

## The Demography of *Miconia prasina* (Melastomataceae) During Secondary Succession in Puerto Rico

John B. Pascarella<sup>1,2,3</sup>, T. Mitchell Aide<sup>3</sup>, and Jess K. Zimmerman<sup>4</sup>

<sup>2</sup>Department of Biology, Valdosta State University, Valdosta, Georgia 31698, U.S.A.

<sup>3</sup>Department of Biology, University of Puerto Rico-Río Piedras, PO Box 23360, San Juan, Puerto Rico 00931, U.S.A.

<sup>4</sup>Institute for Tropical Ecosystem Studies, University of Puerto Rico-Río Piedras, San Juan, Puerto Rico 00936, U.S.A.

### ABSTRACT

*Miconia prasina* (Melastomataceae) is an important colonizing species during early stages of secondary succession in Puerto Rico but its abundance declines with increasing stand age. We studied its demography for 2 yr (1995–1997) in three populations across a pasture to forest chronosequence (1-, 12-, and 25-yr old) and in one population in a hurricane-disturbed older forest (>60-yr old). Vegetative growth was positive in the two young sites, but negative in the two older sites. The highest percentage of plants that flowered occurred in the two younger sites but highest seed production occurred in the 25-yr-old site. Although seed germination occurred in the two older sites, no seedlings established. Vegetative reproduction (root sprouts) was found in all sites, with most sprouts occurring in young sites. The 2 yr of census data were used to construct stage-based transition matrices. In the two young sites, the average population growth rate was positive ( $\lambda > 1$ ), while average population growth was negative in the two older sites ( $\lambda < 1$ ). Elasticity, a measure of the effects of proportional changes in life-history transitions to the long-term population growth rate, varied across both stages and sites. Elasticity shifted from large plants in young sites to small plants in older sites. Across all sites, elasticities related to survival were more important than those of growth or vegetative reproduction. The demographic analysis supported the previous observations of changes in the density of *M. prasina* based on the chronosequence and also suggests that establishment via seeds must occur prior to abandonment in active pastures.

### RESUMEN

*Miconia prasina* (Melastomataceae) es una especie colonizadora durante las etapas tempranas de sucesión secundaria en Puerto Rico, pero su abundancia declina con la edad del bosque. Nosotros estudiamos su demografía durante dos años (1995–1997) en tres poblaciones a lo largo de una cronosecuencia de pastizales a bosque (1, 12, y 25 años de edad) y en una población en un bosque perturbado por un huracán (>60 años de edad). El crecimiento vegetativo fue positivo en los sitios jóvenes, pero negativo en los sitios viejos. El mayor porcentaje de plantas que florecieron ocurrió en los sitios jóvenes, pero la mayor cantidad de semillas fue producida en el sitio de 25 años. Aunque la germinación de semillas ocurrió en los dos sitios viejos, ninguna plántula se estableció. Se encontró reproducción vegetativa (por plántulas establecidas por yemas de las raíces) en todos los sitios, con la mayoría de estas plántulas encontradas en los sitios jóvenes. Los dos años de datos de censo se utilizaron para construir matrices de transición. En los sitios jóvenes, el crecimiento promedio de la población fue positivo ( $\lambda > 1$ ), mientras que el crecimiento promedio fue negativo ( $\lambda < 1$ ) en los dos sitios viejos. La elasticidad, definida como una medida del efecto de los cambios proporcionales en las tasas de transición en el crecimiento poblacional a largo plazo, cambió con respecto a los tamaños y sitios. La elasticidad fue la más alta en las plantas de tamaños grandes en los sitios jóvenes mientras que en los sitios viejos las plantas de tamaños pequeños tuvieron la elasticidad más alta. En todos los sitios, las elasticidades relacionadas a la sobrevivencia fueron más importantes que las relacionadas al crecimiento o reproducción asexual. El análisis demográfico apoyó las observaciones previas de los cambios de abundancia de *Miconia prasina* en una cronosecuencia y sugiere que el establecimiento por semilla debe ocurrir antes del abandono en pastizales activos.

**Key words:** chronosequence; matrix model; Melastomataceae; *Miconia prasina*; pioneer; Puerto Rico; succession; tropical forest regeneration.

AS THE AREA OF SECONDARY FORESTS CONTINUES TO GROW (Rudel *et al.* 2005, Zhang *et al.* 2005), knowledge of the ecology and successional dynamics of secondary tropical forests will be critical for protection of biodiversity, maintenance of ecosystem services, and sustainable forestry use (Finegan 1996, Guariguata 2000, Chazdon 2003). One approach to study tropical secondary forest succession is through the use of chronosequences, the use of sites of varying ages to infer successional processes (Saldarriaga *et al.* 1988, Grau *et al.* 1997, Montgomery & Chazdon 2001, Gonzalez-Iturbe *et al.* 2002, Kennard 2002, Oliveira *et al.* 2004). In the Caribbean island of Puerto Rico, chronosequence studies have been used to examine forest regeneration from both anthropogenic land use (Aide *et al.* 1995, 2000; Rivera & Aide 1998; Pascarella *et al.* 2000; Marciano-

Vega *et al.* 2002) and natural disturbances such as hurricanes (Zimmerman *et al.* 1995, Aide *et al.* 1996, Pascarella *et al.* 2004) and landslides (Guariguata 1990, Myster & Walker 1997).

One of the limitations of the chronosequence study is the generality of the substitution of time for space. One way to validate a chronosequence, but much less frequently done, is to follow individual sites through time (longitudinal tracking; Debussche *et al.* 1996, Foster & Tilman 2000, Pascarella *et al.* 2004). Understanding the demographic transitions that regulate the population dynamics of pioneer species important in the chronosequence should enhance our ability to intervene and increase the chance of successful forest restoration (Guariguata & Pinard 1998; Slocum 2000; Myster 2003, 2004; Jones *et al.* 2004; Slocum *et al.* 2004). Although relatively few studies have focused on variation in demographic characteristics among sites along a successional pathway (Alvarez-Buylla & Martinez-Ramos 1992, Alvarez-Buylla 1994, Pascarella & Horvitz

Received 5 August 2005; revision accepted 23 January 2006.

<sup>1</sup> Corresponding author; e-mail: jbpascarella@valdosta.edu

1998, Ehrlén 2003), these studies have found important differences in population growth rates and elasticity across different environments. Variation in elasticity, or the change in population growth rate due to a proportional change in a life-history transition, can reveal the influence of successional changes on life-history traits.

We took this longitudinal approach to studying the demography of a dominant colonizer of abandoned pastures, the subcanopy tree *Miconia prasina* (Melastomataceae), by determining life-stage-specific vital rates (survival, growth, and reproduction) across a pasture to forest chronosequence (1-, 12-, and 25-yr-old secondary forest) and in a hurricane-damaged forest (>60-yr-old). This more detailed approach also allows us to cover the entire range of life-history transitions for this species, including many components that were not measured in the chronosequence model. These data were used to construct stage-based transition matrices to model the population dynamics of this species in the four successional stages. In this paper, we ask three general questions about the demography of *M. prasina* along a secondary successional pathway:

1. Does the population dynamics of the fine-scale matrix model correspond to that observed by the broad-scale chronosequence sampling? *i.e.*, population growth rates should decline with increasing stand age;
2. How do elasticities change as a function of site age? For example, do life-history transitions related to seed germination contribute less to population growth as a function of site age and does adult survival contribute more?
3. Does *M. prasina* establish new individuals from seed in recently abandoned pastures or does it just exhibit rapid growth of preexisting individuals in these sites?

## METHODS

**STUDY SPECIES AND SITES.**—*Miconia prasina* (SW) DC. (Melastomataceae) is a small tree (1–12 m tall, diameter to 20 cm but usually smaller; Liogier 1995). It is widely distributed in the Neotropics throughout the Caribbean and from southern Mexico to southern South America. Of the 19 native *Miconia* species in Puerto Rico, it is one of the most common species, found in moist coastal, moist limestone, and lower mountain forests, from sea level to 800 m in elevation (Little & Wadsworth 1964). The species has hermaphroditic flowers, an autogamous breeding system with average fruit set of 41 percent, and fruits with  $41.4 \pm 3.1$  seeds (mean  $\pm$  1 SE,  $N = 34$  fruits; J. Pascarella, pers. obs.).

In Puerto Rico, *M. prasina* is an important colonizer of abandoned pastures, often dominating sites for the first 20 yr of secondary succession (Aide *et al.* 1995, 1996, 2000; Pascarella *et al.* 2000). From 20 to 40 yr of succession, it declines in abundance. In older sites and in undisturbed forest, it is not common (Thompson *et al.* 2002, J. Zimmerman, pers. obs.). In addition, *M. prasina* is not very abundant as a colonizer of landslides in primary forest in eastern Puerto Rico (Guariguata 1990, Myster & Walker 1997).

Three sites of known age (three abandoned cattle pastures 1-, 12-, and 25-yr old), and an older forest site that has been continu-

ously forested since 1935 (>60-yr-old) were selected in September 1995. The plots were readily accessible, three were under protection of the Forest Service (all but the 25-yr-old site) and they appeared representative to us of the *M. prasina* populations that we had seen throughout the island (Aide *et al.* 2000). The study sites correspond to the sites 1, 3, 4, and 6 in the Rio Sabana region listed by Aide *et al.* (1995). Soils ranged from clays to silty clay loams and are primarily Ultisols in the Zarzal-Cristal complex (Boccheciamp 1977, Johnston 1992). All populations were between 100 m and 150 m elevation on slight-to-moderately steep slopes and were located within 660 m of each other. The close location of the sites was chosen to minimize any effect of environmental variation on population dynamics.

The four sites varied in vegetation present and degree of canopy development during the study (Aide *et al.* 1995). The two young sites had no continuous canopy present and large *Miconia* individuals were the tallest plants while the two older sites had a canopy of taller trees above the tallest *Miconia* plants. The recently abandoned pasture (1-yr-old site) was dominated by pasture grasses, herbs, and small clumps of *M. prasina*. The 12-yr-old site was dominated by ferns and *M. prasina*. The 25-yr-old site was dominated by a subcanopy of *M. prasina* with a dense understory of *Syngonium podophyllum* (Araceae) and a canopy of *Tabebuia heterophylla* (Bignoniaceae). The old forest site (>60-yr-old) had the highest woody species diversity. *Ficus citrifolia* (Moraceae) and *Cecropia schreberiana* (Moraceae) dominated the canopy and *Psychotria berteriana* (Rubiaceae) was the most abundant understory species. We refer to the sites sampled by site age but this does not necessarily bear any relationship to the age of *M. prasina* individuals in these sites.

**CENSUS METHODS.**—Four  $1 \times 40$  m transects were established in September of 1995 at each site except for the 25-yr-old site. In this site, one  $1 \times 40$  m transect and one  $1 \times 20$  m transect were established due to the high densities of *M. prasina*. To compensate for the low densities in the other three sites, we randomly selected additional individuals located nearby until 50 adults ( $\geq 1$  m in height) were marked with metal tags in each population. In November 1995, all adults in the four sites were censused for height, number of stems, and diameter of stems at 1 m. The census was repeated in November of 1996 and 1997. Within the transects, any new adults recruited into the population were recorded each year.

In each transect, a  $1 \times 1$  m subplot was established every 5 m for 32 subplots/population. In the 25-yr-old site, only 12 subplots were used. All plants in the subplots were tagged and the height was recorded. During the initial census, individuals were assigned to either seedling (plants emerged from seeds) or juvenile stem (unknown establishment) stages. During the census in 1996 and 1997, new individuals derived from vegetative establishment (root sprout) were noted. New individuals derived from root sprouts had more lateral roots, larger leaves, and fewer leaf hairs in comparison to new plants derived from seeds. Seedlings derived from seed germination and root sprouts were censused quarterly beginning in November 1995 until November 1996 and then measured once in November 1997.

Every 2 mo from September 1995 to November 1996, all adults in the four sites were censused for flowering activity and the number of inflorescences was counted. The number of flowering episodes was calculated as the number of times plants flowered with at least a 1-mo separation between flowering. Seed production per individual was estimated as the number of inflorescences  $\times$  average number of flowers per inflorescence  $\times$  average fruit set per inflorescence  $\times$  average number of seeds per fruit, summed across all censuses during the 1995–1996 census period.

**STAGE CLASSIFICATION AND MATRIX MODEL ANALYSIS.**—We used reproductive and size criteria to define four life stages: juveniles (no reproductive individuals) and small, medium, and large adults (Table 1). We used height to distinguish juveniles ( $<1$  m) from adults ( $\geq 1$  m), as no individuals in any site  $<1$  m were found flowering. The summed diameter of stems was used as the size criteria categorizing plants that were  $\geq 1$  m in height (Table 1). Because of the lack of transitions to new individuals from seeds, the resulting matrix did not include seed production or seed–seedling transitions.

In order to maximize the number of observed transitions, we pooled all transitions within a population over the 2 yr to generate the yearly transition rates. For each matrix, we calculated the long-term population growth rate ( $\lambda$ ), stable stage structure, and elasticities using MATLAB (1997) and formulas in Caswell (2001). Elasticities were summed by stage class within each population (de Kroon *et al.* 2000) and were grouped by life-cycle components including vegetative asexual reproduction, survival (stasis and retrogression), and growth (Silverton *et al.* 1993). We calculated the confidence interval for each matrix's long-term population growth rate ( $\lambda$ ) by bootstrap resampling the observed original data 10,000 times, ranking the results, and recording the 250th and 9750th estimates as the confidence intervals around the estimated growth rate (Caswell 2001).

TABLE 1. Stage class criteria for four stages of *M. prasina* in abandoned pastures in Puerto Rico.

Stage	Characteristics		
	Height (cm)	Summed stem DBH (cm) <sup>a</sup>	Reproductive
Nonreproductive			
A. Juvenile (juv)	$<100$		no
Adults			
A. Small (sm)	$\geq 100$	$\leq 3$	yes
B. Medium (med)	$\geq 100$	$>3$ and $\leq 6$	yes
C. Large (lrg)	$\geq 100$	$>6$	yes

<sup>a</sup>Because of multiple stems per plant, the summed diameter of all stems was used to distinguish adult size classes.

## RESULTS

Population structure varied across sites and years. In November 1995, mean individual density was highest in the 25-yr-old site, followed by the 1, 12, and  $>60$ -yr-old sites (Table 2). In November 1995, mean summed diameter/plant was greatest in the 12-yr-old site, was similar in the 1- and 25-yr-old sites, and lowest in the  $>60$ -yr-old site (Fig. 1A). In 1995, mean height/plant increased with site age until 25 yr (Fig. 1B). The mean number of stems/plant was highest in young sites with a peak at 12 yr of age and the 1-yr-old site having nearly four stems/plant (Fig. 1C). These two sites also had 60 percent of the stems showing machete damage from previous pasture maintenance. In contrast, the mean number of stems/plant in the 25- and  $>60$ -yr-old sites were only slightly greater than one and showed little to no damage from human activity.

Vegetative growth was most pronounced in the 1- and 12-yr-old sites (Fig. 1A–C). In the 1- and 12-yr-old sites, positive growth was found for both years in height and mean summed stem diameter. Over the combined 2-yr period, mean number of stems per plant increased in the two young sites. In contrast, plants in the 25- and  $>60$ -yr-old sites had negative growth in diameter and height for both years and had slight negative growth in number of stems over the 2-yr period.

Survival varied across sites and years ( $P < 0.001$ , G-test for both years combined). There was no adult mortality in the 1- and 12-yr-old sites for either year. In contrast, there was higher mortality in the two older sites that varied across the two census years. Ten percent of the adults (7 individuals) in the 25-yr-old site and 2 percent (1 individual) in the  $>60$ -yr-old site died in 1995–1996. Mortality was lower in 1996–1997 for the 25-yr-old site (5%, 3 individuals) but higher for the  $>60$ -yr-old site (13%, 6 individuals). Damage from the passage of two hurricanes in June and September 1996 that brought tropical storm force winds to the region was noted mostly in the 12-, 25- and  $>60$ -yr-old sites with 1, 14, and 8 individuals knocked over by wind or falling canopy debris. However, all damaged individuals resprouted at the base.

Reproductive variables varied across sites, with more plants flowering in younger sites but more inflorescences and greater number of flowering episodes in the 25-yr-old site (Table 2). Number of inflorescences/m<sup>2</sup>, fruits/m<sup>2</sup>, and seeds/m<sup>2</sup> all increased with site age up to age 25 yr, then declined sharply in the  $>60$ -yr-old site. In the field studies, no seed germination was noted in the 1- or 12-yr-old sites. Seed germination was observed during the quarterly surveys in the 25 (989 seedlings) and  $>60$ -yr-old sites (4 seedlings). However, no seedlings survived at either site to the next census interval. Root sprouts (# in parentheses) were noted in the 1 (3), 12 (22), and 25 (3) yr old sites. Recruitment from fragmentation and detachment from a single damaged adult plant was noted in the  $>60$ -yr-old site. Both of these types of recruitment resulted in transitions observed in the adult to juvenile elements of the matrix (Table 3).

Because of the lack of transitions to new individuals from seeds, the resulting matrix did not include seed production or seed–seedling transitions. Thus, we used a  $4 \times 4$  matrix to

TABLE 2. Density and reproductive data of *M. prasina* from four populations (1995–1996) in abandoned pastures in Puerto Rico.

Site (age)	Density (#/m <sup>2</sup> ) of individual plants	Percentage of adult plants flowering <sup>a</sup>	Mean no. of inflorescences (±1 SE) <sup>b</sup>	Mean no. of flowering episodes (±1 SE) <sup>b</sup>	Inflorescences/m <sup>2</sup> (1995–1996)	Fruits/m <sup>2c</sup>	Seeds/m <sup>2d</sup>
1	0.24	58	16.7 ± 3.18 <sup>ab</sup>	2.6 ± 0.26 <sup>ab</sup>	3	201	8,330
12	0.14	50	37.3 ± 8.19 <sup>a</sup>	2.4 ± 0.24 <sup>b</sup>	5.8	370	15,325
25	1.15	39	54.2 ± 10.5 <sup>a</sup>	4.0 ± 0.31 <sup>a</sup>	42	6580	272,402
>60	0.09	12	4.1 ± 1.73 <sup>b</sup>	1.1 ± 0.13 <sup>b</sup>	0.21	13	543

<sup>a</sup>Adult plants are all plants >1m.  $P < 0.0001$ , G-test.

<sup>b</sup>Mean no. of inflorescences ( $P < 0.01$ ) and mean no. of flowering episodes ( $P < 0.001$ ) calculated for all adult plants that flowered at least once. Kruskal–Wallis ANOVA for variation among sites.

<sup>c</sup>Estimated as (total number of inflorescences × mean number of flowers/inflorescence × mean fruit set)/meters in transect.

<sup>d</sup>Estimated as (total number of fruits × mean seed number per fruit)/meters in transects.

characterize only the vegetative dynamics including asexual reproduction through root sprouts (Table 3). In the two youngest sites (1- and 12-yr-old), the long-term asymptotic average population growth rates ( $\lambda$ ) were greater than one, while average growth rates were less than one in the two older sites (Table 4). The highest population growth was noted in the 12-yr-old site (1.15) with the lowest in the old forest site (0.84). Confidence intervals for the average growth rates overlapped each other at one, indicating that none of the sites was significantly different from each other or a stable population ( $\lambda = 1$ ). Stable stage structure varied by site. The 1-yr-old site had mostly medium and large adults while the older sites had mostly juveniles (Table 5).

Elasticities varied, depending on the site and plant stage class. When summed by stage class, the highest elasticities were found in the larger stage classes (small-to-large adults) in the two young sites while the older sites had highest elasticities in the small adults (Fig. 2). The 25-yr-old site also had high elasticity values in the juveniles and the >60-yr-old site had high elasticity in the medium adults. When grouped by life-cycle components, all four populations had the highest elasticity contributions from survival, ranging from 64 percent to 94 percent, with the highest values found in the two older sites (Table 6) and lower values in the young sites. Growth transitions were second most important in all sites, but were lower in the two older sites. Vegetative reproduction was low in elasticity in all populations except for the 12-yr old site where it totaled 12 percent.

## DISCUSSION

Previous chronosequence studies (Aide *et al.* 1995, 1996, 2000; Pascarella *et al.* 2000) suggested that the population growth rate of *M. prasina* declines with stand age after an initial period of growth following pasture abandonment. Although the confidence intervals of long-term population growth rate at all sites overlapped with each other, the average growth rates were in general agreement with the chronosequence model. We found the average population growth rate in the two youngest sites (1- and 12-yr-old) indicated positive

population growth and the average population growth rate in the older successional site (25-yr-old) and in the old forest site (>60 yr) indicated a declining population.

Potential causes of this population decline in older sites may include greater stem density, lower light levels, and increased mortality from tropical storm events. By 25 yr, secondary forests derived from abandoned cattle pastures in Puerto Rico peak in stem density (Aide *et al.* 1995, 1996). In Nicaragua, *M. prasina* was described as a heliophilic pioneer species that showed the highest growth rates in sites with high levels of disturbance from Hurricane Joan (Boucher *et al.* 2001). Our growth data on stem diameter increment and height growth are in agreement with these observations of *M. prasina*, with the highest growth rates found in the most open environments (1- and 12-yr-old sites) and negative growth found in more closed canopy successional (25-yr-old) and older (>60 yr) forested sites. Larger plants found in older sites are also more susceptible to wind damage from the frequent tropical storms and hurricanes that strike Puerto Rico (Walker *et al.* 1991).

*Miconia prasina* populations in older forest sites, such as the 60-yr-old site in this study, may be of recent origin from disturbance. We believe that the population of *M. prasina* at this site was initiated following the disturbance created by Hurricane Hugo in 1989 and was only 6-yr old at the time of the initiation of the study. The abundance of *Cecropia* at this site is a strong indicator of recent hurricane disturbance (Brokaw 1998). In Nicaragua, *M. prasina* recruited into tree size diameters 2 yr after Hurricane Joan and stem and height growth rates were positive for 4 yr before declining as the canopy reformed (Vandermeer *et al.* 1997, 1998). This suggests that in older forest sites, the species is relatively transient, occurring only following severe disturbances such as hurricanes or in more permanent open habitats such as streambeds and riverbanks (Liogier 1995).

How did elasticities change as a function of site age? We predicted that elasticities related to reproduction should be highest in the young sites if population growth in this species is through the recruitment of new individuals via seed in recently abandoned pastures. While flowering occurred in all habitats, with a greater percentage of plants flowering in younger sites, total seed output

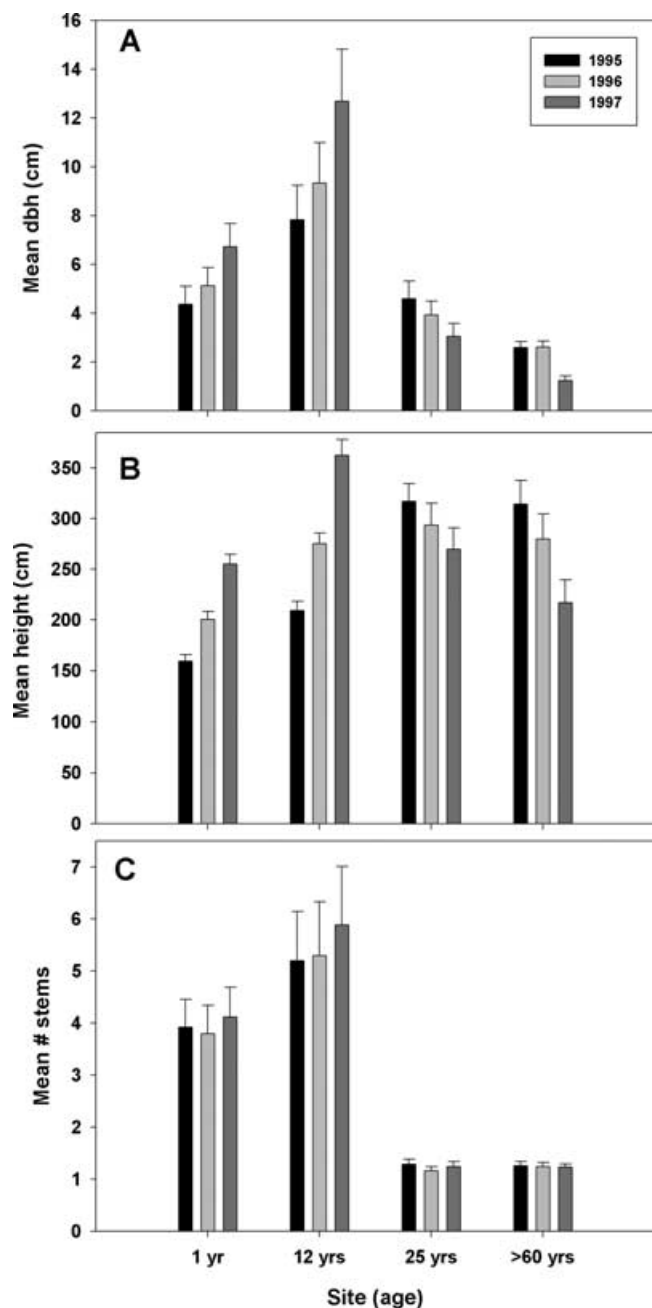


FIGURE 1. Population size variables (mean  $\pm$  1 SE) as a function of site age from 1995–1997 for *M. prasina*. (A) Diameter. (B) Height. (C) Number of stems.

was highest in the 25-yr-old successional habitat. High seed production in this site was also associated with a large number of seedlings. However, none of the seedlings that established in this site survived and no seedlings were ever observed in the two young sites.

Small-seeded species such as *M. prasina* (<0.001 g) typically are unable to establish under litter (Vasquez-Yanes *et al.* 1990, Guzman-Grajales & Walker 1991, Hoffman 1996). Data from a separate

TABLE 3. Pooled transition matrices (1995–1996 and 1996–1997 transitions) by sites for *M. prasina* in abandoned pastures in Puerto Rico. Values are rounded to fit in this table.

Stage at time $t + 1$	Stage at time $t$			
	Juvenile	Small	Medium	Large
A) 1-yr-old abandoned pasture				
Juvenile	0.44	0.23 <sup>a</sup>	0.13	0.06
Small	0.11	0.85	0	0
Medium	0	0.13	0.84	0.13
Large	0	0	0.16	0.87
$N^b$	9	52	32	15
B) 12-yr-old abandoned pasture				
Juvenile	0.31	2.10	1.46	1.22
Small	0.08	0.63	0.07	0
Medium	0	0.37	0.77	0
Large	0	0	0.17	1
$N$	13	43	30	25
C) 25-yr-old abandoned pasture				
Juvenile	0.83	0.22	0.10	0.02
Small	0.01	0.81	0.24	0.10
Medium	0	0.03	0.64	0
Large	0	0	0	0.82
$N$	77	68	50	11
D) >60-yr-old forest				
Juvenile	0.75	0.12	0	0
Small	0	0.76	0.25	0
Medium	0	0.04	0.68	1.0
Large	0	0	0	0
$N$	8	68	28	1

<sup>a</sup>Transition elements in row 1, columns 1–4 of all matrices represent the combination of vegetative reproduction and retrogression from adult size stages.

<sup>b</sup>Number of individuals used to generate transition elements.

field experiment (Zimmerman *et al.* 2000) in the 1-yr-old pasture where 2400 seeds of *M. prasina* were planted under vegetation and in cleared areas found no seedling establishment under either treatment. As we only observed seed germination in tip-up mounds in older forests and in open areas created by cattle in the 25-yr-old site, this suggests that seed germination is linked to exposed soil.

TABLE 4. Population growth rates ( $\lambda$ ) and their bootstrap confidence limits for *M. prasina* in abandoned pastures in Puerto Rico.

Site age (years)	$\lambda$	Lower CL	Upper CL
1	1.019	1	1.078
12	1.145	1	1.397
25	0.889	0.823	1
>60	0.835	0.765	1

TABLE 5. Stable stage distribution for *M. prasina* populations along a forest chronosequence in Puerto Rico.

	Stable stage distribution			
	Site age (years)			
Stage	1	12	25	>60
Juvenile	0.16	0.65	0.78	0.52
Small	0.10	0.11	0.20	0.38
Medium	0.36	0.11	0.02	0.11
Large	0.37	0.13	0	0

Because of the lack of observed recruitment via seeds, we believe that the increase in density of *M. prasina* in recently abandoned pastures is due primarily to vegetative growth of individuals already present in the pasture at the time of abandonment. In these young abandoned pastures, root sprouts may be the primary means of establishment of additional new individuals. Root sprouts had not been previously reported in this species nor is it typical of tropical woody pioneers such as *Cecropia* (Brokaw 1998). However, root sprouts are found in a variety of tropical trees such as *Alseis blackiana* (Guariguata 1992). The formation of root sprouts may be adaptations to the natural riparian habitat of *M. prasina* in Puerto Rico, where root sprouts may help plants recover from erosion from periodic stream flooding.

The relatively high elasticity of vegetative reproduction through root sprouts in the two young sites may be related to

TABLE 6. Elasticity (see text for definition) grouped by life-cycle component for *M. prasina* in abandoned pastures in Puerto Rico.

Life-cycle component	Site (age)			
	1	12	25	>60
Survival	0.88	0.64	0.92	0.94
Growth	0.10	0.24	0.05	0.06
Vegetative reproduction	0.02	0.12	0.03	0.00

the recent history of use as a pasture. Management of pastures in Puerto Rico typically involves the use of machetes to reduce shrub cover, which was undoubtedly employed in the sites we sampled up until the time we began our study. However, we have no precise knowledge of the frequency of the practice in the different sites we sampled so we cannot state with confidence its importance to the population dynamics described here. Nonetheless, the ability to resprout following macheting or grazing would allow *M. prasina* plants to persist in active pastures. Macheting did not appear to have an effect on survival of these species, as there was no mortality of adult stems in either young site. The primary effect of macheting appears to be the development of a multistem shrub morphology over a single-stem subcanopy tree.

As expected, the importance of survival was highest in the oldest sites, reflecting the low probability of either growth or vegetative reproduction. Other studies that have examined demography of plants along a successional sequence have also found major shifts

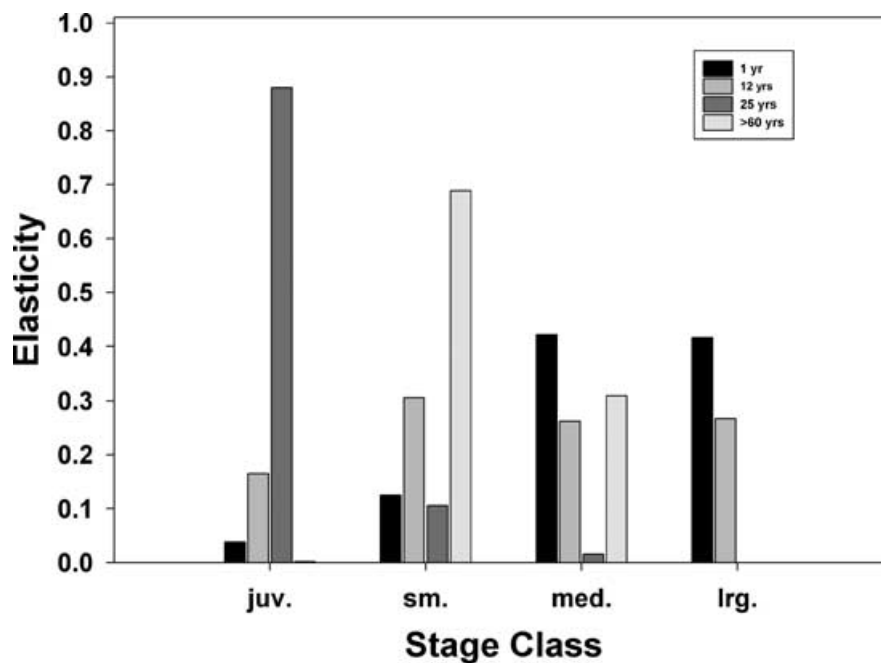


FIGURE 2. The stage-specific elasticities for each stage class in populations of *M. prasina* and site summed by stage class. The total elasticity of all the stage classes within a site is constrained to sum to one (i.e., elasticities are proportional).

in population growth and elasticity. Kowarik (1995) found that populations in West Virginia of the exotic tree *Ailanthus altissima*, normally an invader in open sites, has 100 percent mortality of seedlings but can persist in older successional sites through production of slow-growing clonal ramets. Oostermeijer *et al.* (1996) found significant shifts in population growth rate of *Gentiana pneumonanthe* as a function of succession in wet heathlands in the Netherlands. In their study, elasticities also shifted from dominance of survival in mature or senescent populations that were declining to dominance of fecundity and growth elasticities in young successional habitats that were experiencing positive population growth. Their results are similar to those obtained in this study, reflecting general trade-offs in life-history transitions that relate to environmental quality.

In conclusion, this study provides support for the chronosequence approach by documenting the mechanisms of population growth and decline in the pioneer species *M. prasina*. We suggest that future research examine the timing of establishment of *M. prasina* via seed by examining vegetation change during current deforestation and in active pastures. Additional research on soil seed banks, seed longevity under natural conditions, and seed dispersal of *M. prasina* would enhance our understanding of the long-term dynamics of this species as land-use change continues.

## ACKNOWLEDGMENTS

This project was funded by a grant under the NASA Institutional Research Award program to the University of Puerto Rico and the NSF-CREST program. The U.S. Forest Service allowed access to the populations within the Caribbean National Forest. The University of Puerto Rico undergraduate students Caleb Gonzalez and Anaëli Cintron assisted with data collection. Manuel Guariguata and three anonymous reviewers helped improve the manuscript. Juan Carlos Morales and Agustin M. Abba provided assistance with the Spanish translation.

## LITERATURE CITED

- AIDE, T. M., J. K. ZIMMERMAN, L. HERRERA, M. ROSARIO, AND M. SERRANO. 1995. Forest recovery in abandoned tropical pastures in Puerto Rico. *For. Ecol. Manage.* 77: 77–86.
- AIDE, T. M., J. K. ZIMMERMAN, M. ROSARIO, AND H. MARCANO. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. *Biotropica* 28: 537–548.
- AIDE, T. M., J. K. ZIMMERMAN, J. B. PASCARELLA, L. RIVERA, AND H. MARCANO. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: Implications for restoration ecology. *Restor. Ecol.* 8: 328–338.
- ALVAREZ-BUYLLA, E. R. 1994. Density dependence and patch dynamics in tropical rain forests: Matrix models and applications to a tree species. *Am. Nat.* 143: 155–191.
- ALVAREZ-BUYLLA, E. R., AND M. MARTINEZ-RAMOS. 1992. Demography and allometry of *Cecropia obtusifolia*: A Neotropical pioneer tree and evaluation of the climax-pioneer paradigm for tropical rain forests. *J. Ecol.* 80: 275–290.
- BOCCHICCIAMP, R. A. 1977. Soil survey of the Humacao area of Eastern Puerto Rico. United States Department of Agriculture Soil Conservation Service, San Juan, PR, USA.
- BOUCHER, D. H., J. H. VANDERMEER, I. GRANZOW DE LA CERDA, M. A. MALONE, I. PERFECTO, AND N. ZAMORA. 2001. Post-agriculture versus post-hurricane succession in southeastern Nicaraguan rain forest. *Plant Ecol.* 156: 131–137.
- BROKAW, N. V. L. 1998. *Cecropia schreberiana* in the Luquillo mountains of Puerto Rico. *Bot. Rev.* 64: 91–120.
- CASWELL, H. 2001. Matrix population models, 2nd edition. Sinauer Associates, Inc., Sunderland, Massachusetts.
- CHAZDON, R. L. 2003. Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspect. Plant Ecol. Evol. Syst.* 6: 51–71.
- DEBUSSCHE, M., J. ESCARRÉ, J. LEPART, C. HOUSSARD, AND S. LAVOREL. 1996. Changes in Mediterranean plant succession: Old-fields revisited. *J. Veg. Sci.* 7: 519–526.
- DE KROON, H., J. VAN GROENENDAEL, AND J. EHRLÉN. 2000. Elasticities: A review of methods and model limitations. *Ecology* 81: 607–618.
- EHRLÉN, J. 2003. Fitness components versus total demographic effects: Evaluating herbivore impacts on a perennial herb. *Am. Nat.* 162: 796–810.
- FINEGAN, B. 1996. Pattern and process in Neotropical secondary forests: The first 100 years of succession. *Trends Ecol. Evol.* 11: 119–124.
- FOSTER, B. L., AND D. TILMAN. 2000. Dynamic and static views of succession: Testing the descriptive power of the chronosequence approach. *Plant Ecol.* 146: 1–10.
- GONZALEZ-ITURBE, J. A., I. OLMSTED, AND F. TUN-DZUL. 2002. Tropical dry forest recovery after long term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in northern Yucatan, Mexico. *For. Ecol. Manage.* 167: 67–82.
- GRAU, H. R., M. F. ARTURI, A. D. BROWN, AND P. G. ACENOLAZA. 1997. Floristic and structural patterns along a chronosequence of secondary forest succession in Argentinean subtropical montane forests. *For. Ecol. Manage.* 95: 161–171.
- GUARIGUATA, M. R. 1990. Landslide disturbance and forest regeneration in the upper Luquillo mountains of Puerto Rico. *J. Ecol.* 78: 814–832.
- GUARIGUATA, M. R. 1992. Observations on the vegetative behavior in juveniles of the canopy tree, *Alseis blackiana*, in lowland Panama. *Biotropica* 24: 575–576.
- GUARIGUATA, M. R. 2000. Seed and seedling ecology of tree species in Neotropical secondary forests: Management implications. *Ecol. Appl.* 10: 145–154.
- GUARIGUATA, M. R., AND M. A. PINARD. 1998. Ecological knowledge of regeneration from seed in Neotropical forest trees: Implications for natural forest management. *For. Ecol. Manage.* 112: 87–99.
- GUZMAN-GRAJALES, S. M., AND L. R. WALKER. 1991. Differential seedling responses to litter after Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 23: 407–413.
- HOFFMAN, W. A. 1996. The effects of fire and cover on seedling establishment in a Neotropical savanna. *J. Ecol.* 84: 383–393.
- JOHNSTON, M. H. 1992. Soil-vegetation relationships in a tabonuco forest community in the Luquillo Mountains of Puerto Rico. *J. Trop. Ecol.* 8: 253–263.
- JONES, E. R., M. H. WISHNIE, J. DEAGO, A. SAUTU, AND A. CEREZO. 2004. Facilitating natural regeneration in *Saccharum spontaneum* (L.) grasslands within the Panama Canal Watershed: Effects of tree species and tree structure on vegetation recruitment patterns. *For. Ecol. Manage.* 191: 171–183.
- KENNARD, D. K. 2002. Secondary forest succession in a tropical dry forest: Patterns of development across a 50-year chronosequence in lowland Bolivia. *J. Trop. Ecol.* 18: 53–66.
- KOWARIK, I. 1995. Clonal growth in *Ailanthus altissima* on a natural site in West Virginia. *J. Veg. Sci.* 6: 853–856.
- LIOGIER, A. H. 1995. Descriptive flora of Puerto Rico and adjacent islands. Spermatophyta. Vol. IV: Melastomataceae to Lentibulariaceae. Editorial de la Universidad de Puerto Rico, Rio Piedras, PR, USA.
- LITTLE, E. L. JR., AND F. H. WADSWORTH. 1964. Common trees of Puerto Rico and the Virgin Islands. United States Department of Agriculture Handbook 449, Washington, DC.

- MARCANO-VEGA, H., T. M. AIDE, AND D. BAEZ. 2002. Forest regeneration in abandoned coffee plantations and pastures in the Cordillera Central of Puerto Rico. *Plant Ecol.* 161: 75–87.
- MATLAB VERSION 5. 1997. The Math Works, Inc. Natick, Massachusetts.
- MONTGOMERY, R. A., AND R. L. CHAZDON. 2001. Forest structure, canopy architecture, and light transmittance in tropical wet forests. *Ecology* 82: 2707–2718.
- MYSTER, R. W. 2003. Vegetation dynamics of a permanent pasture plot in Puerto Rico. *Biotropica* 35: 422–428.
- MYSTER, R. W. 2004. Post-agricultural invasion, establishment, and growth of Neotropical trees. *Bot. Rev.* 70: 381–402.
- MYSTER, R. W., AND L. R. WALKER. 1997. Plant successional pathways on Puerto Rican landslides. *J. Trop. Ecol.* 13: 165–173.
- OLIVEIRA, F. A. T., D. A. CARVALHO, E. A. VILELA, N. CURI, AND M. A. L. FONTES. 2004. Diversity and structure of the tree community of a fragment of tropical secondary forest of the Brazilian Atlantic Forest domain 15 and 40 years after logging. *Revista Brasil. Bot.* 27: 685–701.
- OOSTERMEIJER, J. G., M. L. BRUGMAN, E. R. DEBOER, AND J. C. DENNIJS. 1996. Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. *J. Ecol.* 84: 153–166.
- PASCARELLA, J. B., AND C. C. HORVITZ. 1998. Hurricane disturbance and the population dynamics of a tropical understory shrub: Megamatrix elasticity analysis. *Ecology* 79: 547–563.
- PASCARELLA, J. B., T. M. AIDE, M. I. SERRANO, AND J. K. ZIMMERMAN. 2000. Land-use history and forest regeneration in the Cayey mountains, Puerto Rico. *Ecosystems* 3: 217–228.
- PASCARELLA, J. B., T. M. AIDE, AND J. K. ZIMMERMAN. 2004. Short-term response of secondary forests to hurricane disturbance in Puerto Rico, USA. *For. Ecol. Manage.* 199: 379–393.
- RIVERA, L. W., AND T. M. AIDE. 1998. Forest recovery in the Karst region of Puerto Rico. *For. Ecol. Manage.* 108: 63–75.
- RUDEL, T. K., O. T. COOMES, E. MORAN, F. ACHARD, A. ANGELSEN, J. C. XU, AND E. LAMBIN. 2005. Forest transitions: Towards a global understanding of land use change. *Glob. Environ. Change* 15: 23–31.
- SALDARRIAGA, J. C., D. C. WEST, M. L. THARP, AND C. UHL. 1988. Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. *J. Ecol.* 76: 938–958.
- SILVERTON, J., M. FRANCO, I. PISANTY, AND A. MENDOZA. 1993. Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *J. Ecol.* 81: 465–476.
- SLOCUM, M. G. 2000. Logs and fern patches as recruitment sites in a tropical pasture. *Restor. Ecol.* 8: 408–413.
- SLOCUM, M. G., T. M. AIDE, J. K. ZIMMERMAN, AND L. NAVARRO. 2004. Natural regeneration of subtropical montane forest after clearing fern thickets in the Dominican Republic. *J. Trop. Ecol.* 20: 483–486.
- THOMPSON, J., N. BROKAW, J. K. ZIMMERMAN, R. B. WAIDE, E. M. EVERHAM, D. J. LODGE, C. M. TAYLOR, D. GARCIA-MONTIEL, AND M. FLUET. 2002. Land use history, environment, and tree composition in a tropical forest. *Ecol. Appl.* 12: 1344–1363.
- VANDERMEER, J., A. BRENNER, AND I. GRANZOW DE LA CERDA. 1998. Growth rates of tree height six years after hurricane damage at four localities in Eastern Nicaragua. *Biotropica* 30: 502–509.
- VANDERMEER, J., I. GRANZOW DE LA CERDA, AND D. BOUCHER. 1997. Contrasting growth rate patterns in eighteen tree species from a post-hurricane forest in Nicaragua. *Biotropica* 29: 151–161.
- VASQUEZ-YANES, C., A. OROZCO-SEGOVIA, E. RINCÓN, M. E. SÁNCHEZ-CORONADO, P. HUANTE, J. R. TOLEDO, AND V. L. BARRADAS. 1990. Light beneath the litter in a tropical forest: Effect on seed germination. *Ecology* 71: 1952–1958.
- WALKER, L. R., D. J. LODGE, N. V. L. BROKAW, AND R. B. WAIDE. 1991. An introduction to hurricanes in the Caribbean. *Biotropica* 23: 313–316.
- ZHANG, Q. F., D. DEVERS, A. DESCH, C. O. JUSTICE, AND J. TOWNSHED. 2005. Mapping tropical deforestation in Central Africa. *Environ. Monit. Assess.* 101: 69–83.
- ZIMMERMAN, J. K., T. M. AIDE, M. ROSARIO, M. SERRANO, AND L. HERRERA. 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. *For. Ecol. Manage.* 77: 65–76.
- ZIMMERMAN, J. K., J. B. PASCARELLA, AND T. M. AIDE. 2000. Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restor. Ecol.* 8: 350–360.