Lack of Interspecific Plant Competition With a Dominant Grass in the Understory of a Lowland Forest in Colombia

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ABSTRACT

I analyzed a natural experiment of competition involving a dominant herb in Tinigua Park, Colombia. *Pharus virescens* is a dominant monocarpic grass that synchronously produces seeds once every 5 yr, after which all individuals die. I found no difference in species richness, density, or diversity comparing plots with and without the grass in 381 quadrats (4 m²) and there was no negative relationship between the abundance of the grass and that of other plants.

**Key words:** *Pharus virescens*, seedling species richness; Tinigua National Park; tropical rain forest; understory plant density.

**WESTERN AND CENTRAL AMAZONIAN TROPICAL FORESTS** are known to be some of the most diverse ecosystems on earth (Ter Steege *et al.* 2003). Various theories have been proposed to explain geographical patterns of plant diversity, but we still know relatively little about the influence that each of the proposed factors has on diversity, and different mechanisms may play different roles in different localities. Wright (2002) stressed that there is good empirical evidence indicating the importance of niche differences, host-specific pests, and density-dependent effects as the main factors promoting plant diversity. Furthermore, he proposed a stronger competitive effect of adult plants on seedlings than among seedlings (Coomes & Grubb 2000, Lewis & Tanner 2000). In these scenarios, competition among seedlings and herbs may not be an important cause driving competitive exclusion between species in tropical forests. However, there is evidence that, under some conditions, understory plants may limit seedling populations (Harms *et al.* 2004, Wang *et al.* 2004), and aboveground- and belowground competition in tropical plants may affect growth and seedling survival (Coomes & Grubb 1998, Barberis & Tanner 2005).

Some influential hypotheses are based on the idea that plant competition may be strong enough to affect diversity patterns. For example, it has been proposed that limited recruitment promotes species diversity because it lowers the potential that the better-adapted species have to exclude less-fit sympatric species (Hurtt & Pacala 1995, Hubbell *et al.* 1999). Although some theories on plant diversity are based on the effect of strong interspecific plant competition, there are only a few studies testing its strength in tropical forest and the results differ among studies and ecological settings (Marquis *et al.* 1986, Brown & Whitmore 1992, Goldberg & Barton 1992, Coomes & Grubb 1998, Barberis & Tanner 2005). The purpose of this study was to describe the results of a natural experiment to test the effect of removing the dominant grass species on the density and diversity of plants in the understory of a lowland tropical rain forest.

The study area was the CIEM (Centro de Investigaciones Ecológicas La Macarena), located on the west margin of Rio Duda (240’ N, 7410’ W, 350–400 m asl.), Departamento del Meta, Colombia. The station trail system covers at 4 km² at the eastern border of Tinigua National Park (201,875 ha). Rainfall is seasonal in the region, with a 2–3 mo dry period occurring between December and March. Average annual precipitation during three study years was 2782 mm (Stevenson 2002). The topography of the area includes relatively flat flooded areas along the river and hilly upland terra firme forests (Stevenson 2002).

**Terra firme forests** are dominated in the understory by *Pharus virescens* Doell. This species ranked first according to an importance index based on relative density and frequency in 30 4-m² quadrats (Index = 84.3 vs. 58.8 for the second species, Stevenson 1995). It was estimated that this species reaches 10,587 individuals/ha in nonflooded forests, and it was present on 63 percent of 381 4-m² plots with a range of abundance of 0–20 individuals (Stevenson 2002). *Pharus virescens* leaves grow from partly erect pseudo-rhizomes, and clumps of leaves can reach 50 cm in height (Fig. 1). It is a monocarpic bambusoid grass that produces seeds simultaneously only once every 5 yr (Kobayashi & Izawa 1992). Most seeds are dispersed by epizoochory between September and December in each reproductive year (e.g., 1990, 1995, and 2000). Afterwards, the whole population dies off, leaving open space in the understory for about 2 yr. The remaining seeds germinate in the rainy season of the year following seed production, producing a new generation (Kobayashi & Izawa 1994). Thus, the reproductive episodes of this species provide more light and nutrients for other plants in years following reproduction (e.g., 1996, 2001), which might release other species from aboveground and belowground competition (Coomes & Grubb 1998, Lewis & Tanner 2000).

If interspecific competition with this grass affects the density or diversity of other plant species on the forest floor, I expected to find the following patterns: (1) Among years: a higher number of individuals and a higher diversity when *P. virescens* was absent than when it was fully grown; (2) Among plots: a negative association between the abundance of the grass and that of other plants. To assess the
influence of competition of this dominant species on diversity and individual densities. I compared density and diversity of seedlings and herbs (defined as all plants <1 cm dbh) between some years when *P. virescens* was dominant (2 yr before fruit set) and when it was absent or very small (2 yr after reproduction). Average plant height in some plots, excluding *P. virescens*, was 22.5 cm (SE = 2.1, N = 87), and <10 percent of the individuals in these plots were taller than fully grown *P. virescens*, suggesting there are few well-developed individuals in the plots that may not be overshadowed by the grass and thus are free from aboveground competition with the grass.

I measured the density and diversity of plants in the understory using 4-m² quadrats either along line transects or within 1-ha plots (Stevenson 2002). When quadrats were located on transects, each was set every 50 m, 2 m from the path, and the direction was set randomly among four cardinal directions. When the plots were located within larger plots, each was located in a corner of a 10 × 10-m subplot (the corner chosen at random). I censused a total of 208 plots in years when *P. virescens* was fully grown (73 in 1994, 68 in 1999, and 67 in 2000), and 173 when it was absent or small (14 in 1996 and 159 in 2001). None of the plots established in different years coincided in location because identification of seedlings generated some perturbation and death of plants, and thus, this methodology might change density and diversity patterns for recensused plots. I identified all individuals within the plots (<1 cm dbh) following nomenclature in Stevenson et al. (2000); otherwise, I assigned each plant to a particular morphotype and counted the number of individuals of each species or morphotype. I excluded recently germinated seedlings (*i.e.*, seedlings without true leaves). For some species with rhizomes, I calculated density from the number of apparently independent individuals (*i.e.*, without subterranean connections).

I estimated plant diversity as species richness (the number of species in each 4-m² plot) and the number of species per stem was also analyzed to assess the importance of density on species richness (Hubbell et al. 1999). I also used Fisher’s alpha index of diversity, which produced quantitatively similar results than species per stem (data not shown). I ran *t*-tests and ANOVA to test for differences in species and individual densities, using the JMP program (SAS Institute 1994). I used *a posteriori* Tukey–Kramer tests to assess differences between particular years. The analyses among years were performed excluding individuals of *P. virescens*, the ones that are forming the competing matrix. However, the inclusion of the species gave quantitatively similar results (data not shown). A linear regression analysis was done between the number of fully grown *P. virescens* individuals and the number of other plants.

I found that the mean number of individuals in plots was similar between periods when *P. virescens* was fully grown and virtually absent (fully grown: mean = 40.6, SE = 1.1, N = 208; absent: mean = 39.7, SE = 1.2, N = 173; t = −0.56, P = 0.58). I found differences in plant density among years (F = 18.9, P < 0.001), but the pattern did not consistently show fewer species in years when *P. virescens* was present (Fig. 1A). In fact, *a posteriori* comparisons showed higher density in 1999 than in any other year, when the grass was fully grown.

I recorded a total of 484 plant species in the plots and ca 200 additional morphotypes that were not identified to species level. I found the mean number of species/quadrat to be similar between periods when *P. virescens* was fully grown and absent (fully grown: mean = 22.9, SE = 0.52; absent: 23.6, SE = 0.57; t = 0.92, P = 0.36, sample size as before). Although I found differences in species richness among years (F = 14.2, df = 4, P < 0.001), the pattern followed a similar trend as the one found for density (Fig. 1B). Actually, the mean number of species was highest in 1999 when *P. virescens* was tall (although the difference was not statistically different between 1999 and 1994).

The number of species per stem showed no differences between periods with and without *P. virescens* (fully grown: mean = 0.58, SE = 0.01; absent: mean = 0.55, SE = 0.01, t = 1.61, P = 0.11). I found differences among years (F = 5.54, df = 4, P = 0.0002; Fig. 1C), and the lowest mean values were found in 1999, in sharp contrast with previous analyses. *A posteriori* analyses showed more species per stem in both 2000 and 2001 than in 1999.

Using years as replicates to compare species richness, density, and diversity implies a very limited analysis, with only 3 yr with full grown *P. virescens* and two without them. The results indicated that none of the parameters showed differences (mean species richness: 23.3 ± 2.0 vs. 23.3 ± 2.4 SE; density: 41.3 ± 4.8 vs. 38.1 ± 5.8; species per stem: 0.60 ± 0.02 vs. 0.63 ± 0.03; all χ² < 0.34, P > 0.55).

At the plot level, the number of fully grown *P. virescens* individuals was not a good predictor of species richness, density, nor species per stem (Fig. 1; all R² < 0.03, F < 0.1, P > 0.66, N = 381). Similarly, I found no significant relationship between the abundance of the grass and the density of seedlings of trees and lianas, excluding herbs (F = 0.09, P = 0.77).

In summary, the results of this study do not support predictions of the hypothesis that there is competition between understory plants and the dominant *P. virescens*. Neither overall diversity nor species density increased when this grass was virtually absent, and there were no signs of consistent delayed responses. For instance, according to delayed responses from competition with *P. virescens*, one should expect a similar pattern along the 5-yr cycle, but in the first fruiting episode density was similar one year before and one year after production (1994–1996) and in second episode density decreased between 1999 and 2001 (Fig. 1A).

The highest number of species found in 1999 were mainly driven by differences in plant density and might be caused by annual variation in seed predation, seed production patterns, or climatic factors (Engelbrecht & Kursar 2003, Bunker & Carson. 2005, Wright et al. 2005, Norden et al. 2007). Since a large number of plots were randomly situated on well-drained terra firme forests, it is unlikely that biased patterns in local conditions are generating the differences among years. Future studies would be necessary to establish the causes originating differences in seedling densities in this system.

The results of this study show that, at least in this tropical forest, competition with a dominant understory species is not the main factor controlling diversity patterns of seedlings and herbs. The results are consistent with some studies showing a weak
influence of interspecific competition among understory plants on diversity (Marquis et al. 1986). It could be that seed predation and early seedling mortality is high enough to keep seedlings at such low numbers that, in general, they do not strongly compete. It is also possible that these effects are not apparent in our system, because of the short window of time when the grass is fully grown, which contrast with other studies where long-lived understory palms limit seedling growth and survival (Harms et al. 2004, Wang & Augspurger 2004). Therefore, the results do not rule out the possibility of competition among species other than *P. virescens*, or competition between adult plants and seedlings (Wright 2002). It would be necessary to undertake experiments to test whether canopy plants or other plants reduce seedling densities, which may be caused by root or light competition (Coomes & Grubb 2000).

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SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: www.blackwell-synergy.com/loi/btp

Figure S1. (A) View of the understory of a mature forest with a high density of *Pharus virescens* in Tinigua National Park, Colombia. This photograph was taken in 1994, when the grass was about 3-yr old. Each ramet may shade an area of approximately 0.2 m². (B) Recently germinated *P. virescens* seedlings growing on the forest soil in 1991 after a reproductive year (courtesy of M. Kobayashi).

LITERATURE CITED


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