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SHRUB- VS. GRASS-PATCH EFFECTS ON THE SEED RAIN AND SEED BANK OF A FIVE-YEAR PASTURE IN PUERTO RICO

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INTRODUCTION

The conversion of tropical forests for pasture and agriculture is the main cause of deforestation in the Neotropics (Uhl *et al*. 1988, Fearnside 1993), and hence recovery of these areas after abandonment affects critical tropical social and ecological issues (Borhidi 1988). To begin an understanding of the recovery process, researchers must have knowledge of pasture structural phases over time. In the beginning, processes are dominated by the past crop in a field which is either seeded (e.g., for pastures *Setaria sphacelata* can be used: Myster 2004a,b) or invading naturally (*Panicum* sp. and *Brachiaria subquadripara* in the study pasture: Myster 2003b) due to the actions of cattle, such as soil compaction, hummock creation, and dung deposition. This is followed by the patch dynamics of remnant past crops, grasses, forbs, ferns, and predominantly asexual shrubs (e.g., *Cordia multispicata*, *Psidium guajava*, *Baccharis trinervis*, and *Miconia* sp. in the tropics [Vieira *et al.* 1994, Holl 1998b, Zahawi & Augspurger 1999, Holl 2002, Myster 2003b] and *Rhus* sp. in temperate old fields [Myster 1993]). Then we have the invasion of trees in microsites created by those patch dynamics, and finally the closed canopy of a secondary forest is created (see Uhl 1987, Uhl *et al*. 1988, Nepstad *et al*. 1996).

These structural phases have been observed in long-term permanent plot sampling in five pastures, which is part of the Long-Term Ecological Research Program in the Luquillo Mountains of Puerto Rico (http://luq.lternet.edu, Myster 2003b). Included in that research is one pasture in particular that has been extensively studied for processes ranging from trace gases and atmospheric fluxes (Reiners *et al*. 1994) to exotic earthworms and decomposition (Liu & Zou 2002), as well as various plant regeneration mechanisms (Zimmerman *et al*. 2000, Myster 2003a,c, unpublished data). What has been needed in these research projects is a patch-wise approach that combines sampling of the regeneration mechanisms controlling seed availability with synthesis of field-experiment patch effects on those seed and seedling mechanisms that control survival and growth (Myster 2004b). These mechanisms are critical to an understanding of forest recovery in an abandoned pasture because they drive the individual plant-plant replacements that may lead to the changes in composition called "succession" (Myster 2001).

For these reasons, and because of the low levels of advanced regeneration after agriculture (Purata 1986, Uhl *et. al*. 1988), I sampled both the seed rain, by setting out seed traps, and the seed bank, by germinated soil samples, in grass and shrub patches of a five-year-old Puerto Rican pasture. I compared species composition, species richness, seed and seedling abundances, and alpha diversity (appropriate in tropical studies: Valencia et al. 1994) between those patch types. Finally, I synthesized several studies done in this specific pasture and these specific patch types, covering all plant regeneration mechanisms, in order to more deeply understand pasture patch dynamics and restoration.

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STUDY SITE AND METHODS

This study was conducted in the Luquillo Experimental Forest (LEF) Puerto Rico, USA (18°20'N, 65° 45'W; Myster & Fernandez 1995). LEF is located between 325 m and 1080 m in elevation, experiences between 2 m and 5 m of rainfall a year, and is classified as tropical lower montane wet forest (Edministen 1970). February to April is the dry season with an average monthly rainfall of 0.22 m and a mean temperature of 24° and September to December is the wet season with an average monthly rainfall of 0.32 m and a mean temperature of 27° (Garcia-Mantiel 1996). The study pasture is 4 ha in size, borders the northwest corner of the LEF near the town of Sabana, Puerto Rico at 350 m elevation (Zou & Gonzalez 1997), and has been abandoned since 1996. Before that, it had been in agriculture and pasture since 1936 (Myster 2003b). Currently, the pasture consists of a mosaic of patches where trees from the forest are slowly invading microsites created by advancing shrubs (Myster 2003a).

Seed rain and seed bank were sampled in the pasture starting in March 2001. Seed rain was collected in 1-m^2 area seed traps and identified to species after five months in the field (protocol also used in Myster & Fernández 1995, Myster & Sarmiento 1998). The traps were constructed with a 5-cm^2 wire mesh on top to deter seed predators with cloth underneath for collecting seeds that fall through the mesh, and with 1-m plastic PVC poles both for support and for keeping the traps off the ground to reduce predation. The traps were placed in the center of each of five grass patches and of each of five *Miconia* sp. shrub patches. The patches were chosen randomly between 10 and 20 m from the forest edge to reduce possible confounding forest edge effects (as seen in Myster & Pickett 1993, Myster 2003a).

To estimate the seed bank, in March 2001 one soil sample was collected in each of the ten patches by insertion of a 12-cm diameter metal ring into the soil to a depth of 10 cm. This depth was used because recruitment is typically limited to the uppermost soil layers (Vazquez-Yanes & Orozco-Segovia 1993). From each sample, a 10-g (approximately 10% of the total sample) horizontal ground layer sub-sample was removed after mixing and germinated by spreading the soil on top of sterile potting mix at a 1-cm thickness. Germination was monitored for three months in a greenhouse located at the LTER research station in the LEF (also see Myster & Fernandez 1995), after which Liogier & Martorell (1982) was used as the taxonomic source to identify the germinated seedlings. Fisher's alpha diversity (a diversity index independent of sample size recommended for the Neotropics: Valencia *et al.* 1994) was computed for seeds and seedlings in both patch types, using the procedure in Rosenzweig (1995). Finally, statistical analysis consisting of one-way analysis of variance (SAS 1985) was performed on seed and seedling parameters, where treatment groups were defined by patch type and individual seed process (i.e., seed rain, seed bank).

RESULTS

Approximately half of the species were found in both the seed rain and the seed bank (Tables 1, 2), and these

TABLE 1. Total trapped seeds in the five grass patches and five shrub patches of a five-year-old Puerto Rican pasture. Lifeforms are tree (T), shrub (S), vine (V), forb (F) and graminoid (G).

Species	lifeform	grass patch	shrub patch
Mimosa sp.	H	3	0
Miconia prasina	S	13	326
Tabebuia heterophylla	T	0	3
Nepsera aquatica	H	16	0
Desmodium spp.	H	5	5
Ipome setifera	H	1	2
Total species		5	4
Total seeds		41	336
Alpha diversity		1.78	1.01

TABLE 2. Total germinated seedlings in the five grass patches and five shrub patches of a five-year-old Puerto Rican pasture. Lifeforms are tree (T), shrub (S), vine (V), forb (F) and graminoid (G).

Species	lifeform	grass patch	shrub patch
Panicum maxima	G	20	20
Urena lobata	H	0	1
Miconia prasina	S	0	4
Nepsera aquatica	H	5	0
Hedyotis corymbosa	H	9	10
Paspalum millegrana	G	25	10
Desmodium spp.	H	2	0
Unknown fern		3	2
Total species		6	6
Total seedlings		64	47
Alpha diversity		1.69	1.78

species (forest understory shrub *Miconia prasina* and pasture herbs *Nepsera aquatica*, *Desmodium* spp.) maintained their relative loads in specific patch types regardless of seed process. In addition, for both processes *Nepsera aquatica* was the only species to be present in the grass patches, but not in the shrub patches. Species richness was significantly greater in the seed bank (eight in total) compared to the seed rain (six in total: F = 6.52, df = 1, p = 0.03), with little species richness difference between patch types within each seed process. In particular, woody seeds were greater under shrub patches for both seed processes (F = 12.22, df = 1, p = 0.005). The total number of dispersed seeds in the shrub traps was significantly greater than in the grass traps (F = 30.32, df = 1, p = 0.0001), whereas the total number of emerged seedlings from soil samples was significantly greater in the grass patches (F = 8.72, df = 1, p = 0.01). The number of seedlings in the seed bank was less compared with the seed rain (F = 15.22, df = 1, p = 0.004). Finally, alpha diversity was greatest for seed traps in the grass patches compared with the shrub patches (F = 14.66, df = 1, p = 0.001) and for emerged seedlings in the shrub patches compared with the grass patches (F = 5.66, df = 1, p = 0.004).

DISCUSSION

Total seed rain was comparable with pastures in Colombia (Aide & Cavelier 1994) and Costa Rica (Holl 1998a,b, 2002), but more seedlings emerged in Ecuadorian fields (Myster 2004a), Brazilian fields (Garcia 1995, Nepstad *et al.* 1996), and in pastures in Colombia (Aide & Cavelier 1994). However, milpa fields (corn, squash, and beans grown together) in Mexico (Quintania-Ascencio *et al.* 1996) had more seedling emergence from soil samples than the study pasture. *Miconia* spp. were the most common genus among these studies. In general, the number of seedlings in the seed bank was less (Vazquez-Yanes & Orozco-Segovia 1993, Myster 2004a) compared to the seed rain (F = 15.22, df = 1, p = 0.004) with woody species rare everywhere (Nepstad *et al.* 1996, Zimmerman *et al.* 2000).

These same patches and pasture were also used for both a seed predation and a seedling survivorship/growth field experiment. The results of the seed predation study (Myster 2003c) showed (1) patch type effects, where seed survivorship was higher for seeds in the *Miconia* spp. patches (mean of 35%) compared with seeds in the grass patches (mean of 31%), (2) species effects, where 50% of the seeds of the tree species *Syzygium jambos* remained after two weeks, *Solanum torvum* had 35% remaining, *Piper aduncum* 21%, and the shrub *Miconia prasina* 24%, and (3) species x patch type interaction effects, where *M. prasina* had 3% mean seeds remaining in the grass patches vs. 33% mean seeds remaining in the *Miconia* sp. patches. In addition, in a seedling experiment done in this same pasture and these same patch-types (Netherton 2003) survivorship did not differ between patch types and most seedlings survived after 10 months in the field. However, *Tabebuia heterophylla* seedlings grew more in grass patches compared with *Miconia* spp. patches, but *Guarea guidonia* and *Inga laurina* showed no significant patch differences. Finally exclusion of below-ground competition increased growth for all three tree species, with the greatest effect occurring when covering vegetation was also clipped.

Putting all these same pasture studies together allows a more complete understanding of how regeneration mechanisms vary between patch types and how they may result in patch dynamics. The most basic result is that pasture succession is species-specific (see Myster 1993), with grass or shrub patches having both positive and negative effects depending on species and regeneration mechanisms at work. In general, grass patches had more germinated seedlings and more seedling growth but shrub patches had more dispersed seeds and less seed predation. These facilitating shrub effects have been shown elsewhere in the Neotropics (e.g., Vieira *et al.* 1994, Rhodes *et al.* 1998, Holl 2002).

In general in the Neotropics, animal dispersal is more important than wind dispersal in providing seeds to disturbed areas, and such dispersal is best facilitated when the vegetation is complex enough to provide perches and cover for animals (Wunderle 1997) as happens with shrub invasion. In fact several researchers have found more seeds under shrubs compared with other patches or kinds of plant cover (Uhl *et al.* 1982, Guevara *et al.* 1986, Willson and Crome 1989, Guevara *et al.* 1992, Vieira *et al.* 1994, Silva *et al.* 1996). In addition results here show an order of magnitude increase of seeds under *Miconia* spp. shrubs compared with grass patches, just as Vieira *et al.* (1994) found under *Cordia multispicata* shrubs.

Furthermore, several general results from temperate pasture/old field studies relate well to this study being also species-specific and patch-type dependant: (1) woody patches inhibited tree seedling growth (Burton 1989) with more seed predation (Myster & Pickett 1993) and seed dispersal (McDonnell & Stiles 1983) than other patches, with a net result of greater established tree seedling densities in woody patches (Myster & Pickett 1992a); (2) the seed bank for tree seeds was low (Gill & Marks 1991), and (3) facilitation was suggested when woody litter inhibits herbaceous growth and shrubs can reduce competition from grass and herbs, increase seed germination, and bring up nutrients from deep soil layers (see Myster 1993).

Finally, results from the several studies done in this Puerto Rican pasture may lead to better restoration strategies. In particular, synthesis with other similar studies suggests that (1) seeds and seedlings should be added near patches where they occur naturally (see Myster 2003b), (2) nutrients should be added to patches low in them (Rhodes *et al.* 1998), (3) substrate materials should be added to patches exposed to the sun in order to reduce desiccation and enhance germination, (4) exotic species should be removed, especially those known to inhibit trees, and (5) saplings, small trees, and shrubs should be planted in the pasture to act as recruitment foci or nurse trees as seen in this study and elsewhere (Holl 1998, 2002). Long-term sampling of pastures (Myster 2003b) and association analysis of such data (Myster & Pickett 1992b) may also be used to suggest key species for these pasture additions, in order to facilitate the key pasture recovery process of tree invasion and growth.

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