removal plots exhibited similar distributional shifts

significant decrease in litterfall N content, indicative of responses to nutrient limitation by individual trees at our litter-removal plots. Although there are no results from this system quantifying the increased magnitude of nutrient limitation resulting from litter removal, the fact that the removal of 4–5 times the initial P stocks in above-ground fine litter over a 5-year period did not appreciably influence the demography of our study species at such a nutrient-poor site is surprising and merits further investigation.

Second, it is important to consider the possibility that species with different life history strategies could be more susceptible to changes in water and nutrient availability than our focal taxa (McCook 1994). Past research conducted at our study site suggest that other species may be more responsive to changes in water availability than our two focal species. A study of changes in whole-stand ANPP in response to water availability found that whole-stand diameter increment was linked to changes in water availability resulting from irrigation and previous dry season rainfall (Vasconcelos 2006). Although the growth of *L. pubescens* individuals in size class 3 tracked the change in ANPP for the whole stand, no other vital did. Furthermore, shifts in the size distribution of the two focal species resulted in a drastic decrease in their population numbers, and suggest the dynamics of these two species may be different from others in the stand (Fig. 5). Nevertheless, it is important to recognize that *L. pubescens* and *M. sylvatica* represent very distinct species in the community of successional trees found in our study site, and are the dominant successional species in the region's secondary forests (L. Fortini, unpublished data). Hence, their response to our experimental manipulations—or lack thereof—will have important implications for the trajectory of succession.

Third**,** it is important to remember that the demographic responses of a species to changes in abiotic constraints will be influenced by how other species—which can be either competitors or facilitators—respond to the same changes (Goldberg 1996; Choler et al. 2001; Liancourt et al. 2005; Suter et al. 2007). In secondary forests this is further complicated by changes in the strength and direction of competitive interactions over the course of a stand's successional trajectory (McCook 1994; Kobe et al. 1995; Mal et al. 1997). The relative importance of different limiting factors can also change as succession proceeds, further shifting the competitive balance between species. As such, the response of focal species to the same changes in abiotic constraints may have differed if we had conducted these experiments at earlier or later successional stages. At our study stand, the shifts in diameter distribution for all species present in the stand during the study period indicate an ongoing dynamic development of the forest (Araújo et al. 2005). Further support for this conclusion is that despite continued fruiting by the two study species (L. Fortini, personal observation), seedling recruitment by the end of the study period was appreciably lower; this suggests that the possibility of a delayed recruitment response to either treatment is unlikely. This dynamism, and the myriad other factors that also influence demography, work in a complex fashion to influence a species' interactions with competitors; this competitive balance in turn alters population and stand structure, leading to feedback changes in light availability and other abiotic constraints.

While understory light availability did not vary with respect to experimental treatment (L. Fortini, unpublished data), there is evidence suggesting light plays an important role in the demography of our focal species as seen elsewhere (Kobe et al. 1995; Graham et al. 2003). Although neither study species was suffering from high overstory mortality or low reproductive output (L. Fortini, unpublished data), both species showed clear bottlenecks in their understory size classes. Almost no *L. pubescens* individuals recruited in spite of ample fruiting, including in litter-removal plots where the elimination of the litter layer should have resulted in increased understory recruitment (Facelli and Pickett 1991). Furthermore, there was also an understory bottleneck in *M. sylvatica*—despite ample understory recruitment, nearly no individuals survived to reach the smaller reproductive size classes. Given the previously documented impacts of water and nutrient availability on stand- and individual-level processes at our study site and elsewhere, we expected controls over forest succession were potentially more complex than overriding autogenic control through light availability (Huston and

Smith 1987). Our results suggest that, for some species and at certain successional stages, light availability may still overshadow prolonged alterations of other ecosystem properties posited critical for forest function.

Our results suggest a set of research directions and related experiments that merit further exploration. First, it is necessary to explore the role of autogenic successional factors (e.g., light availability, root competition) in mediating population response to exogenous abiotic constraints. This could be done by monitoring of seedlings to adults from a number of species of contrasting life history traits in similar manipulative experiments, therefore ensuring a better representation of species under varied strengths of autogenic control from stand structure. Alternatively, one could explore the effects of experimental manipulations of abiotic factors along a chronosequence representing different stages of succession. Second, applied treatments should ideally include multidirectional manipulations (e.g., irrigation and exclusion) to properly evaluate limitations to typical and atypical stress conditions. Finally, such experiments should monitor how treatments impact competitive ability/relative fitness of individuals over time to begin understanding the potentially complex response of populations in a diverse community setting. Such experimental approaches, coupled with recent theoretical advances (Caswell 2007), could help investigate the potentially important role of transient population dynamics.

Lastly, it is also worth noting how the contrasting demographic patterns for the two focal species clearly reflect their distinct successional roles. *L. pubescens* establishes stand dominance early on, but soon declines in abundance. We found no consistent temporal patterns in *L. pubescens* demographic rates, suggesting the patterns of demography we observed reflect ecological influences that preceded our monitoring of the stand. In contrast, *M. sylvatica*'s inverse-J population structure, high survival of smaller size classes, and initially high understory recruitment are consistent with the observation that its dominance in the successional community lags behind that of *L. pubescens*. Nevertheless, the near absence of recruitment into *M. sylvatica*'s understory stages and the smallest overstory size class implies the long-term persistence of *M. sylvatica* is unlikely. If so, this gives rise to increased dominance of other species in the successional progression of these stands, although it does not exclude the possibility of *M. sylvatica*'s return from the seed bank or from younger neighboring stands following disturbance.

Conclusion

With the growing interest in the mitigation of anthropogenic disturbance and changes in global C dynamics, research on processes and factors constraining tropical forest regrowth is flourishing (Vester and Cleef 1998; Coomes et al. 2000; Johnson et al. 2000; Moran et al. 2000; de Jong et al. 2001; Guariguata and Ostertag 2001; Capers et al. 2005; Vasconcelos 2006). While our results suggest the population growth rates of secondary forest tree species are resilient to altered precipitation regimes or land-use-induced nutrient limitation, the complex mechanisms underlying this response clearly indicate a need for work in other systems and with a broad diversity of species. If climate change results in increases in precipitation for the region (Marengo 2004), our results suggest that the demography and population dynamics of some species will be minimally affected by increases in the frequency of dry season rainfall. However, if climate change results in more intense dry seasons (Harris et al. 2008), rainfall-exclusion experiments are more likely to take plants into water stress levels beyond those commonly experienced in typical dry seasons and thus may be valuable complements to our present study (Nepstad et al. 2007). In effect, while addressing the consequences of climate change on tree populations in the Amazon, both irrigation and rainfall-exclusion experiments only offer partial answers. Similarly, nutrient limitation comparable to that in our experimental manipulations would also be predicted to have limited effects on demography.

Acknowledgments We thank Osorio Oliveira, Glebson Sousa, and Evandro da Silva for their assistance in the field, and Raimundo Nonato da Silva (UFRA) and Débora Aragão for logistical support. This research was conducted under cooperative agreements between the University of Florida, Universidade Federal Rural da Amazonia and Embrapa Amazônia Oriental and supported by a grant from the Andrew Mellon Foundation to D. J. Z., a grant from Conselho Nacional de Desenvolvimento Científico e Tecnológico—CNPQ to I. S. M. and an EPA STAR fellowship to L. B. F. All conducted experiments comply with current Brazilian laws.

References

Aide TM, Zimmerman JK, Pascarella JB, Rivera L, Marcano-Vega H (2000) Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. Restor Ecol 8:328–338

Aragão DV, Fortini LB, Mulkey S, Zarin DJ, Araujo MM, Carvalho CJR (2005) Correlation but no causation between leaf nitrogen and maximum assimilation: the role of drought and reproduction in gas exchange in an understory tropical plant *Miconia ciliata* (Melastomataceae). Am J Bot 92:456–461

Araújo MM, Tucker JM, Vasconcelos SS, Zarin DJ, Oliveira W, Sampaio PD, Rangel-Vasconcelos LGT, Oliveira FDA, Coelho RFR, Aragão DV, Miranda I (2005) Padrão e processo sucessionais em florestas secundárias de diferentes idades na Amazônia oriental. Ciência Florestal 15:343–357

Ayuba HK, Aweto AO, Abubakar SM (2000) Soil nutrient dynamics under small-holder agricultural practices in Konduga, north-eastern Nigeria. Trop Agric 77:116–118

Brown S, Lugo AE (1990) Tropical secondary forests. J Trop Ecol 6:1–32

Bruna EM (2003) Are plant populations in fragmented habitats recruitment limited? Tests with an Amazonian herb. Ecology 84:932–947

Bruna EM, Oli MK (2005) Demographic effects of habitat fragmentation on a tropical herb: life-table response experiments. Ecology 86:1816–1824

Bunker DE, Carson WP (2005) Drought stress and tropical forest woody seedlings: effect on community structure and composition. J Ecol 93:794–806

Burns JH (2008) Demographic performance predicts invasiveness of species in the Commelinaceae under high-nutrient conditions. Ecol Appl 18:335–346

Capers RS, Chazdon RL, Brenes AR, Alvarado BV (2005) Successional dynamics of woody seedling communities in wet tropical secondary forests. J Ecol 93:1071–1084

Caswell H (2001) Matrix population models: construction, analysis, and interpretation, 2nd edn. Sinauer, Sunderland

Caswell H (2007) Sensitivity analysis of transient population dynamics. Ecol Lett 10:1–15

Ceccon E, Huante P, Campo J (2003) Effects of nitrogen and phosphorus fertilization on the survival and recruitment of seedlings of dominant tree species in two abandoned tropical dry forests in Yucatan, Mexico. For Ecol Manage 182:387–402

Chazdon RL, Coe FG (1999) Ethnobotany of woody species in second-growth, old-growth, and selectively logged forests of northeastern Costa Rica. Conserv Biol 13:1312–1322

Chazdon RL, Brenes AR, Alvarado BV (2005) Effects of climate and stand age on annual tree dynamics in tropical second-growth rain forests. Ecology 86:1808–1815

Choler PR, Michalet R, Callaway RM (2001) Competition and facilitation on gradients in alpine communities. Ecology 82:3295–3308

Clements FE (1916) Plant succession: an analysis of the development of vegetation (publication 242). Carnegie Institute, Washington

Coelho RFR, Zarin DJ, Miranda IS, Tucker JM (2004) Análise florística e estrutural de uma floresta em diferentes estágios sucessionais no município de Castanhal, Pará. Acta Amazon 33:563–582

Condit R (1998) Ecological implications of changes in drought patterns: shifts in forest composition in Panama. Clim Chang 39:413–427

Coomes OT, Grimard F, Burt GJ (2000) Tropical forests and shifting cultivation: secondary forest fallow dynamics among traditional farmers of the Peruvian Amazon. Ecol Econ 32:109–124

Davidson EA, Carvalho CJR, Vieira ICG, Figueiredo RDO, Moutinho P, Ishida FY, Santos MTPD, Guerrero JB, Kalif K, Saba RT (2004) Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. Ecol Appl 14:S150–S163

De Jong W, Freitas L, Baluarte J, Van De Kop P, Salazar A, Inga E, Melendez W, Germana C (2001) Secondary forest dynamics in the Amazon floodplain in Peru. For Ecol Manage 150:135–146

Engelbrecht BMJ, Kursar TA (2003) Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. Oecologia 136:383–393

Facelli JM, Pickett STA (1991) Plant litter—its dynamics and effects on plant community structure. Bot Rev 57:1–32

Fortini LB, Mulkey SS, Zarin DJ, Vasconcelos SS, Carvalho CJR (2003) Drought constraints on leaf gas exchange by *Miconia ciliata* (Melastomataceae) in the understory of an Eastern Amazonian regrowth forest stand. Am J Bot 90:1064–1070

Gavin MC (2004) Changes in forest use value through ecological succession and their implications for land management in the Peruvian Amazon. Conserv Biol 18:1562–1570

Gehring C, Denich M, Kanashiro M, Vlek PLG (1999) Response of secondary vegetation in Eastern Amazonia to relaxed nutrient availability constraints. Biogeochemistry 45:223–241

Giardina CP, Binkley D, Ryan MG, Fownes JH, Senock RS (2004) Belowground carbon cycling in a humid tropical forest decreases with fertilization. Oecologia 139:545–550

Goldberg DE (1996) Competitive ability: definitions, contingency and correlated traits. Philos Trans R Soc B 351:1377–1385

Gower ST (1987) Relations between mineral nutrient availability and fine root biomass in two Costa Rican tropical wet forests: a hypothesis. Biotropica 19:171–175

Graham EA, Mulkey SS, Kitajima K, Phillips NG, Wright SJ (2003) Cloud cover limits net CO_2 uptake and growth of a rainforest tree during tropical rainy seasons. PNAS 100:572–576

Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. For Ecol Manage 148:185–206

Halpern SL, Underwood N (2006) Approaches for testing herbivore effects on plant population dynamics. J Appl Ecol 43: 922–929

Harris PP, Huntingford C, Cox PM (2008) Amazon basin climate under global warming: the role of the sea surface temperature. Philos Trans R Soc B 363:1753–1759

Hopkins MS, Reddell P, Hewett RK, Graham AW (1996) Comparison of root and mycorrhizal characteristics in primary and secondary rainforest on a metamorphic soil in North Queensland, Australia. J Trop Ecol 12:871–885

Hughes RF, Kauffman JB, Jaramillo VJ (1999) Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. Ecology 80:1892–1907

Huston M, Smith T (1987) Plant succession: life history and competition. Am Nat 130:168–198

Jipp PH, Nepstad DC, Cassel DK, Carvalho CRJ (1998) Deep soil moisture storage and transpiration in forests and pastures of seasonally dry Amazonia. Clim Chang 39:395–412

Johnson CM, Zarin DJ, Johnson AH (2000) Post-disturbance aboveground biomass accumulation in global secondary forests. Ecology 81:1395–1401

Juo ASR, Manu A (1996) Chemical dynamics in slash-and-burn agriculture. Agric Ecosyst Environ 58:49–60

Kitajima K, Mulkey SS, Wright SJ (1997) Seasonal leaf phenotypes in the canopy of a tropical dry forest: photosynthetic characteristics and associated traits. Oecologia 109:490–498

Kobe RK, Pacala SW, Silander JA, Canham CD (1995) Juvenile tree survivorship as a component of shade tolerance. Ecol Appl 5:517–532

Laurance WF, Fearnside PM, Laurance SG, Delamonica P, Lovejoy TE, Merona JMR, Chambers JQ, Gascon C (1999) Relationship between soils and Amazon forest biomass: a landscape-scale study. For Ecol Manage 118:127–138

Lawrence D (2001) Nitrogen and phosphorus enhance growth and luxury consumption of four secondary forest tree species in Borneo. J Trop Ecol 17:859–869

Lean J, Bunton CB, Nobre CA, Rowntree PR (1996) The simulated impact of Amazonian deforestation on climate using measured ABRACOS vegetation characteristics. In: Gash JHC, Nobre CA, Roberts JM, Victoria RL (eds) Amazonian deforestation and climate. Wiley, New York, pp 549–576

Liancourt P, Callaway RM, Michalet R (2005) Stress tolerance and competitive-response ability determine the outcome of biotic interactions. Ecology 86:1611–1618

Mal TK, Lovett-Doust J, Lovett-Doust L (1997) Time-dependent competitive displacement of *Typha angustifolia* by *Lythrum salicaria*. Oikos 79:26–33

Malhi Y, Nobre AD, Grace J, Kruijt B, Pereira MGP, Culf A, Scott S (1998) Carbon dioxide transfer over a Central Amazonian rain forest. J Geophys Res 103(D24):31593–31612

Marengo JA (2004) Interdecadal variability and trends of rainfall across the Amazon Basin. Theor Appl Climatol 78:79–96

Mayor X, Roda F (1994) Effects of irrigation and fertilization on stem diameter growth in a Mediterranean Helm Oak Forest. For Ecol Manage 68:119–126

McCook LJ (1994) Understanding ecological community succession—causal-models and theories, a review. Vegetatio 110:115–147

McGrath DA, Smith CK, Gholz HL, Oliveira FD (2001) Effects of land-use change on soil nutrient dynamics in Amazonia. Ecosystems 4:625–645

McGraw JB, Caswell H (1996) Estimating of individual fitness from life-history data. Am Nat 147:47–64

Mirmanto E, Proctor J, Green J, Nagy L, Suriantata (1999) Effects of nitrogen and phosphorus fertilization in a lowland evergreen rainforest. Philos Trans R Soc B 354:1825–1829

Moran EF, Brondizio ES, Tucker JM, Silva-Forsberg MC, McCracken S, Falesi I (2000) Effects of soil fertility and land-use on forest succession in Amazonia. For Ecol Manage 139:93–108

Morris WF, Doak DF (2002) Quantitative conservation biology: theory and practice of population viability analysis. Sinauer, Sunderland

Nepstad DC, Moutinho P, Dias-Filho MB, Davidson E, Cardinot G, Markewitz D, Figueiredo R, Vianna N, Chambers J, Ray D, Guerreiros JB, Lefebvre P, Sternberg L, Moreira M, Barros L, Ishida FY, Tohlver I, Belk E, Kalif K, Schwalbe K (2002) The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. J Geophys Res 107(D20):8085. doi:10.1029/2001JD000360

Nepstad D, Lefebvre P, Silva UL, Tomasella J, Schlesinger P, Solorzano L, Moutinho P, Ray D, Benito JG (2004) Amazon drought and its implications for forest flammability and tree growth: a basin-wide analysis. Glob Chang Biol 10:704–717

Nepstad DC, Tohver IM, Ray D, Moutinho P, Cardinot G (2007) Mortality of large trees and lianas following experimental drought in an Amazon forest. Ecology 88:2259–2269

Noble IR, Slatyer RO (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43:5–21

Olschewski R, Benitez PC (2005) Secondary forests as temporary carbon sinks? The economic impact of accounting methods on reforestation projects in the tropics. Ecol Econ 55:380–394

Pavlis J, Jenik J (2000) Roots of pioneer trees in the Amazonian rain forest. Trees Struct Funct 14:442–455

Pearson HL, Vitousek PM (2001) Stand dynamics, nitrogen accumulation, and symbiotic nitrogen fixation in regenerating stands of *Acacia koa*. Ecol Appl 11:1381–1394

Pickett STA (1976) Succession: an evolutionary interpretation. Am Nat 110:107–119

Rangel-Vasconcelos LGT, Zarin DJ, Carvalho CJR, Santos MML, Vasconcelos SS, Oliveira FA (2005) Carbono, nitrogȩnio e atividade da biomassa microbiana de um solo sob vegetação secundária de diferentes idades na Amazônia oriental. Rev Ciênc Agrárias 44:49–64

Sayer EJ (2006) Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. Biol Rev 81:1–31

Shuttleworth WJ, Gash JHC, Lloyd CR, Moore CJ, Roberts J, Filho ADOM, Fisch G, Filho VDPS, Ribeiro MDNG, Molion LCB, Sá LDDA, Nobre JCA, Cabral OMR, Patel SR, De Moraes JC (1984) Eddy correlation measurements of energy partition for Amazonian forest. Q J R Meteorol Soc 110:1143–1162

Smith J, Ferreira S, Van De Kop P, Ferreira CP, Sabogal C (2003) The persistence of secondary forests on colonist farms in the Brazilian Amazon. Agrofor Syst 58:125–135

Suter M, Ramseier D, Guesewell S, Connolly J (2007) Convergence patterns and multiple species interactions in a designed plant mixture of five species. Oecologia 151:499–511

Tanner EVJ, Barberis IM (2007) Trenching increased growth, and irrigation increased survival of tree seedlings in the understorey of a semi-evergreen rain forest in Panama. J Trop Ecol 23:257–268

Tenório ARM, Graça JJC, Góes JEM, Mendez JGR, Gama JRMF, Da Silva PRO, Das Chagas PSM, Da Silva RNP, Américo RR, Pereira WLM (1999) Mapeamento dos solos da estação de piscicultura de Castanhal, PA. FCAP Inform Téc 25:5–26

Vasconcelos SS (2006) Moisture and nutrient constraints to ecosystem processes in a forest regrowth stand in Eastern Amazonia, Brazil. Ph.D dissertation. Gainesville, University of Florida

Vasconcelos SS, Zarin DJ, Mulkey SS, Carvalho CJR, Fortini LB (2002) Water use efficiency increases in response to drought for *Vismia guianensis* in the overstory of an Eastern Amazonian regrowth forest. LBA Science Conference, Manaus, Brazil. http://lba.cptec.inpe.br/beija-flor/

Vasconcelos SS, Zarin DJ, Capanu M, Littell R, Davidson EA, Ishida FY, Santos EB, Araujo MM, Aragão DV, Rangel-Vasconcelos LGT, Oliveira FD, Mcdowell WH, Carvalho CJR (2004) Moisture and substrate availability constrain soil trace gas fluxes in an eastern Amazonian regrowth forest. Glob Biogeochem Cycles 18:1–10

Vasconcelos SS, Zarin DJ, Rosa MBDS, Oliveira FDA, Carvalho CJR (2007) Leaf decomposition in a dry season irrigation experiment in eastern Amazonian forest regrowth. Biotropica 35:593–600

Vasconcelos SS, Zarin DJ, Araujo MM, Rangel-Vasconcelos LGT, Carvalho CJR, Staudhammer CL, Oliveirat FD (2008) Effects of seasonality, litter removal, and dry-season irrigation on litterfall quantity and quality in eastern Amazonian forest regrowth, Brazil. J Trop Ecol 24:27–38

Veluci-Marlow RM (2007) Seasonal and experimental effects on microbial composition and dynamics in tropical forest regrowth. Ph.D dissertation. Gainesville, University of Florida

Vester HFM, Cleef AM (1998) Tree architecture and secondary tropical rain forest development—a case study in Araracuara, Colombian Amazonia. Flora 193:75–97

Vitousek PM, Sanford JRL (1986) Nutrient cycling in moist tropical forest. Annu Rev Ecol Syst 17:137–167

Yarranton GA, Morrison RG (1974) Spatial dynamics of a primary succession: nucleation. J Ecol 62:417–428

Yavitt JB, Wright SJ (2008) Seedling growth responses to water and nutrient augmentation in the understorey of a lowland moist forest, Panama. J Trop Ecol 24:19–26