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# Impacts of Herbicide Application and Mechanical Cleanings on Growth and Mortality of Two Timber Species in *Saccharum spontaneum* Grasslands of the Panama Canal Watershed

Dylan Craven,[1,2] Jefferson Hall,[1] and Jean-Marc Verjans[3]

## Abstract

**Reforestation has been suggested as a strategy to control *Saccharum spontaneum*, an invasive grass that impedes regeneration in disturbed areas of the Panama Canal Watershed (PCW). In this study, the effects of different intensities of herbicide application and mechanical cleanings on the growth and mortality of *Terminalia amazonia* and *Tectona grandis* saplings were evaluated in *S. spontaneum* grasslands within the PCW. Both species exhibited greater height, basal diameter, wood volume index, wider crown diameters, deeper live crowns, and lower mortality with increasing intensity of mechanical cleanings and herbicide application. Height and competition of *S. spontaneum* correlated negatively with intensity of mechanical cleanings and herbicide application. Grass control costs did not differ between tree species but did increase significantly with intensity of mechanical cleanings and herbicide application. We recommend fire suppression, annual herbicide application, and at least four mechanical cleanings per year in *Tec. grandis* plantations during the first 3 years of plantation establishment. Given the slower initial growth and mortality patterns of *Ter. amazonia*, aggressive grass control treatments should be continued until individuals are sufficiently large to effectively shade *S. spontaneum*. Results from this study suggest that reforestation with commercial timber species can rapidly establish and control *S. spontaneum* growth in the PCW. Reforestation of areas already invaded or at risk of being invaded by *S. spontaneum* appears to be a viable strategy to reduce its abundance and subsequent negative ecological effects in the PCW.**

**Key words:** **invasive grass species, Panama, reforestation, *Tectona grandis*, *Terminalia amazonia*.**

## Introduction

The Panama Canal Watershed (PCW) is an area of dynamic land uses and diverse forest types that is of vital economic and ecological importance. At present, the PCW provides passage for approximately 38% of the trade between Asia and the East Coast of the United States and provides 95% of potable water for the inhabitants of the cities of Panama City, Colon, and San Miguelito (Autoridad del Canal de Panamá 2006, 2007). Despite covering a relatively small geographic area, 3,396 km$^2$, the forests within the PCW are among the world's most diverse, containing 850–1,000 tree species, 650 bird species, 93 amphibian species, and 70 mammal species (Fleming 1973; Condit et al. 2001; Martínez et al. 2006). As of 2003, 46.8% of the PCW in terms of area was under forest cover, which was evenly divided between intact primary and secondary forest types (Martínez et al. 2006). Productive land uses like cattle ranching and agriculture account for 34.5% of the PCW, and nonproductive cover types, such as water (12.7%), populated areas (1.64%), areas dominated by the invasive grass species *Saccharum spontaneum* (2.6%, equivalent to 89.79 km$^2$), and other uses (1.8%), occupy the remaining non-forested areas (Martínez et al. 2006). Between 1985 and 2003, deforestation within the PCW (−0.358%) was lower than in other regions of the country and occurred principally near populated areas and small watersheds (Martínez et al. 2006). Natural regeneration, less illegal logging, and reforestation programs increased forest cover between 1998 and 2003 by 0.05% (Martínez et al. 2006).

Invasive, exotic grass species such as *S. spontaneum* threaten the viability of forest ecosystems pantropically, as they promote fire and prevent natural regeneration (Vitousek et al. 1997). *Saccharum spontaneum* L., a $C_4$ grass native to Asia, was first introduced to Panama in 1928 as part of the Canal Zone Experiment Gardens to propagate multiple varieties of sugarcane; it did not become invasive in disturbed areas along the Panama Canal until the 1960s and 1970s (The Canal Zone Experiment Gardens 1931; Standley 1933; N. Smith 2007, Smithsonian

[1] Native Species Reforestation Project (PRORENA), Applied Ecology Program, Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Avenida Roosevelt 401, Balboa, Ancon, Republic of Panama
[2] Address correspondence to D. Craven, email dylan.craven@yale.edu
[3] Eco-Forest S.A., Apartado 32, Balboa, Ancon, Republic of Panama

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Tropical Research Institute, Panama City, Panama, personal communication). Its vigorous early growth and multiple propagation strategies enable it to rapidly colonize areas degraded by cattle grazing and slash-and-burn agriculture, eventually leading to less diverse plant communities with few native plant species (Hammond 1999; Brooker 2006). During the dry season in the PCW, anthropogenic fires occur frequently in *S. spontaneum*–dominated areas and inhibit seedling regeneration (Hooper et al. 2002). Small-seeded species disperse into the grasslands in greater numbers than large-seeded species, yet suffer greater mortality as seedlings (Nepstad et al. 1996; Hooper et al. 2002, 2005). Seed rain of large-seeded species in grasslands declines as forested areas reduce in size and increasingly reflects extant vegetation (Nepstad et al. 1996). Direct competition from grasses for water and soil nutrients also limits seedling growth (Nepstad et al. 1990; Hooper et al. 2005; Brooker 2006).

The physical barriers to forest regeneration presented by invasive grass species—dry season forest regime, seed dispersal limitation, and competition for water and soil nutrients—are difficult to overcome without directed intervention. Efforts to control invasive grass species, such as *S. spontaneum*, *Pennisetum setaceum*, and *Imperata cyclindrica*, consist of four principal components: fire exclusion, shading, chemical application, and mechanical cleaning (Anoka et al. 1991; Kuusipalo et al. 1995; Hammond 1999; Otsamo 2000; Chikoye et al. 2002). Fire exclusion promotes secondary forest regeneration by increasing germination, establishment, growth, and seedling species richness in grasslands (Cabin et al. 2002; Hooper et al. 2005; Shono et al. 2007). The competitive advantage shifts toward tree seedlings in shaded environments by decreasing the photosynthetic capacity of the invasive grass species and improving microsite conditions for seedling establishment (Anoka et al. 1991; Kuusipalo et al. 1995; Otsamo 2000; Cabin et al. 2002; Kim et al. 2006). Intense mechanical cleanings can further facilitate the germination and establishment of native plant species by reducing the root biomass of the invasive grass (Cabin et al. 2002).

The reforestation of degraded areas in the PCW might be the most effective strategy for eliminating *S. spontaneum* and improving biodiversity and carbon sequestration (Condit et al. 2001; Jones et al. 2004; Wishnie et al. 2007). Previous studies in the PCW found that the shade cover provided by trees is the best way to eliminate *S. spontaneum* (Hooper et al. 2005; Kim et al. 2006). Tree plantations mitigate the harsh environmental conditions of abandoned lands and facilitate seedling regeneration in the understory (Parrotta 1992; da Silva Junior et al. 1995; Guariguata et al. 1995; Cusack & Montagnini 2004). Seed dispersal increases in tree plantations, as their structural characteristics increase visitation by seed dispersal agents (Jones et al. 2004; Hooper et al. 2005; Zamora & Montagnini 2007). Tree cover provided by tree plantations, live fences, and isolated trees has also been associated with greater bird, animal, butterfly, and ant diversity in Central America (Jones et al. 2004; Harvey et al. 2005; Sáenz 2006; Griscom et al. 2007).

Timber plantations, by replacing *S. spontaneum* and providing taller, more complex vegetative cover, can improve the structural connectivity between large, continuously forested areas in the PCW. Extensive information exists about the ecology of *S. spontaneum* (Hammond 1999; Hooper et al. 2002, 2005; Jones et al. 2004) and its response to shading (Kim et al. 2006); the ecological and economical feasibility of reforesting in *S. spontaneum*–dominated areas of the PCW has not been tested quantitatively. For the present study, we formulated the following hypotheses to examine whether weed control treatments of varying intensities affected tree growth and mortality of two timber species (*Tectona grandis* and *Terminalia amazonia*) and the costs of grass control treatments in *S. spontaneum* grasslands:

(1) Structural characteristics and growth of both species will increase with the intensity of grass control treatments. Mortality for both species will decrease as the intensity of grass control treatments increases.
(2) More frequent mechanical treatments and herbicide application will reduce *S. spontaneum* height and the level of competition between it and surrounding trees.
(3) For both species, grass control costs will increase with herbicide application and frequency of mechanical cleanings. Furthermore, direct costs of grass control will be lower for *Tec. grandis* than for *Ter. amazonia*, because we expect the initial growth of *Tec. grandis* to be faster than that of *Ter. amazonia*.

## Methods

### Study Site

The research was performed within the concession granted to Eco-Forest S.A. in the PCW near Santa Clara, Republic of Panama, south of Barro Colorado Island National Monument (lat 9°09′N, long 79°51′W), a field site administered by the Smithsonian Tropical Research Institute. The study site is adjacent to seasonally wet tropical forest that receives 2,600 mm of rain, 95% of which falls during the wet season (Croat 1978; Leigh & Windsor 1982; Windsor 1990; Wieder & Wright 1995; Leigh 1999). Mean daily temperature is 27 ± 9°C (Dietrich et al. 1996). The soils are predominantly Aquic Ustropepts with minor components of Aquic Humitropepts and Typic Haplohumults and are moderately deep, well drained, and mildly acidic (5.65 pH) (Eco-Forest S.A., unpublished data; Vásquez Morera 1999).

### Species Studied

*Tectona grandis* L. f. and *Terminalia amazonia* (J.F.Gmel.) Exell were selected for this study because of their widespread use in timber plantations and reforestation programs in Central America and Panama; both species produce valuable timber that is sold in local and global markets. Teak is used in 48% of plantations in Panama (Gutiérrez & Díaz 1999; FAO 2007) and is the third most widely planted tropical hardwood worldwide in terms of area (Kraenzel et al. 2003). *Terminalia amazonia* is distributed widely across the neotropics from Mexico to Brazil and Peru in wet lowland forests (Carrasquilla 2005). Despite the limited use of *Ter. amazonia* in commercial plantations in Panama, it is used widely in Costa Rica for its carbon sequestration and timber production potential (Montero & Kanninen 2003). Rotation cycles of *Ter. amazonia* plantations in Costa Rica range between 20 and 30 years (Petit & Montagnini 2004; Redondo-Brenes 2005); Eco-Forest S.A. manages its teak plantations on an 18- to 25-year rotation cycle (J. M. Verjans 2007, Eco-Forest S.A., Panama City, Panama, personal communication).

#### Experimental Design

In June 2003, the study area was established on 2.8 ha of *Saccharum spontaneum*–dominated grasslands. All vegetation was cleared initially with machete. Seedlings of *Tec. grandis* and *Ter. amazonia* were planted in the cleared area in 56 pure plots, each measuring 21 × 18 m; 56 seedlings were planted in each plot at a spacing of 3 × 3–m spacing. Fire was excluded from the entire experimental area, given the expected effects on seedling mortality (Hooper et al. 2005). Seven combinations of chemical and mechanical weed control treatments were equally distributed across all plots. Half of the study plots received annual applications in the middle of the wet season (July/August) of granulated Round Up Max (glyphosate) (Monsanto Company, St. Louis, MO, U.S.A.) diluted in water at a concentration of 73.33 L $H_2O$/kg Round Up. Within two herbicide application treatments (herbicide; no herbicide), mechanical cleanings were performed at four different intensities (once, twice, four, and seven times per year). Treatments receiving one or two mechanical cleanings per year were realized in the wet season (June/July). Treatments receiving four and seven mechanical cleanings were performed every 2 months throughout the year. The herbicide + one mechanical cleaning combination was not implemented.

#### Field Measurements

Height (m), basal diameter (cm), live crown height (m), crown diameter (m), and tree mortality (number) were measured annually in July on all individuals from 2003 until 2006. All herbicide applications and mechanical cleanings were directly observed. For herbicide applications, the number of workers, time, total time (number of workers × minutes), total liters of herbicide applied, and height of *S. spontaneum* (m) were recorded on a per plot basis. The level of competition between *S. spontaneum* and trees was visually estimated using a scalar (1–4, 4 signifying a high level of competition and 1 very little) on a per plot basis per Wishnie et al. (2007). For each mechanical cleaning, the number of workers, time, total time (number of workers × time), *S. spontaneum* height (m), and competition scalar were recorded.

#### Data Analysis

The choice to plant *Tec. grandis* or *Ter. amazonia* is a management decision that involves primarily economic concerns in addition to ecological ones. Unless otherwise indicated, we analyzed these species separately to reflect the dichotomous nature of this decision. We tested for differences among weed control treatments in structural characteristics (height, basal diameter, live crown height, and crown diameter) separately by species using analysis of variance (ANOVA) and Tukey's honestly significant differences (HSD). All variables complied with normality assumptions. Where significant interactions of main effects were present, the Slice command was used in SAS (Schabenberger et al. 2000).

After 3 years of growth, there was a large variation in tree size between species and treatment combinations, and few individuals were large enough to have usable wood. We calculated wood volume index ($m^3$/ha) for both species as a means for comparing total productivity between treatments, because it integrates both height and basal diameter measurements. Wood volume index per tree was calculated using the following formula adapted from Newbould (1967):

$$\text{Wood Volume Index} = \left(\frac{\pi(\frac{D}{2})^2 h}{2}\right)1{,}111,$$

where $D$ was basal diameter (converted to meters) and $h$ was height (m). Wood volume index per hectare was calculated assuming a density of 1,111 trees/ha. Species-specific form factors were not available for the studied species and were not included in the calculation of wood volume index. Wood volume index per hectare was natural log transformed to meet normality assumptions. Differences between weed control treatments were tested using ANOVA and Tukey's HSD for both species.

Total mortality was calculated as the number of dead trees per plot for both species and was tested for differences between species and grass control treatments using a log-linear model of the GENMOD procedure with a negative binomial distribution and the natural log transformed value of the total number trees in each plot as the offset variable (Affleck 2006). Differences in annual mortality were tested for both species using the repeated statement of the GENMOD procedure.

To test for differences between grass control treatments for grass competition for each species, we used a simulated chi-square test because the dataset was a multiway contingency table with nonstructural zeroes (Gotelli & Entsminger 2004). Grass competition and grass height were regressed against total mortality using a log-linear model as previously described for total mortality.

The direct Cost of Mechanical Cleanings was calculated on a per plot basis in the following manner:

$$\text{Cost of Mechanical Cleaning} = \text{Total Minutes} \times \text{Hourly Wage},$$

where hourly salary is $1.25 in the PCW (J. M. Verjans 2007, Eco-Forest S.A., Panama City, Panama, personal communication). The cost of mechanical cleaning was then scaled up to a per hectare estimate for analysis. The direct cost of herbicide application was calculated per plot in the following manner:

$$\text{Cost of Chemical Treatments} = (\text{Total Minutes} \times \text{Hourly wage}) + (\text{Liters} \times \text{Herbicide Cost}),$$

where Herbicide Cost represents the per liter cost of the herbicide Round Up Max, estimated at $0.1023 (J. M. Verjans 2007, Eco-Forest S.A., Panama City, Panama, personal communication). The total cost of mechanical and chemical treatments was calculated by adding together the separate costs of mechanical and chemical treatments. For each species, differences were tested using an ANOVA and Tukey's HSD. This cost analysis does not include land purchase, seedling purchase, transportation, pesticide purchase, and application. Direct costs reflect their cost the year incurred. Because the Panamanian balboa is dollarized, further adjustments were not made to direct costs. We performed all statistical analyses using SAS version 9.1.3, unless indicated otherwise (SAS Institute, Inc., Cary, NC, U.S.A.).

## Results

### Tree Growth and Mortality

*Terminalia amazonia* saplings after 3 years of growth differed significantly for both mechanical cleaning and herbicide treatments (Table 1). Herbicide application significantly improved growth for all parameters (Figs. 1 & 2). In treatments with and without herbicide, individuals in higher frequency mechanical treatments had greater basal diameter, height, live crown height, crown diameter, and wood volume index (Figs. 1 & 2). For basal diameter, crown diameter, and wood volume index, the saplings in the no-herbicide treatment with the most frequent mechanical cleanings had statistically similar values as those in the herbicide treatment with two mechanical cleanings per year (Figs. 1 & 2). *Terminalia amazonia* saplings grew faster in total height and basal diameter in the last year of the study in all treatments receiving herbicide and in the no-herbicide treatment with four and seven mechanical cleanings (Fig. 1).

**Table 1.** ANOVA of structural characteristics of *Terminalia amazonia* in *Saccharum spontaneum* grasslands of the PCW under seven different grass control treatments.

| | | *p Value* | |
|---|---|---|---|
| *Response Variable* | $r^2$ *(%)* | *Mechanical* | *Herbicide* |
| Basal diameter (cm) | 50.30 | <0.0001 | <0.0001 |
| Height (m) | 44.07 | <0.0001 | <0.0001 |
| Live crown height (m) | 45.09 | <0.0001 | <0.0001 |
| Crown diameter (m) | 45.58 | <0.0001 | <0.0001 |
| Wood volume index ($m^3$/ha)* | 53.90 | <0.0001 | <0.0001 |

* Natural log transformed for analysis.

*Tectona grandis* saplings responded similarly to the seven treatment combinations as *Ter. amazonia* saplings, exhibiting significant differences for herbicide and mechanical cleaning treatments (Table 2). For all structural characteristics, all paired comparisons of mechanical cleaning within herbicide application and herbicide application within mechanical cleaning were significantly different. Individuals of *Tec. grandis* in the herbicide treatment with the most frequent mechanical cleanings had the highest values for all morphological variables (Fig. 1). There were no significant differences between individuals receiving four and seven annual mechanical cleanings in plots receiving herbicide applications. Individuals in the no-herbicide treatment with seven annual cleanings had similar values to those in the herbicide treatment with two annual cleanings for all morphological variables (Fig. 1). Total height and basal diameter growth of *Tec. grandis* saplings were relatively even across the 3 years of the study and did not exhibit faster growth in the last year of the study as was the case for *Ter. amazonia* saplings (Fig. 1).

Total mortality of both species did not differ significantly by species (log-linear model, Pearson statistic $= 1.3344$, $p = 0.3266$) nor by the combination of species and weed control treatments ($p = 0.0771$) but did by weed control treatment ($p < 0.0001$). Total mortality of *Ter. amazonia* decreased with increasing frequency of mechanical cleanings for both herbicide treatments (Fig. 3). There were significant differences for mortality between mechanical cleanings (log-linear model, negative binomial distribution, dispersion parameter $= 1.3356$, $p < 0.0001$) and herbicide treatments ($p = 0.0224$) but not for the combination of the two treatments ($p = 0.0672$). Mortality of *Tec. grandis* saplings was also negatively correlated with the frequency of mechanical cleanings for both herbicide treatments (Fig. 3). There were significant differences between mechanical cleaning treatments (log-linear model, dispersion parameter $= 1.3078$, $p = 0.0306$) and herbicide treatments ($p = 0.0002$) but not for the combination of herbicide and mechanical treatments ($p = 0.894$). For both species, annual mortality also varied significantly (log-linear model, negative binomial distribution, $df = 2$, *Ter. amazonia*, dispersion parameter $= 1.147$, $p = 0.0158$; *Tec. grandis*, Pearson statistic $= 0.9141$,

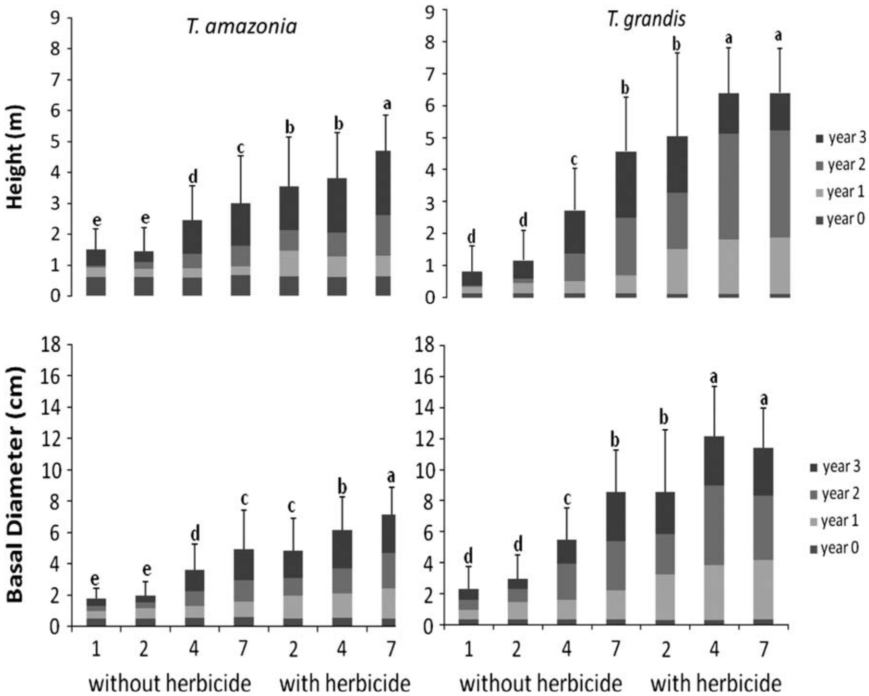


Figure 1. ANOVA of structural characteristics of two timber species in *Saccharum spontaneum* grasslands in the PCW under seven different grass control treatments (ANOVA, Tukey's HSD, 95% confidence interval, $\alpha = 0.05$, $df = 6$).

$p = 0.0004$). Annual mortality patterns differed by species, with mortality generally increasing for *Ter. amazonia* and decreasing for *Tec. grandis* (Fig. 3). After minimal mortality in year 1 across all treatments, *Ter. amazonia* seedlings in treatments receiving no herbicide and one or two mechanical cleanings and those receiving herbicide and two mechanical cleanings suffered considerable mortality in years 2 and 3 (Fig. 3). The majority of mortality in the aforementioned treatments occurred in year 3 (Fig. 3). Conversely, *Tec. grandis* seedlings in treatments receiving no herbicide suffered considerable mortality in year 1 relative to those in treatments receiving herbicide (Fig. 3). In year 2, *Tec. grandis* seedlings in treatments not receiving herbicide and one or two mechanical cleanings suffered more than 50% of its total mortality (Fig. 3). Across all treatments, mortality in year 3 was negligible for *Tec. grandis* (Fig. 3).

#### Canal Grass Height and Competition

After 3 years, *Saccharum spontaneum* height in pure plots of *Tec. grandis* decreased significantly by mechanical cleaning (Fig. 4; generalized linear model [GLM], $r^2 = 81.64\%$, $F = 84.37$, $p < 0.0001$) and herbicide treatments (Fig. 4; GLM, $r^2 = 81.64\%$, $F = 9.31$, $p = 0.005862$) but not by the combination of the two treatments (Fig. 4; GLM, $r^2 = 81.64\%$, $F = 4.1445$, $p = 0.053988$). In pure plots of *Ter. amazonia*, height of *S. spontaneum* also decreased by mechanical cleaning (Fig. 4; GLM, $r^2 = 79.49\%$, $F = 47.6483$, $p < 0.0001$) and herbicide application (Fig. 4; GLM, $r^2 = 79.49\%$, $F = 24.971$, $p < 0.0001$) but not by the combination of the two main effects (Fig. 4; GLM, $r^2 = 79.49\%$, $F = 1.0048$, $p = 0.3287$). *Saccharum spontaneum* competition differed significantly by the combination of herbicide and mechanical cleanings in plots of *Tec. grandis* (simulated $\chi^2 = 62.00$, $p = 0.000$) and *Ter. amazonia* ($\chi^2 = 52.00$, $p = 0.000$).

Mortality of *Ter. amazonia* saplings was predicted significantly by *S. spontaneum* height (log-linear model, dispersion statistic $= 1.4455$, $\chi^2 = 16.84$, $p < 0.0001$) and the *S. spontaneum* competition scalar (log-linear model, dispersion statistic $= 1.7473$, $\chi^2 = 11.85$, $p = 0.0006$). *Tectona grandis* sapling mortality was significantly predicted by both the *S. spontaneum* height (log-linear model, dispersion statistic $= 0.9805$, $\chi^2 = 11.23$, $p = 0.0008$) and the *S. spontaneum* competition scalar (log-linear model, dispersion statistic $= 0.9669$, $\chi^2 = 8.38$, $p = 0.0038$).

#### Direct Costs

Direct costs of grass control did not differ significantly between species (ANOVA, $df = 1$, $r^2 = 0.001\%$, $F = 0.03$, $p = 0.867$). In plots of *Ter. amazonia*, grass control costs varied significantly by herbicide application (GLM, $r^2 = 89.84\%$, $F = 31.89$, $p < 0.0001$), mechanical cleanings (GLM, $r^2 = 89.84\%$, $F = 46.05$, $p < 0.0001$), and the combination of both treatments (GLM, $r^2 = 89.84\%$, $F = 7.86$, $p = 0.0028$). All paired comparisons of herbicide application within mechanical cleaning were significant, whereas only mechanical cleaning within herbicide application comparisons at intermediate frequencies (two and four

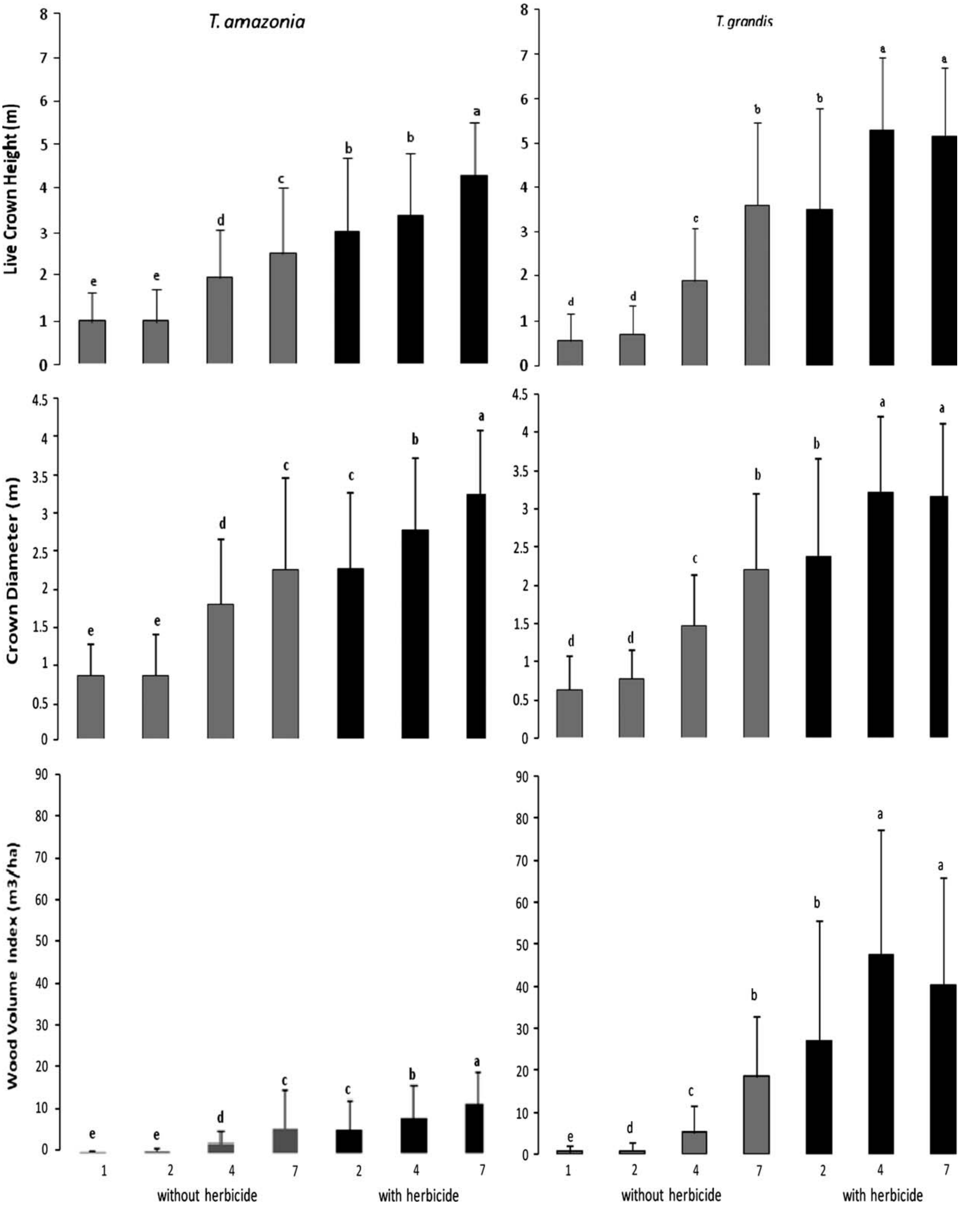


Figure 2. ANOVA of structural characteristics of two timber species in *Saccharum spontaneum* grasslands in the PCW under seven different grass control treatments (ANOVA, Tukey's HSD, 95% confidence interval, $\alpha = 0.05$, $df = 6$).

annual cleanings) were significantly different. Plots that were mechanically cleaned with the greatest frequency were equally expensive for both herbicide treatments (Fig. 5). Grass control costs increased significantly with the frequency of mechanical cleanings for both herbicide treatments (Fig. 5). Grass control costs of *Tec. grandis*

**Table 2.** ANOVA of structural characteristics of *Tectona grandis* in *Saccharum spontaneum* grasslands of the PCW under seven different grass control treatments.

| | | *p Value* | |
|---|---|---|---|
| *Response Variable* | $r^2$ *(%)* | *Mechanical* | *Herbicide* |
| Basal diameter (cm) | 62.36 | <0.0001 | <0.0001 |
| Height (m) | 62.69 | <0.0001 | <0.0001 |
| Live crown height (m) | 55.93 | <0.0001 | <0.0001 |
| Crown diameter (m) | 52.23 | <0.0001 | <0.0001 |
| Wood volume index ($m^3$/ha)* | 68.65 | <0.0001 | <0.0001 |

* Natural log transformed for analysis.

plots were significantly different for mechanical cleanings (GLM, $r^2 = 69.64\%$, $F = 15.44$, $p < 0.0001$) but not for herbicide application (GLM, $r^2 = 69.64\%$, $F = 0.29$, $p = 0.5976$) nor for the combination of the two main effects (GLM, $r^2 = 69.64\%$, $F = 0.50$, $p = 0.6138$). The most expensive grass control treatment in *Tec. grandis* plots was the combination of no herbicide and seven annual mechanical cleanings (Fig. 5). Grass control costs increased with the frequency of mechanical cleanings for both herbicide treatments (Fig. 5).

## Discussion

### Tree Growth and Mortality

The combinations of mechanical cleanings and herbicide application used for this experiment were designed to shift the competitive advantage in *Saccharum spontaneum*–dominated areas in order to facilitate the growth of *Tectona grandis* and *Terminalia amazonia* saplings. The annual application of herbicide and more frequent mechanical cleanings prevented *S. spontaneum* from overtopping and shading out the seedlings. For all variables of tree growth, both species responded significantly to herbicide application and mechanical cleanings. In plots receiving herbicide and frequent mechanical cleanings, trees were taller, had thicker stems, and had wider, deeper crowns.

For all growth parameters, individuals of *Tec. grandis* receiving herbicide and four mechanical cleanings did not differ significantly from those receiving herbicide and seven mechanical cleanings. *Terminalia amazonia* seedlings continued to respond positively to more frequent mechanical cleanings, because there were significant differences for all growth characteristics between individuals receiving herbicide and four mechanical cleanings and those receiving herbicide and seven mechanical cleanings. Not only did saplings of both species grow better in plots that received herbicide and frequent mechanical cleanings, but they also suffered lower total mortality. *Terminalia amazonia* was more tolerant of initial growing conditions than *Tec. grandis* in terms of mortality, most notably in treatments receiving no herbicide. Annual mortality trends shifted dramatically by year 3 for both species, increasing for *Ter. amazonia* in treatments receiving less frequent mechanical cleanings and decreasing uniformly for *Tec. grandis*. These results corroborate those of a *P. setaceum* control study in Hawaii, in which native plant cover increased significantly in more aggressive grass control treatments (Cabin et al. 2002). Differences in all growth characteristics between species were notable, especially wood volume index, although they were not analyzed quantitatively.

These results support previous studies of young plantations in Costa Rica and Panama in which exotic species (including *Tec. grandis*) exhibited superior growth to that of native species (Piotto et al. 2003; Wishnie et al. 2007). Differences in species-specific growth patterns possibly explain the relatively superior initial growth of *Tec. grandis*, as *Ter. amazonia* grew slowly during the first 2 years of this study before accelerating its growth in year 3. Inorganic fertilizer application did not increase *Ter. amazonia* growth significantly in degraded pastures in Costa Rica after 2 years, while a pattern of increased growth after 4 and 8 years was observed when *Ter. amazonia* was intercropped

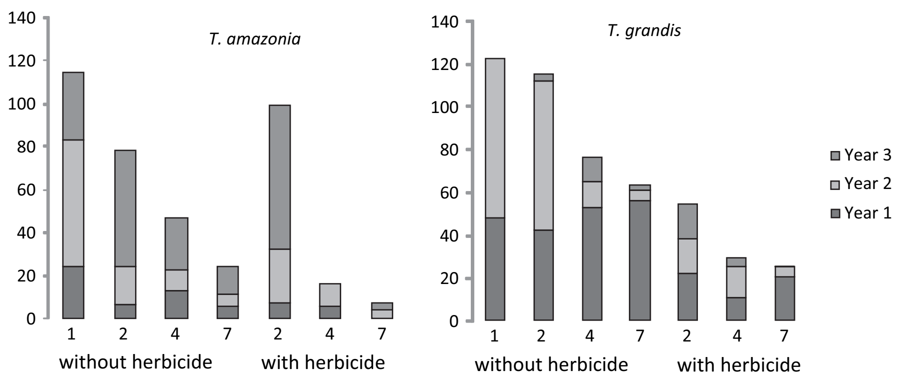


Figure 3. Mortality of two timber species in *Saccharum spontaneum* grasslands in the PCW under seven different grass control treatments after 3 years (*Terminalia amazonia*, initial amount of live saplings = 1,568, total dead saplings = 386; *Tectona grandis*, initial amount of live saplings = 1,586, total dead saplings = 486).

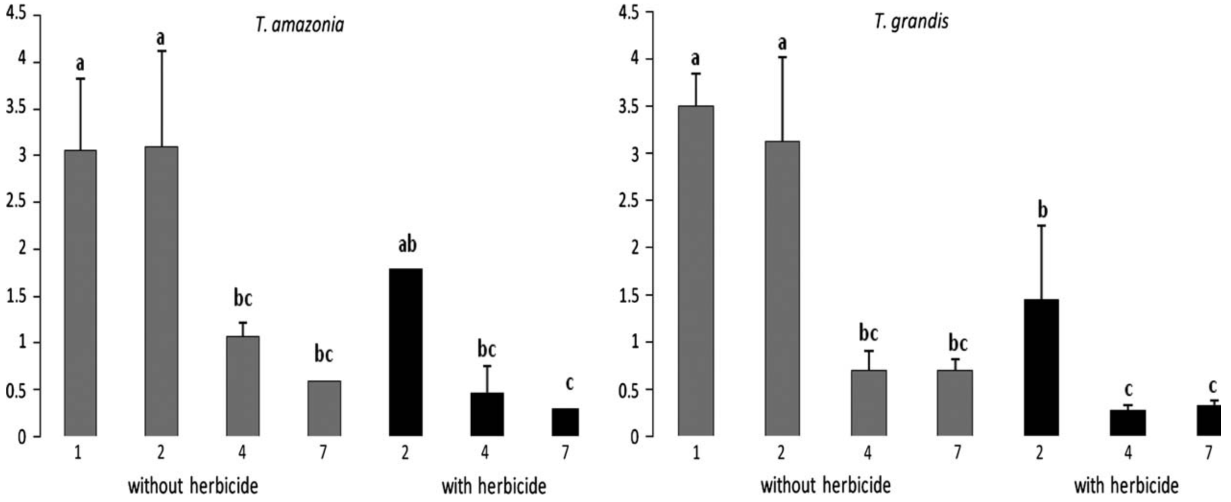


Figure 4. Canal grass height after 4 years in plots of two timber species in the PCW under seven different grass control treatments (ANOVA, Tukey's HSD, 95% confidence interval, $\alpha = 0.05$, $df = 6$).

with woody N-fixing species (Nichols & Carpenter 2006). As we have presented 3-year growth data for timber species with estimated harvest rotations of approximately 20–25 years, it would be premature to extrapolate these results because growth rates of native tropical species can change unexpectedly over time (Redondo-Brenes 2005; Ugalde Arias & Gómez Flores 2006; F. Montagnini 2007, Yale University School of Forestry and Environmental Studies, New Haven, CT, personal communication).

### Canal Grass Height and Competition

Non-native grass species represent the greatest impediment to forest regeneration in many tropical ecosystems (Holl et al. 2000). Via shading, tree plantations can eliminate invasive grass species and facilitate natural forest succession (Anoka et al. 1991; Kuusipalo et al. 1995; Otsamo 2000; Jones et al. 2004; Hooper et al. 2005; Kim et al. 2006). In the present study, frequent mechanical cleanings and herbicide application significantly reduced the height growth of *S. spontaneum* and its ability to compete with *Ter. amazonia* and *Tec. grandis* saplings. Total mortality of both tree species studied decreased significantly in plots receiving frequent mechanical cleanings and herbicide application. The greater tree height, live crown height, and crown diameter of saplings in more intensive grass control treatments effectively shaded *S. spontaneum*, thereby limiting its height growth and ability to compete with surrounding vegetation. These results are not surprising as researchers have demonstrated the effectiveness of shading as a method for controlling invasive grass species in abandoned pasturelands in the tropics

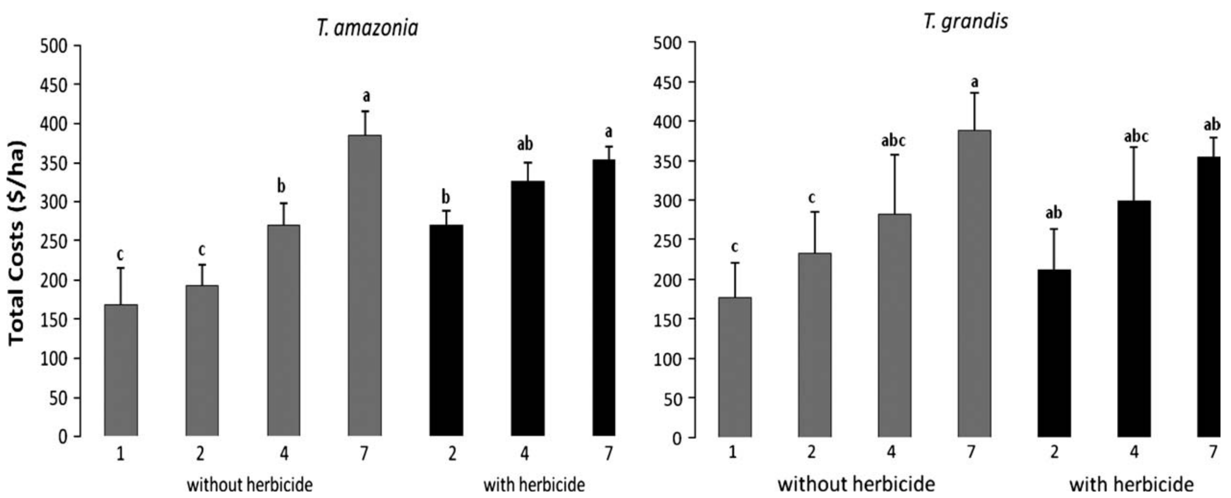


Figure 5. Grass control costs of two timber species in the PCW under seven different grass control treatments (ANOVA, Tukey's HSD, 95% confidence interval, $\alpha = 0.05$, $df = 6$).

(Kuusipalo et al. 1995; Cabin et al. 2002; Hooper et al. 2002, 2005; Kim et al. 2006).

Saplings of both species suffered greater total mortality and lower growth in treatments receiving less frequent mechanical cleanings and no herbicide application, corroborating results from previous studies in Panama, Costa Rica, and India (Cabin et al. 2002; MacDonald 2004; Hooper et al. 2005). *Terminalia amazonia*, however, has demonstrated good survival and growth with no grass control in abandoned pastures of Costa Rica (Nichols 1994). Low-intensity grass control treatments did not alter the competitive advantage of *S. spontaneum* over *Tec. grandis* and *Ter. amazonia* seedlings; *S. spontaneum* was approximately 1.0–2.0 m taller than saplings in these treatments. The focal species responded differently to the competition presented by *S. spontaneum* in these treatments over time. *Tectona grandis* mortality was greater in years 1 and 2 and tapered drastically in year 3; mortality of *Ter. amazonia* seedlings exhibited the opposite pattern, increasing significantly in year 3 after having suffered relatively low mortality in years 1 and 2. *Saccharum spontaneum* limited seedling growth in low-intensity grass control treatments by outcompeting the seedlings for light, as suggested by other studies in tropical pastures (Gerhardt & Fredrikkson 1995; Loik & Holl 1999, 2001). Competition for belowground resources, such as water and nutrients, might also have contributed to the physiological stress and greater mortality experienced by seedlings and their competitive disadvantage relative to *S. spontaneum* in low-intensity grass control treatments (Nepstad et al. 1990). Ecophysiological studies of both species under more controlled conditions could provide greater insight into the contrasting mortality patterns of *Ter. amazonia* and *Tec. grandis* seedlings in low-intensity grass control treatments.

### Direct Costs

The direct costs of *S. spontaneum* control did not differ between the studied species, reflecting the similar crown morphology—deep, relatively narrow crowns—of both species at the sapling stage. Grass control costs increased with the intensity of the effort to control *S. spontaneum* growth. Although more frequent mechanical cleanings increased grass control costs in plots of both species, only in *Ter. amazonia* plots did herbicide application significantly increase grass control costs. Herbicide application did not increase the cost for controlling *S. spontaneum* in *Tec. grandis* plots, indicating that the additional cost of herbicide application was mitigated by a decrease in time required to perform the mechanical cleanings.

It is important to note that the direct costs of seven different grass control treatments reported in the present study represent the partial costs of plantation establishment after 3 years in *S. spontaneum*–dominated areas of the PCW. Per hectare estimates of total plantation establishment costs in the PCW range between $1,590 and $2,570 in year 1, $620 and $1,980 in year 2, and $550 and $1,880 in year 3 (PRORENA 2007, unpublished data; Ugalde Arias & Gómez Flores 2006). Even the most expensive grass control treatment (approximately $400 over 3 years) represents only 6–14% of total plantation establishment costs after 3 years.

This analysis did not incorporate valuation methods that account for environmental services generated by reforestation, such as biodiversity, watershed protection, or carbon sequestration (Condit et al. 2001; Cusack & Montagnini 2004; Nichols & Carpenter 2006; Zamora & Montagnini 2007). Such valuation methods might have increased the value of young *Ter. amazonia* plantations, which have been found to provide complexly structured habitat for wildlife (Nichols & Carpenter 2006).

The dramatic differences across growth characteristics of both studied species between *S. spontaneum* control treatments suggest that land managers in the PCW should aggressively control *S. spontaneum* in order to optimize timber production. Based on our results, we recommend fire suppression, annual herbicide application, and at least four mechanical cleanings per year in *Tec. grandis* and *Ter. amazonia* plantations during the first 3 years of establishment. The relatively slow growth of *Ter. amazonia* suggests the need to continue aggressive grass control beyond the first 3 years of establishment. Aggressive grass control might also reduce mortality in the latter stages of establishment, because *Ter. amazonia* saplings remained susceptible to competition from *S. spontaneum*. Intercropping *Ter. amazonia* with native N-fixing tree species, such as *Inga* spp., could promote better growth of the focal species given its preference for organic nitrogen as well as limit competition with *S. spontaneum* (Jones et al. 2004; Nichols & Carpenter 2006).

## Conclusions

Our results suggest that reforestation of *Saccharum spontaneum* grasslands is both ecologically and economically feasible in the PCW, particularly when land managers exclude fire and invest in aggressive grass control strategies. The two commercial species studied, *Terminalia amazonia* and *Tectona grandis*, responded positively in terms of growth characteristics to increasing intensity of mechanical cleanings and herbicide application. Grass control treatments of increasing intensity reduced the growth and the competitive ability of *S. spontaneum*, thereby catalyzing tree growth, whereas costs of grass control treatments increased with intensity. The rapid accumulation of wood volume was enabled by frequent mechanical cleanings and herbicide application. The slow growth of *Ter. amazonia*, relative to that of *Tec. grandis*, suggests the need to continue grass control treatments beyond the initial 3 years of establishment. Further studies are needed to evaluate whether intercropping *Ter. amazonia* with a nitrogen-fixing legume adequately controls *S. spontaneum* while also promoting faster growth of *Ter. amazonia*.

As suggested in previous studies, the greater structural connectivity provided by tree cover in rural landscapes has been correlated positively with biodiversity (e.g., Harvey et al. 2005; Nichols & Carpenter 2006; Sáenz 2006). Individuals of both species in treatments receiving frequent mechanical cleanings and herbicide application exhibited structural characteristics associated with those that promote greater biodiversity of multiple taxa. Given the apparent feasibility of reforestation in *S. spontaneum* grasslands and the conservation value of the PCW, further studies are still needed to better understand the role of reforested areas in improving the structural connectivity between protected areas and national parks within the PCW. Current regulations established by the Panama's Ministry of the Environment for the PCW have resulted in a modest increase in forest cover in the past 5 years; more aggressive efforts to reforest the region could increase dramatically its biodiversity and hydrological value, carbon sequestration potential, and income of its inhabitants.

### Implications for Practice

- Aggressive grass control, despite its higher direct costs, is needed to minimize mortality and maximize growth of timber species in *Saccharum spontaneum* grasslands.
- Mixed native species plantations that combine fast-growing leguminous species with timber species are likely to reduce direct costs related to grass control, as well as fertilization costs.
- Reforested areas in the PCW might help to maintain biodiversity in a human-dominated landscape by providing greater structural connectivity between protected areas and national parks.

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## LITERATURE CITED

Affleck, D. 2006. Poisson mixture models for regression analysis of stand-level mortality. Canadian Journal of Forest Research **36:** 2994–3006.

Anoka, U. A., I. O. Akobundu, and S. N. C. Okonkwo. 1991. Effects of *Gliricidia sepium* (Jacq.) Steud and *Leucaena leucephala* (Lam.) de Wit on growth and development of *Imperata cylindrica* (L.) Raeuschel. Agroforestry Systems **16:**1–12.

Autoridad del Canal de Panamá. 2006. Propuesta de ampliación del Canal de Panamá. Autoridad del Canal de Panamá, Panama City, Panama.

Autoridad del Canal de Panamá. 2007. Panama City, Panama (available from http://www.pancanal.com/esp/general/así-es-el-canal.html) accessed 1 May 2007.

Brooker, R. W. 2006. Plant-plant interactions and environmental change. New Phytologist **171:**271–284.

Cabin, R. J., S. G. Weller, D. H. Lorence, S. Cordell, L. J. Hadway, R. Montgomery, D. Goo, and A. Urakami. 2002. Effects of light, alien grass, and native species additions on Hawaiian dry forest restoration. Ecological Applications **12:**1595–1610.

Carrasquilla, L. G. 2005. Árboles y arbustos de Panamá [Trees and shrubs of Panama]. Editora Novo Art, Panama City, Panama.

Chikoye, D., V. M. Manyong, R. J. Carsky, F. Ekeleme, G. Gbehouno, and A. Ahanchede. 2002. Response of speargrass (*Imperata cylindrica*) to cover crops integrated with handweeding and chemical control in maize and cassava. Crop Protection **21:**145–156.

Condit, R., W. D. Robinson, R. Ibáñez, S. Aguilar, A. Sanjur, R. Martínez, et al. 2001. The status of the Panama Canal Watershed and its biodiversity at the beginning of the 21st century. BioScience **51:**389–398.

Croat, T. B. 1978. The flora of Barro Colorado Island. Stanford University Press, Palo Alto, California.

Cusack, D., and F. Montagnini. 2004. The role of native species plantations in recovery of understory diversity in degraded pasturelands of Costa Rica. Forest Ecology and Management **188:**1–15.

da Silva Junior, M. C., F. R. Scarano, and F. De Souza Cardel. 1995. Regeneration of an Atlantic forest formation in the understorey of a *Eucalyptus grandis* plantation in south-eastern Brazil. Journal of Tropical Ecology **11:**149–152.

Dietrich, W. E., D. M. Windsor, and T. Dunne. 1996. Geology, climate, and hydrology of Barro Colorado Island. Pages 21–46 in E. G. Leigh, A. S. Rand, and D. M. Windsor, editors. The ecology of a tropical forest. Smithsonian Institute Press, Washington, D.C.

FAO (Food and Agricultural Organization of the United Nations). 2007. Forestry country profiles. FAO (available from http://www.fao.org/forestry/site/18308/en/pan/) accessed 26 March 2007.

Fleming, T. H. 1973. Numbers of mammal species in North and Central American forest communities. Ecology **54:**555–563.

Gerhardt, K., and D. Fredrikkson. 1995. Biomass allocation by broad-leaf mahogany seedlings, *Swietenia macrophylla* (King), in abandoned pasture and secondary dry forest in Guanacaste, Costa Rica. Biotropica **27:**174–182.

Gotelli, N. J., and G. L. Entsminger. 2004. EcoSim: null models software for ecology (version 7). Acquired Intelligence, Inc. and Kesey-Bear, Jericho, Vermont (available from http://garyentsminger.com/ecosim/index.html) accessed 15 April 2007.

Griscom, H. P., E. K. V. Kalko, and M. S. Ashton. 2007. Frugivory by small vertebrates within a deforested, dry tropical region of Central America. Biotropica **39:**278–282.

Guariguata, M. R., R. Rheingans, and F. Montagnini. 1995. Early woody invasion under tree plantations in Costa Rica: implications for forest restoration. Restoration Ecology **3:**252–260.

Gutiérrez, R. R., and H. I. Díaz. 1999. Memoria de las estadísticas de los recursos forestales de Panama. Workshop for Forest Resources Assessment Programme (FRA 2000). Turrialba, Costa Rica, 17–21 May 1999.

Hammond, B. 1999. *Saccharum spontaneum* (Gramineae) in Panama: the physiology and ecology of invasion. Pages 23–38 in M. S. Ashton, J. O'Hara, and R. Hauff, editors. Protecting watershed areas: case of the Panama Canal. Haworth Press, Binghamton, New York.

Harvey, C. A., C. Villanueva, J. Villacis, M. Chacon, D. Munoz, M. Lopez, et al. 2005. Contribution of live fences to the ecological integrity of agricultural landscapes in Central America. Agriculture, Ecosystems & Environment **111:**200–230.

Holl, K. D., M. E. Loik, E. H. V. Lin, and I. A. Samuels. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. Restoration Ecology **8:** 339–349.

Hooper, E., R. Condit, and P. Legendre. 2002. Responses of 20 native tree species to reforestation strategies for abandoned farmland in Panama. Ecological Applications **12:**1626–1641.

Hooper, E., P. Legendre, and R. Condit. 2005. Barriers to forest regeneration of deforested and abandoned land in Panama. Journal of Applied Ecology **42:**1165–1174.

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. Forest Ecology and Management **191:**171–183.

Kim, T. J., F. Montagnini, N. Cedeño, D. Dent, and E. Mariscal. 2006. Investigation of shading as a method for controlling wild sugarcane on abandoned lands (Panama). Ecological Restoration **24:**203.

Kraenzel, M., A. Castillo, T. Moore, and C. Potvin. 2003. Carbon storage of harvest-age teak (*Tectona grandis*) plantations, Panama. Forest Ecology and Management **173:**213–225.

Kuusipalo, J., G. Adjers, Y. Jafarsidik, A. Otsamo, K. Tuomela, and R. Vuokko. 1995. Restoration of natural vegetation in degraded *Imperata cylindrica* grassland: understorey development in forest plantations. Journal of Vegetation Science **6:**205–210.

Leigh, E. G. 1999. Tropical forest ecology: a view from Barro Colorado Island. Oxford University Press, New York.

Leigh, E. G., and D. Windsor. 1982. Forest production and regulation of primary consumers on Barro Colorado Island. Pages 111–122 in E. G. Leigh Jr, A. S. Rand, and D. Windsor, editors. Ecology of a tropical forest. Smithsonian Institution, Washington, D.C.

Loik, M. E., and K. D. Holl. 1999. Photosynthetic responses to light for rainforest seedlings planted in abandoned pasture, Costa Rica. Restoration Ecology **7:**382–391.

Loik, M. E., and K. D. Holl. 2001. Photosynthetic responses of tree seedlings in grass and under shrubs in early-successional tropical old fields, Costa Rica. Oecologia **127:**40–50.

MacDonald, G. E. 2004. Cogongrass (*Imperata cylindrica*)—biology, ecology, and management. Critical Reviews in Plant Sciences **23:**367–380.

Martínez, R. E., D. Luque, M. Calderón, A. Somoza, N. Camacho, I. Tejeda, and A. S. Montoya. 2006. Programa de Vigilancia de la Cobertura Vegetal Región Oriental de la Cuenca del Canal. Autoridad Nacional del Ambiente and Autoridad del Canal de Panamá, Panama City, Republic of Panama.

Montero, M., and M. Kanninen. 2003. Biomasa y carbono en plantaciones de *Terminalia amazonia* en la zona Sur de Costa Rica. Revista Forestal Centroamericana **39:**50–56.

Nepstad, D., C. Uhl, and E. A. Serrão. 1990. Surmounting barriers to forest regeneration in abandoned, highly degraded pastures: a case study from Paragominas, Pará, Brazil. Pages 215–229 in A. B. Anderson, editor. Alternatives to deforestation: steps toward sustainable use of the Amazon rain forest. Columbia University Press, New York.

Nepstad, D. C., C. Uhl, C. A. Pereira, and J. M. Cardoso da Silva. 1996. A comparative study of tree establishment in abandoned pasture and mature forest of Eastern Amazonia. Oikos **76:**25–39.

Newbould, P. J. 1967. Methods for estimating the primary production of forests. IBP handbook 2. Blackwell Scientific, Oxford, United Kingdom.

Nichols, J. D. 1994. *Terminalia amazonia* development of a native species for reforestation and agroforestry. Commonwealth Forest Review **73:**9–13.

Nichols, J. D., and F. L. Carpenter. 2006. Interplanting *Inga edulis* yields nitrogen benefits to *Terminalia amazonia*. Forest Ecology and Management **233:**344–351.

Otsamo, R. 2000. Secondary forest regeneration under fast-growing forest plantations on degraded *Imperata cylindrica* grasslands. New Forests **19:**69–93.

Parrotta, J. A. 1992. The role of plantation forests in rehabilitating degraded tropical ecosystems. Agriculture, Ecosystems & Environment **41:**115–133.

Petit, B., and F. Montagnini. 2004. Growth equations and rotation ages of ten native tree species in mixed and pure plantations in the humid neotropics. Forest Ecology and Management **199:**243–257.

Piotto, D., Montagnini, F., Ugalde, L., and Kanninen, M. 2003. Performance of forest plantations in small- and medium-sized farms in the Atlantic lowlands of Costa Rica. Forest Ecology and Management **175:**195–204.

Redondo-Brenes, A. 2005. Payment for environmental services in Costa Rica: carbon sequestration estimations of native tree plantations. Tropical Resources Institute Bulletin **24:**20–29.

Sáenz, J. 2006. Biodiversity in agricultural landscapes—the need for new focuses for its conservation. Pages 33–39 in D. Craven, editor. Biodiversity in human-impacted landscapes. Vol. 1. Summary of conference proceedings, 19 November 2006, Panama City, Panama.

Schabenberger, O. S., T. G. Gregoire, and F. Kong. 2000. Collections of simple effects and their relationship to main effects and interactions in factorials. The American Statistician **54:**210–214.

Shono, K., S. J. Davies, and Y. K. Chua. 2007. Performance of 45 native tree species on degraded lands in Singapore. Journal of Tropical Forest Science **19:**25–34.

Standley, P. C. 1933. The flora of Barro Colorado Island, Panama. The Arnold Arboretum of Harvard, Jamaica Plain, Massachusetts.

The Canal Zone Experiment Gardens. 1931. Science **74:**362.

Ugalde Arias, L., and M. Gómez Flores. 2006. Perspectivas económicas y ambientales de las plantaciones de teca bajo manejo sostenible, en Panamá. Centro Agronómico Tropical de Investigación y Enseñanza, Turrialba, Costa Rica.

Vásquez Morera, A. 1999. Estudio semidetallado de suelos y determinación de la capacidad de uso de las tierras (globos sur, central y norte). Ecos S.A., San José, Costa Rica.

Vitousek, P. M., K. M. D'Antonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997. Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology **21:** 1–16.

Wieder, R. K., and S. J. Wright. 1995. Tropical forest litter dynamics and dry season irrigation on Barro Colorado Island, Panama. Ecology **76:**1971–1979.

Windsor, D. M. 1990. Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. Smithsonian Institution Press, Washington, D.C.

Wishnie, M. H., D. H. Dent, E. Mariscal, N. Cedeño, J. Deago, D. Ibarra, R. Condit, and P. M. S. Ashton. 2007. Initial performance and reforestation potential of 24 tropical tree species planted across a precipitation gradient in the Republic of Panama. Forest Ecology and Management **243:**39–49.

Zamora, C. O., and F. Montagnini. 2007. Seed rain and seed dispersal agents in pure and mixed plantations of native trees and abandoned pastures at La Selva Biological Station, Costa Rica. Restoration Ecology **15:**453–461.