COMMUNITY ECOLOGY - ORIGINAL PAPER

# Seedling interactions in a tropical forest in Panama

**J. -C. Svenning · T. Fabbro · S. J. Wright**

**Abstract** Competition is believed to be a central force limiting local diversity and controlling the structure of plant communities. However, it has been proposed that the stressed understory environment limits total understory plant density to such low levels that competitive exclusion cannot be an important factor limiting the local diversity of understory plants. To evaluate the importance of inter-seedling competition, we performed a seedling competition experiment with five shade-tolerant species in a tropical moist forest in Panama. Three-month-old seedlings were transplanted into the forest singly or with their roots intertwined with a single conspecific or heterospecific seedling in all pairwise species combinations. If competition is important, performance (survival, stem height, and number of leaves after one and six years) would be expected to be lowest with a conspecific neighbor and greatest without a neighbor. The experiment was replicated in five $0.24$-$m^2$ plots at each of 20 sites in tall secondary forest. To test whether seedling performance differed among treatments we fitted linear mixed models (LMM) and generalized linear mixed models (GLMM), treating species identity and microsite (site and plot) as random effects. The five shade-tolerant study species all experienced good establishment with relatively high survival and growth rates. The neighbor treatment consistently affected seedling performance, but the effect was always very small, both in absolute terms and relative to the much stronger species and microsite effects. Seedlings with a conspecific neighbor consistently performed worse than seedlings with a heterospecific neighbor, but having no neighbor generally did not cause superior performance relative to the other treatments. We conclude that direct competitive interactions are relatively unimportant among understory plants in humid tropical forests.

**Keywords** Barro Colorado Island · Competition · Generalized linear mixed models · Plant community assembly · Neutral theory

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## Introduction

Competition is believed to be a central force limiting local diversity and controlling the structure of plant communities (Grime 1979; Tilman 1982; Goldberg and Barton 1992). Competitive niche partitioning has been proposed to be an important mechanism allowing hundreds of species to coexist locally in humid tropical forests (Ashton 1993; Tilman and Pacala 1993; Kobe 1999; Svenning 2001; Montgomery and Chazdon 2002; Wright 2002). In a diametrically opposed hypothesis, dispersal structures tropical forest plant communities, and competition only plays a role as a neutral interaction independent of species identity (Hubbell et al. 1999; Hubbell 2001). Experiments to evaluate

the role of competition are needed to help determine whether competitive niche partitioning or neutral dispersal assembly structure tropical forest plant communities.

All forest species that germinate in the soil must regenerate from the understory or from tree fall gaps. The understory, therefore, includes seedlings of canopy trees and lianas as well as all life stages for the shrubs and terrestrial herbs that comprise 40–60% of plant species in wet tropical forests (Gentry and Dodson 1987). Which mechanisms allow large numbers of plant species to coexist in tropical forest understories? It has been proposed that the stressed understory environment of humid tropical forests limits total understory plant density to such low levels that competitive exclusion cannot be an important factor limiting the local diversity of suppressed understory plants (Wright 1992, 2002). Several mechanisms reduce plant densities in the understory of closed canopy tropical forests. Seed supplies limit the recruitment of most species (Hubbell et al. 1999; Dalling et al. 2002; Muller-Landau et al. 2002, 2004; Makana and Thomas 2004; Svenning and Wright 2005). Herbivores and pathogens further reduce understory plant growth and density (reviewed by Wright 2002). Finally, canopy trees and lianas dominate the internal forest environment, both above- and belowground, and suppress the growth and densities of understory plants (Coomes and Grubb 2000; Barberis and Tanner 2005). A similar suite of factors affects understory plants in temperate forests (Collins et al. 1985; Ehrlén and Eriksson 2000; Packer and Clay 2000; Turnbull et al. 2000; Thomsen et al. 2005). If total understory plant density is limited to sufficiently low levels, there would be little scope for direct competition among understory individuals because plants only compete directly with near-neighbors whose zones of resource depletion overlap. In this extreme, competitive exclusion cannot be an important limiting factor for the local coexistence of understory plant species (Wright 1992, 2002).

The hypothesis that direct competition is unimportant among suppressed understory plants represents a special case of the hypothesis that competition is unimportant for plants in unproductive environments (Grime 1979). Experiments will be necessary to evaluate this hypothesis for understory plants in humid tropical forests. Three experiments have removed a portion of the understory plants and then followed the response of the remaining understory plants in tropical forests. Twice the remaining understory plants failed to show competitive release (Marquis et al. 1986; Brown and Whitmore 1992), in agreement with the hypothesis that competition is limited among understory plants. The third partial understory removal experiment had mixed results, with increased recruitment of lianas and herbs, but not of trees, shrubs, palms, or epiphytes in mature forest (Benitez-Malvido 2006). Here, we take a different approach and test for competition between closely

adjacent seedlings. We experimentally evaluate the importance of seedling competition by planting seedlings of five shade-tolerant species either alone or as close together as possible with a single conspecific or with a single heterospecific. By planting seedlings immediately adjacent to one another, we sought to evaluate the potential for seedling interactions when it was at its greatest. If seedling competition is important, we predict that seedlings without neighbors will perform best and seedlings with conspecific neighbors will perform worst.

## Materials and methods

### Study site

Barro Colorado Island (BCI; 9°09′N, 79°51′W) is a 16-km$^2$ former hilltop elevated 27–160 m a.s.l. and located in Gatun Lake, Republic of Panama. Yearly precipitation averages ca. 2,600 mm, the climate is seasonally dry, and the vegetation is tropical semi-deciduous forest. Half of BCI is covered with old-growth forest, at least parts of which have escaped fire and agriculture for 1,500 years or more (Leigh 1999). The remaining secondary forest dates mostly from the 1800s (Foster and Brokaw 1996). Detailed descriptions of the climate, geology, and biota of BCI can be found in Croat (1978), Gentry (1990), Leigh et al. (1996), and Leigh (1999). Nomenclature follows Croat (1978).

### Experimental design

Our field competition experiment was designed to maximize the potential impact of seedling interactions and to contrast this with effects of species identity and microsite (represented by site and plot effects). The experiment was replicated at 20 sites in tall secondary forest. All sites contained a small, natural canopy opening. At each site, five 0.24-m$^2$ plots were located along a gradient ranging from the completely closed canopy to the center of the canopy opening. Therefore, the plot effect includes any effect of this environmental gradient. The mean maximum distance among plots within a site was 13.0 m ($\pm$3.0 SD).

Seedlings, herbs and large obstructing branches were removed from within 10 cm of each plot, plots were divided into contiguous 10 by 10 cm subplots, and 20 treatments were randomly assigned to one subplot within each plot. Fifteen treatments included two seedlings planted with their roots intermingled and their stems as close together as possible to maximize the potential for interaction. The two-seedling treatments included all possible con- and heterospecific pairs of the treelet *Lacistema aggregatum* (Lacistemataceae), the shrubs *Hybanthus prunifolius* (Violaceae),

*Psychotria limonensis* and *P. marginata* (Rubiaceae), and the grass *Streptochaeta sodiroana* (Poaceae). All five species are shade-tolerant and germinate, survive, and grow in the shaded understory. Five additional one-seedling treatments included a single seedling of each species. Thus, each species was represented by seven seedlings in each plot. To avoid pseudoreplication, we randomly selected one seedling from each conspecific pair for the analyses, so that each species was represented by six seedlings in each plot.

Seedlings were grown in a well-shaded greenhouse from seeds collected in March–May 2000 and were transplanted to the center of a randomly assigned subunit in September 2000. The mean number of leaves when transplanted were 3.9 for *Hybanthus*, 2.6 for *Lacistema*, 2.5 for *P. limonensis*, 2.2 for *P. marginata*, and 3.5 for *Streptochaeta* ($n$ = the 600 seedlings selected for the 2001 analysis for each species). Naturally emerged seedlings less than one year old recorded in a long-term monitoring study had similar numbers of leaves on BCI (mean ($n$): *Hybanthus*, 3.3 (3337); *Lacistema*, 4.5 (22); *P. limonensis*, 2.1 (43); *P. marginata*, 2.7 (106); *Streptochaeta*, no data; S.J. Wright, unpublished data). Dead or severely damaged seedlings were replaced with healthy seedlings through October 2000. Plots were maintained every 2–4 weeks during the first year by weeding and by removal of palm fronds or similarly massive debris.

A first-year census was conducted in October 2001, 13 months after transplanting. A final sixth-year census was conducted in September–October 2006. At both censuses, seedlings were noted as being dead or alive and the number of unfolded leaves (not cotyledons) and the height of the stem (not for the herbaceous *Streptochaeta*) was measured for all live seedlings. Therefore, we have three measures of seedling performance, namely survival and the two size measures, stem height and number of leaves, after both one and six years.

The seedling density planted into the experimental plots (146 seedlings per m$^2$) was considerably greater than the natural density of plants ≤50 cm tall (mean $26 \pm 14$ SD plants per m$^2$, $n$ = 20), which was determined for 60 by 50 cm plots located 2 m from the third plot within each site. Nonetheless, the small size of the planted seedlings limited direct interactions among seedlings in different subplots. Rather, direct interactions would primarily have been between those pairs of experimental seedlings planted into a single subplot with their roots intertwined.

Data analysis

If competition occurs among neighboring seedlings, we expect seedlings without neighbors to perform best and seedlings with conspecific neighbors to perform worst. Therefore, for the analyses the impact of seedling interactions was represented by a three-state categorical neighbor variable indicating whether a seedling was (1) planted alone, (2) planted with a conspecific neighbor, and (3) planted with a heterospecific neighbor. This treatment effect was contrasted with the effects of species identity and microsite (represented by site and plot effects) on performance. In the modeling we considered treatment as a fixed factor and species identity, sites, and plots nested within sites as random factors. Therefore, to test whether seedling performance differed among treatments we fitted linear mixed models (LMM) and generalized linear mixed models (GLMM; Pinheiro and Bates 2001) using lme4 (Bates and Sarkar 2007) in R 2.4.1 (R Development Core Team 2007). In contrast to a traditional mixed model ANOVA, the LMM/GLMM approach straightforwardly allows us to handle binary and continuous response variables in a single framework. Furthermore, maximum likelihood and restricted maximum likelihood solutions (for fixed and random effects, respectively) were used for estimating and testing because the ANOVA method is known to be more sensitive to unbalanced data and outliers (McCulloch and Searle 2001). Within the treatment factor two planned orthogonal comparisons were estimated and tested, namely the difference between seedlings planted alone versus planted with a con- or heterospecific, and the difference between seedlings planted with a conspecific versus a heterospecific.

To estimate and test differences in survival to 2001 and 2006 we used GLMM with a logistic link function, while stem height and number of leaves after one year and after six years were modeled using LMM. The herbaceous *Streptochaeta* was not included in the analyses of stem height. The most complex model considered included fixed treatments and variance components due to random effects of species identity, site, and plot nested within site (Tmt + species + site + plot (site)). More complex models that also included random heterogeneity in the treatment effect due to plot and species identity could not generally be fit due to insufficient replication and were therefore not considered. To assess the precision of estimates and the significance of the individual model terms we used likelihood ratio tests as suggested by Pinheiro and Bates (2001). The size of the likelihood test statistics was also used to compare the relative strengths of the fixed treatment effect and the random species, site, and plot effects.

We inspected the model assumptions for the within-group errors (independent and identically normally distributed within-group errors, with mean zero and constant variance, independent of random effects) as well as the distributional assumptions of the random effects (normally distributed with mean zero) using plots constructed with the R-package asuR (Fabbro 2007) and its inherited packages in R 2.4.1. Stem height and number of leaves were carefully

transformed (see "Results") to avoid violations of model assumptions. We note that for number of leaves a really good model could not be achieved without excluding the seedlings with zero leaves (defoliated or stressed individuals). However, since the results with and without these seedlings were qualitatively the same, we report the models based on all live seedlings.

## Results

The five shade-tolerant study species all experienced good establishment with relatively high survival and growth rates (Table 1). Survival, stem height, and number of leaves after one and six years as a function of the seedling neighbor treatments are shown in Figs. 1, 2. It is clear that the overall effect of the treatments was at most small, although a tendency for lower performance when planted with a conspecific is apparent, in particular for survival (both years) and stem height (2006). These patterns were confirmed by the GLMM and LMM analyses: species identity and to a lesser extent plot and site had strong effects on all aspects of seedling performance (survival, stem height, number of leaves) after both one and six years (Table 2). In contrast, the seedling neighbor treatment had only minor effects on seedling performance (Tables 2, 3, 4); however, the effect was significant for survival after one and six years and number of leaves after one year, although only borderline-significant for stem height after one and six years and number of leaves after six years. In all cases performance was or tended to be lower when growing with a conspecific than with a heterospecific neighbor (Tables 2, 3, 4). However, for number of leaves an additional pattern was present: after one year seedlings planted alone had more leaves than seedlings planted with a neighbor (Table 4). We note that the poor performance in the conspecific neighbor treatment also applied to each species individually in most cases. For 2001, the odds of survival were lowest for the conspecific neighbor treatment for all five species, stem height was shortest for the conspecific neighbor treatment for three of four species (stem height was not measured for the grass *Streptochaeta*), and number of leaves was lowest for the
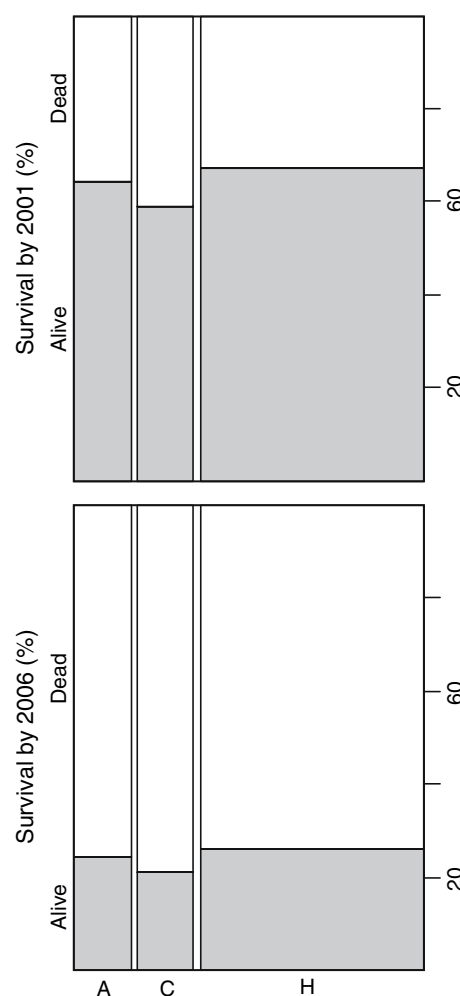


**Fig. 1** Seedling survival after one year (2001) and six years (2006) as a function of treatment (planted alone (*A*), with a conspecific (*C*) or with heterospecific (*H*) seedling). *Bar width* is proportional to sample size

conspecific neighbor treatment for all five species (comparing numbers without testing, results not shown). For 2006, the respective numbers were three out of five, all four, and four of five species. Best performance was seen about equally often in the no-neighbor and heterospecific neighbor treatments, with no obvious species-specific patterns (results not shown).

**Table 1** Seedling survival rate, mean stem height, and mean number of leaves per individual (±SD) after one year (2001) and six years (2006)

|  | Survival (%) 2001/2006 | Stem height (cm) 2001/2006 | Number of leaves 2001/2006 |
|---|---|---|---|
| *Hybanthus* | 71/28 | 8.9 / 22.4 (±3.9/16.9) | 4.0/6.3 (±2.2/5.7) |
| *Lacistema* | 76/41 | 8.1/33.3 (±3.1/19.7) | 6.6/10.9 (±2.8/11.5) |
| *P. limonensis* | 52/19 | 6.8/39.9 (±3.3/31.6) | 4.9/10.9 (±2.6/9.4) |
| *P. marginata* | 68/20 | 5.0/23.7 (±2.3/22.4) | 4.8/13.1 (±2.7/13.5) |
| *Streptochaeta* | 61/18 | –/– | 5.2/12.5 (2.5/8.1) |

**Fig. 2** Seedling stem height and number of leaves after one year (2001) and six years (2006) as a function of treatment [planted alone (*A*), with a conspecific (*C*) or with heterospecific (*H*) seedling]. The data illustrated is the same as in Tables 3, 4. *Box plots* indicate the median and the first and third quartile (the hinges), with the *whiskers* extending to the most extreme data point which is no more than 1.5 times the interquartile range. *Box plot width* is proportional to the square root of the number of observations in a group. *Box plot notches* are constructed so that if the notches do not overlap there is "strong evidence" that the groups have different medians (R Development Core Team 2007)
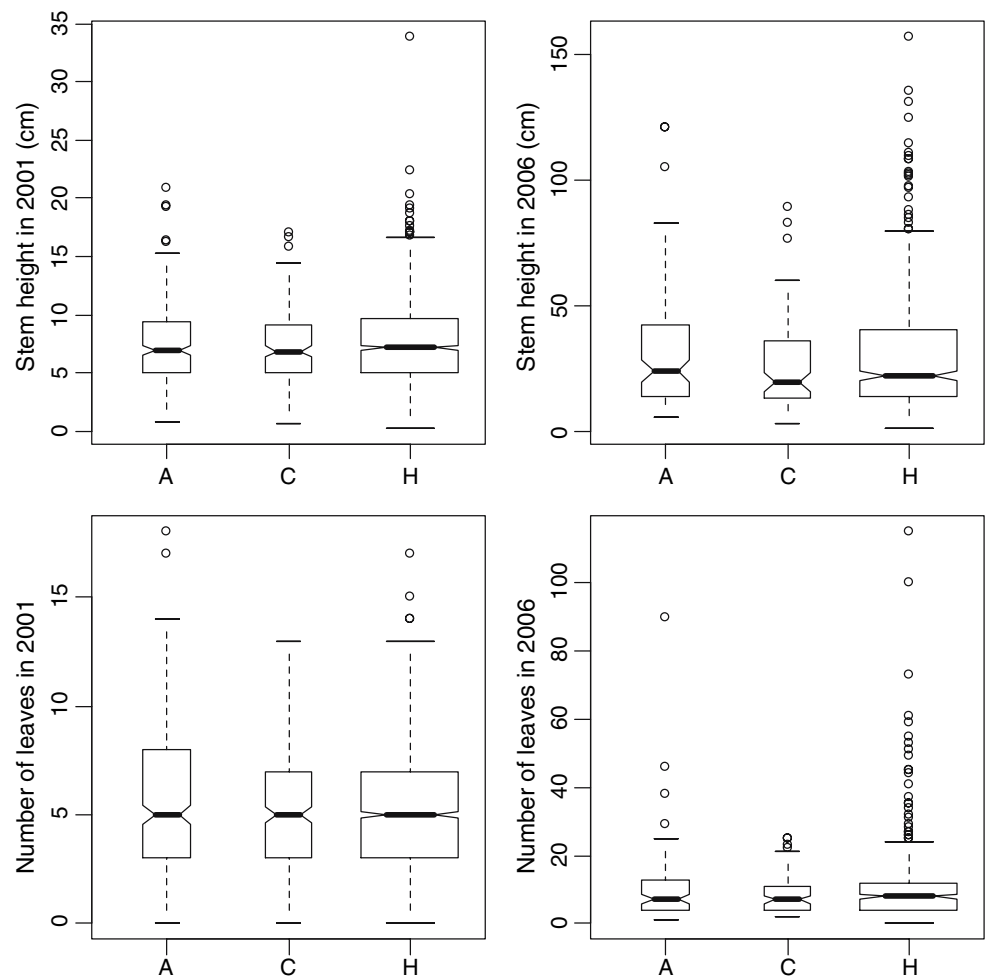


## Discussion

Competition is often argued to be a strong structuring force in plant communities (e.g., Grime 1979; Tilman 1982; Goldberg and Barton 1992; Tilman and Pacala 1993; Coomes and Grubb 2000), and competitive niche partitioning has been proposed to be an important mechanism for the maintenance of high local species richness in humid tropical forests (Ashton 1993; Tilman and Pacala 1993; Kobe 1999; Svenning 1999, 2001; Montgomery and Chazdon 2002; Wright 2002). However, disagreement exists over the relative importance of competition for plant community structure (Callaway and Walker 1997; Crawley 1997; Reynolds 1999). Notably, a controversial view posits that plant communities in tropical forests and other ecosystems are structured by dispersal, and that competition only plays a role as a neutral interaction independent of species identity (Hubbell et al. 1999; Hubbell 2001). As a more radical alternative it has been proposed that the stressed understory environment of humid tropical forests limits total understory plant density to such low levels that competitive exclusion cannot be an important factor limiting the local

diversity of suppressed understory plants (Wright 1992, 2002). The experimental results reported here provide conditional support for the latter view. Field competition experiments manipulate single species in pairwise experiments or large numbers of species simultaneously (Goldberg and Scheiner 1993). Our experiment is the first example of a pairwise competition experiment conducted in tropical forest. Pairwise experiments include a small number of species (five in this study), which limits the extent to which results can be generalized to the community as a whole (Goldberg and Scheiner 1993). However, since our results were relatively consistent among all five study species, i.e., across three growth forms and four distantly related families as well as two congeners, we might expect similar results for most other shade-tolerant plant species from this tropical forest.

The simplest question one can ask about competition is whether it occurs in a given setting (Goldberg and Scheiner 1993). Our experiment was designed to answer this question with respect to seedlings in the tropical forest understory on BCI. Despite purposefully planting seedlings with their roots intermingled to maximize the potential for

**Table 2** Results from generalized linear mixed model (GLMM) analyses of seedling survival after (a) one year (2001) and (b) six years (2006) as a function of treatment [Tmt: planted alone (A), with a conspecific (C) or with heterospecific (H) seedling]

| Survival | Estimates | | Test statistics |
|---|---|---|---|
| (a) 2001 | | | |
| Tmt | Odds ratio | | $\chi^2_{(2)} = 15.2$*** |
| | A vs. C + H: | 1.06 | $z = 0.51$ |
| | C vs. H: | 0.63 | $z = -3.96$**** |
| Species | Variance: | 0.23 | $\chi^2_{(1)} = 97.8$**** |
| Site | Variance: | 0.83 | $\chi^2_{(1)} = 15.8$**** |
| Plot (site) | Variance: | 0.55 | $\chi^2_{(1)} = 183.5$**** |
| $n$ | | | 3,000 |
| (b) 2006 | | | |
| Tmt | Odds ratio | | $\chi^2_{(2)} = 6.6$* |
| | A vs. C + H: | 1.08 | $z = 0.56$ |
| | C vs. H: | 0.71 | $z = -2.55$* |
| Species | Variance: | 0.31 | $\chi^2_{(1)} = 122.1$**** |
| Site | Variance: | 0.52 | $\chi^2_{(1)} = 9.3$** |
| Plot (site) | Variance: | 1.18 | $\chi^2_{(1)} = 193.5$**** |
| $n$ | | | 3,000 |

Also included in the analyses were the random effects of species identity, site, and plot, nested within site (plot (site))

*$P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ****$P < 0.0001$

**Table 3** Results from linear mixed model (LMM) analyses of seedling stem height after (a) one year (2001) and (b) six years (2006) as a function of treatment [Tmt: planted alone (A), with a conspecific (C) or with heterospecific (H) seedling]

| Stem height | Estimates | | Test statistics |
|---|---|---|---|
| (a) 2001 | | | |
| Tmt | Mean difference | | $\chi^2_{(2)} = 5.46$† |
| | A vs. C + H: | 0.050 | $t = 0.20$ |
| | C vs. H: | −0.548 | $t = -2.28$* |
| Species | Variance: | 4.44 | $\chi^2_{(1)} = 399$**** |
| Site | Variance: | 2.18 | $\chi^2_{(1)} = 18.9$**** |
| Plot (site) | Variance: | 2.75 | $\chi^2_{(1)} = 150$**** |
| $n$ | | | 1,596 |
| (b) 2006 | | | |
| Tmt | Mean difference | | $\chi^2_{(2)} = 5.64$† |
| | A vs. C + H: | 0.0894 | $t = 1.43$ |
| | C vs. H: | −0.142 | $t = -2.26$* |
| Species | Variance: | 0.103 | $\chi^2_{(1)} = 110$**** |
| Site | Variance: | 0.110 | $\chi^2_{(1)} = 21.8$** |
| Plot (Site) | Variance: | 0.066 | $\chi^2_{(1)} = 33.1$**** |
| $n$ | | | 644 |

Also included in the analyses were the random effects of species identity, site, and plot, nested within site (plot (site)). Stem height in 2001 was $\sqrt{y} + \sqrt{(y+1)}$ transformed, while stem height in 2006 was $\log(y)$ transformed. Only live individuals were considered, and the herbaceous species *Streptochaeta* was not included in the analyses

†$P < 0.10$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$

**Table 4** Results from linear mixed model (LMM) analyses of the number of leaves per seedling after (a) one year (2001) and (b) six years (2006) as a function of treatment [Tmt: planted alone (A), with a conspecific (C) or with heterospecific (H) seedling]

| Leaf number | Estimates | | Test statistics |
|---|---|---|---|
| (a) 2001 | | | |
| Tmt | Mean difference | | $\chi^2_{(2)} = 18.7$**** |
| | A vs. C + H: | 0.262 | $t = 3.62$* |
| | C vs. H: | −0.247 | $t = 3.41$* |
| Species | Variance: | 0.188 | $\chi^2_{(1)} = 227$**** |
| Site | Variance: | 0.150 | $\chi^2_{(1)} = 20.5$**** |
| Plot (site) | Variance: | 0.150 | $\chi^2_{(1)} = 80.9$**** |
| $N$ | | | 1,959 |
| (b) 2006 | | | |
| Tmt | Mean difference | | $\chi^2_{(2)} = 4.98$† |
| | A vs. C + H: | 0.0795 | $t = 1.30$ |
| | C vs. H: | −0.134 | $t = -2.15$† |
| Species | Variance: | 0.0216 | $\chi^2_{(1)} = 103$**** |
| Site | Variance: | 0.0676 | $\chi^2_{(1)} = 19.5$*** |
| Plot (site) | Variance: | 0.0749 | $\chi^2_{(1)} = 7.94$** |
| $N$ | | | 750 |

Also included in the analyses were the random effects of species identity, site, and plot, nested within site (plot (site)). Leaf number in 2001 was $\sqrt{y} + \sqrt{(y+1)}$ transformed, while leaf number in 2006 was $\log(y+1)$ transformed. Only live individuals were considered

†$P < 0.10$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$

competition, we only found evidence for a minor effect of seedling interactions. The experimental neighbor treatment did, however, consistently affect seedling performance. Nevertheless, the effect was always very small both in absolute terms and relative to the much stronger species and microsite (especially plot) effects. The strong species effects are consistent with previous studies of tropical forest species (e.g., Kitajima 1994; Kobe 1999; Svenning 2001; Montgomery and Chazdon 2002; Barberis and Tanner 2005). Given that plots at each site were located across a small gap center to understory gradient, the strong plot effect at least partly reflects this gradient in light availability and other gap-related environmental factors. The strong influence of light availability on the abundance and performance of shade-tolerant seedlings is well-known in humid tropical forests (e.g., MacDougal and Kellman 1992; Kitajima 1994; Cintra and Horna 1997; Kobe 1999; Svenning 2000, 2002; Montgomery and Chazdon 2002; Paz and Martínez-Ramos 2002).

What is the nature of the weak but consistent seedling neighbor treatment effects? If competitive interactions occur among neighboring seedlings, seedlings without neighbors should perform best and seedlings with conspecific neighbors should perform worst. This expectation was only partially fulfilled. Seedlings with a conspecific

neighbor consistently performed worse than seedlings with a heterospecific neighbor. However, having no neighbor only resulted in superior performance relative to the con- and heterospecific neighbor treatments for one performance measure (number of leaves) in one year (2001). If the negative interactions between conspecifics are not caused by competition, but instead reflect facilitation of species-specific pests, this could potentially be more consistent with negative interactions being restricted to conspecific neighbors. It would not matter for seedling performance if a seedling was grown with a heterospecific or without neighbors, as only conspecific neighbors would interact. Strong negative conspecific density-dependence has been reported for the BCI seedling community and is believed to be mediated by pests (Augspurger and Kelly 1984; Harms et al. 2000; Gilbert et al. 2001; Wright et al. 2005). However, competition and pest facilitation can make very similar predictions in terms of seedling performance, and our results do not allow us to conclude in favor of either hypothesis.

Our results provide evidence for negative interactions among seedlings in the understory of tropical semi-deciduous forest on BCI. However, the strength of the interactions was small for all measures of seedling performance and was nearly exclusively between conspecifics. As we purposefully planted experimental seedlings with their roots intermingled to maximize the possibility of detecting interactions, we conclude that interspecific interactions are relatively unimportant for seedling performance during the first year of seedling life as well as during the subsequent establishment phase and clearly less important than intrinsic variability among species or variation in microsite conditions. The experimental removal of a large portion of all understory plants has twice had no detectable effect and once had mixed effects on those understory plants left in situ (Marquis et al. 1986; Brown and Whitmore 1992; Benitez-Malvido 2006). Again, the evidence suggests that negative interactions among understory plants are relatively weak. Under more fertile soil and wetter, less seasonal climatic conditions, understory plant densities can exceed those on BCI and competitive interactions may be stronger (Harms et al. 2004). Additional pairwise competition experiments and understory thinning experiments are needed to determine whether direct negative interactions occur among understory plants at later life stages, among other species, and for other tropical forests. In the meantime, the available evidence suggests that direct competitive interactions are relatively unimportant among understory plants in humid tropical forests, and thereby provide support for the hypothesis that competitive exclusion is not an important factor limiting the local diversity of understory plants in humid tropical forests (Wright 1992, 2002).

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