New Forests (2015) 46:157–165
DOI 10.1007/s11056-014-9448-2

SHORT COMMUNICATION

Forest regeneration under *Tectona grandis* and *Terminalia amazonia* plantation stands managed for biodiversity conservation in western Panama

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Received: 24 October 2013 / Accepted: 7 August 2014 / Published online: 20 August 2014

Abstract Plantations of *Tectona grandis* in Central America are widely perceived to suppress forest regeneration in their understories, yet few studies have tested this assumption. We surveyed the understory woody vegetation growing in 7-year-old stands of *T. grandis* and the native tree species *Terminalia amazonia* in a plantation in western Panama that was managed with both commercial timber and biodiversity conservation objectives. We predicted that if *T. grandis* suppressed forest regeneration then the understories of *T. grandis* stands would have a lower density of woody stems, smaller stems, and fewer species than stands of *T. amazonia*. None of our predictions were supported. Densities of woody stems were $0.56 \pm 0.21\ m^{-2}$ (mean ± SE) and $0.64 \pm 0.10\ m^{-2}$ in *T. grandis* and *T. amazonia* understories, respectively. Stem height structure was similar under both species, where stems <1 m height dominated. Understory species richness did not differ between the two species; in total, 27 and 30 woody species were sampled in *T. grandis* and *T. amazonia* stands, respectively. However, understory species composition differed between the two crop species. Overall, our results are inconsistent with the idea that *T. grandis* plantations suppress forest regeneration and suggest that the lack of woody vegetation in other *T. grandis* plantation understories may be attributable to management actions, such as understory thinning, rather than species effects of *T. grandis*. Further

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research is needed to compare *T. grandis* and native species for their effects on forest regeneration.

Keywords Diversity · Native species · Reforestation · Restoration

Introduction

Reforesting degraded lands in the tropics, such as abandoned cattle pastures, has the potential to restore ecosystem services and biodiversity (Martinez-Garza and Howe 2003; Ciccarese et al. 2012). Tree plantations are often promoted as a means of encouraging forest regeneration on degraded lands because they stabilize soils and accelerate the development of diverse communities, including plants, birds, and insects (Lugo 1992; Yirdaw 2001; Hartley 2002). Tree plantations tie economic incentives to ecological rehabilitation, providing a practical option for large-scale reforestation in developing countries that occupy most tropical areas (Lamb 1998). When ecological rehabilitation goals are incorporated into tree plantations, it is important to understand how decisions such as species selection affect forest regeneration in plantation understories.

On highly degraded lands, barriers to recolonization by native forest species, such as a lack of seed arrival, grass invasion, and topsoil loss, inhibit secondary forest regeneration (Lamb et al. 2005). Studies throughout the tropics have found that tree plantations can serve as 'catalysts' for secondary regeneration in these areas, whereby they increase the stem density and species richness of understory plant communities compared to areas without planted trees (Parrotta et al. 1997; Lamb et al. 2005). The mechanisms responsible for these increases are thought to be trees' ability to attract seed-dispersers (Wunderle 1997), suppress grasses through shading (Kuusipalo et al. 1995; Jones et al. 2004), and improve soil conditions through litter inputs (Parrotta 1992). However, tree species vary greatly in their effects on understory regeneration (Powers et al. 1997; Slocum and Horvitz 2000). For example, among four crop tree species in experimental trials in Costa Rica, the density and species richness of understory woody stems ranged 0.15–0.79 stems m^{-2} and 0.10–0.26 species m^{-2}, respectively, 6 years after plantation establishment (Carnevale and Montagnini 2002).

Throughout Central America, *Tectona grandis* L.f. (teak)—a species native to Southeast Asia—is commonly used in commercial plantations. For example, in 2008 it accounted for 63.7 % of the plantation area in Panama (ANAM 2009). *T. grandis* is widely perceived to inhibit understory forest regeneration and cause soil erosion, yet there is remarkably little evidence that its effects are different from those of native species (Pandey and Brown 2000; Healey and Gara 2003; Evans and Turnbull 2004; Leopold and Salazar 2008). We used a timber plantation in western Panama that was planted in a mosaic of monocultures of various tree species to compare the understory vegetation in stands of *T. grandis* and the native species *Terminalia amazonia* (J.F. Gmel.) Exell. (Hereafter, the two focal crop species are referred to by genus name.) Experimental and commercial plantations of *Terminalia* have been shown to encourage recruitment of seedlings in the understory compared to unplanted areas (Cusack and Montagnini 2004; Butler et al. 2008). We predicted that if *Tectona* inhibits understory regeneration, then the understory in stands of *Tectona* would have lower density of woody stems, stems with smaller stature, and lower species richness compared to stands of *Terminalia*.

Methods

Study site

This study was conducted in Las Lajas, Panama (81°53′W, 8°15′N), located within the wet tropical zone, with mean annual rainfall of 4,600 mm and a three-month dry season between January and April (van Breugel et al. 2011). The study site is 50 m above sea level and 8 km from the Pacific coast. Underlying soils are loamy clay and cattle pasture is the dominant land-use in the region. Data were collected on the Los Rios plantation owned by Futuro Forestal SA. Native forest was cleared in the 1920s for use as cattle pasture, which was abandoned in the 1990s and left fallow and relatively undisturbed until 1998–1999 when the naturally regenerating vegetation (except large trees of select species) was cleared by hand and tractor and the plantation was established.

The plantation was composed of 7-year-old monocultures of *Tectona*, *Terminalia*, and four other native tree species interspersed in a 68.9 ha area (Fig. 1). Plantation management embraced many of the biodiversity-enhancing actions proposed by Lamb (1998), e.g. wide bands near an intersecting river were left uncleared and unplanted to allow natural forest regeneration. Within the monoculture plantation stands, *Tectona* was planted at 3 m × 3 m spacing while *Terminalia* was planted at 5 m × 5 m spacing. Understory vegetation was cut with machetes for 2 years following planting. In the *Tectona* stands, vegetation was subsequently uncut except for vines that wrapped around crop trees. In the *Terminalia* stands, rows ca. 2.5 m wide were regularly cut with machetes in the vegetation around crop trees. Spaces between rows were left uncut except for branches that entered cut rows. The most recent of these cuts was made 6 weeks prior to sampling. Organic “bokatchi” fertilizer (a mix of fermented chicken manure, calcium, rice pellets, sawdust, ashes, and other ingredients) was applied to a <1 m diameter circle around each crop tree twice annually for three to 4 years following planting. Crop trees of both species were thinned one to 3 months prior to sampling.

Sampling design and analysis

In stands of each of the focal crop species, understory vegetation was sampled within eight randomly located 10 m × 10 m plots (Fig. 1). In October–November 2005, all free-standing woody plants with height >15 cm were measured for height and identified in the field or collected for later identification at the herbarium of the Smithsonian Tropical Research Institute, Panama City, Panama. Diameter at breast height (DBH, 130 cm height) was measured for individuals with DBH > 1 cm. For analyses of understory vegetation we excluded stems > 10 cm DBH, which were likely present when the plantations were established and therefore not subject to the influence of crop species during recruitment. Previous studies have effectively detected differences in understory plant communities among crop tree species with similar or smaller sapling areas (e.g. Powers et al. 1997; Carnevale and Montagnini 2002; Jones et al. 2004). A 20 m × 20 m plot was centered on each understory-sampling plot in which crop trees were measured for DBH with a diameter tape and height with a clinometer. These data were then used to calculate the crop-tree stem density, basal area, mean height, and mean DBH in each stand.

To test whether stem density of understory plants varied between stands of *Tectona* and *Terminalia*, we used Student’s *t* test with Welch’s correction for unequal variance. We tested whether understory stem height structure varied between stands of the two crop species by grouping stems into height classes (15–99, 100–200, >200 cm) and assessing

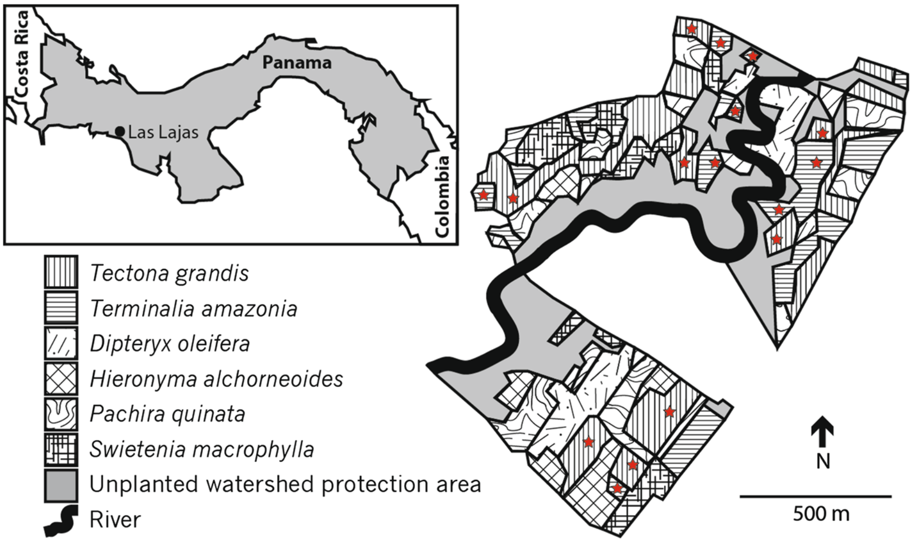


Fig. 1 Map of the study area with *inset* showing the location of the study site, Las Lajas, Panama. *Stars* indicate the locations of sample plots in stands of *Tectona* and *Terminalia*

the density of stems of each height class within each plot. ANOVA was used to test for differences in stem density among plots with crop species, height class within plot, and their interaction as fixed effects. For this analysis, stem density was log transformed to obtain homoscedasticity.

To examine the effect of crop species on understory species richness we constructed species-accumulation curves using individual-based rarefaction in EstimateS version 9 (Colwell 2013). We used the criteria of overlapping 95 % confidence intervals to determine whether the accumulation curves differed between crop species. To assess whether understory plant communities differed between crop species, we used non-metric multidimensional scaling (NMDS) to graphically represent variation in species composition among plots. For this analysis we used the metaMDS function in the R package vegan (Oksanen et al. 2013), which calculated the Bray-Curtis distance between each pairwise plot combination using a Wisconsin transformation of the square root of species abundances. To test whether the understory communities differed between crop species, we used a permutational multivariate analysis of variance (PERMANOVA) with the adonis function in vegan (Oksanen et al. 2013). For this analysis, the Bray-Curtis distance between plots was used as the response variable.

Results

A total of 950 woody plants of 39 species and 24 families were sampled in the plantation understory (woody plants <10 cm DBH; Table 1). Woody plant density was similar in the understories of *Tectona* and *Terminalia* stands; 0.56 ± 0.21 m^{-2} (mean ± SE) and 0.64 ± 0.10 m^{-2}, respectively ($t = 0.46$, $df = 9.95$, $P = 0.66$). The height structure of understory vegetation was also similar between the crop species (Fig. 2). Stems <100 cm tall were dominant under both crop species ($F = 51.7$; $df = 2, 28$; $P < 0.001$) while stem

Table 1 Number of plants of each species sampled in stands of *Tectona grandis* and *Terminalia amazonia*

Family	Species	Crop species	
		Tectona	*Terminalia*
Melastomataceae	Melastomataceae sp5	185	35
Annonaceae	*Xylopia frutescens* Aubl.	73	9
Melastomataceae	*Miconia argentea* (Sw.) DC.	56	51
Flacourtiaceae	*Casearia arguta* Kunth	28	83
Rubiaceae	*Genipa americana* L.	24	6
Dilliniaceae	*Curatella americana* L.	8	6
Tiliaceae	Tiliaceae sp1	8	4
Flacourtiaceae	*Casearia commersoniana* Cambess.	6	4
Anacardiaceae	*Mangifera indica* L. *	6	0
Piperaceae	*Piper hirtellipetiolum* C. DC.	6	67
Siparunaceae	*Siparuna guianensis* Aubl.	6	17
Malpighiaceae	*Byrsonima crassifolia* (L.) Kunth	5	8
Rutaceae	*Zanthoxylum setulosum* P. Wilson	5	12
Sterculiaceae	*Guazuma ulmifolia* Lam.	3	1
Cecropiaceae	*Cecropia peltata* L.	2	4
Melastomataceae	Melastomataceae sp1	2	1
Annonaceae	*Xylopia aromatica* (Lam.) Mart.	2	106
Fabaceace	*Pseudosamanea guachapele* (Kunth) Harms	1	0
Boraginaceae	*Cordia alliodora* (Ruiz & Pav.) Oken	1	33
Fabaceae	*Diphysa americana* (Mill.) M. Sousa	1	2
Myrtaceae	*Eugenia* sp1	1	0
Fabaceace	Fabaceae sp1	1	0
Rubiaceae	*Psychrotria* sp1	1	0
Araliaceae	*Schefflera morototoni* (Aubl.) Maguire, Stey. & Frod.	1	1
Simaruaceae	*Simaba cedron* Planch.	1	0
Anacardiaceae	*Spondias mombin* L.	1	0
Lamiaceae	*Tectona grandis* L.f. *	1	0
Clusiaceae	*Vismia baccifera* (L.) Tr. & Pl.	1	21
Anacardiaceae	*Anacardium excelsum* (Bert. & Balb. ex Kunth) Skeels	0	5
Meliaceae	*Cedrela odorata* L.	0	1
Coccolospermaceae	*Cochlospermum vitifolium* (Willd.) Spr.	0	4
Tiliaceae	*Luehea seemannii* Triana & Planch.	0	9
Melastomataceae	Melastomataceae sp2	0	11
Melastomataceae	Melastomataceae sp3	0	1
Melastomataceae	Melastomataceae sp4	0	2
Lauraceae	*Nectandra* sp1	0	1
Annonaceae	*Oxandra* sp1	0	1
Apocynaceae	*Stemmadenia* sp1	0	2
Combretaceae	*Terminalia amazonia* (J.F. Gmel.) Exell	0	6

Species that were identified only to the level of family or genus are listed with codes consisting of the family name or genus name, respectively, followed by a morphospecies number. Asterisks indicate species that are not native to Panama

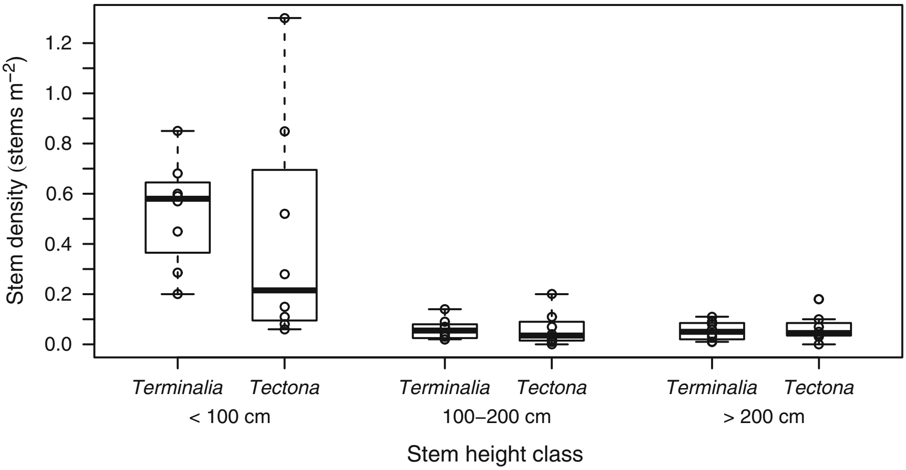


Fig. 2 Stem density of woody understory vegetation, stratified by size class, in stands of *Terminalia* and *Tectona*. Each *circle* represents one plot. *Boxes* enclose the 25th and 75th quartiles and are bisected by the medians. *Bars* extend to the 5th and 95th quartiles

density did not vary between crop species in any height class ($P > 0.42$). However, the structure of crop trees did vary between the two species; *Tectona* trees were larger and more closely spaced than *Terminalia* trees (Table 2).

The total number of species sampled was similar in the *Tectona* and *Terminalia* stands, 27 and 30 species, respectively. Species accumulation curves indicated no significant difference between the two crop species in their understory species richness, the 95 % confidence intervals overlapped throughout the curves (Fig. 3).

The composition of the understory plant communities varied between the two crop species. NMDS showed a trend for clustering within crop species, especially along axis 2 (Fig. 4). PERMANOVA analysis confirmed this visual trend; there was a significant effect of crop species on understory species composition ($F = 2.06$; $df = 1, 15$; $P = 0.023$). Twenty species were shared between stands of the two crop species, while eight species were restricted to *Tectona* stands and 11 were restricted to *Terminalia* stands. The most abundant species sampled in the *Tectona* and *Terminalia* stands were Mestomataceae sp5 (42 % of sampled plants) and *Xylopia frutescens* (22 % of sampled plants), respectively (Table 1). All species sampled in the *Terminalia* stands were native to Panama while two species in the *Tectona* stands were not native to Panama: one *Tectona* seedling and six *Mangifera indica* (mango) seedlings (Table 1).

Discussion

In a timber plantation managed with biodiversity conservation objectives, the understories of *Tectona* and *Terminalia* stands developed similar woody stem density, height structure, and species richness (Figs. 2 and 3). Since *Terminalia* has been shown to foster forest regeneration compared to unplanted abandoned pastureland (Cusack and Montagnini 2004; Butler et al. 2008), our results are inconsistent with the common assumption that *Tectona* suppresses forest regeneration in its understory. Both crop species developed stem densities

Table 2 Crop tree characteristics

Crop species	Stem density (ha^{-1})	DBH (cm)	Tree height (m)	Basal area (m^2 ha^{-1})
Tectona	600 ± 35	15.4 ± 0.6	15.8 ± 0.8	11.2 ± 0.9
Terminalia	409 ± 31	13.2 ± 0.6	13.9 ± 0.4	5.9 ± 0.5
T test results	$t = 4.1$, $df = 13.9$, $P = 0.001$	$t = -2.4$, $df = 14$, $P = 0.03$	$t = -2.2$, $df = 11.2$, $P = 0.05$	$t = 5.2$, $df = 11.6$, $P = 0.0002$

Values are stand-level mean ± SE

within the range of similarly aged (7 years-old) experimental plantations of native tree species in Costa Rica (0.01–25.86 m^{-2}; Powers et al. 1997).

The species composition of understory woody stems differed between *Tectona* and *Terminalia* stands (Fig. 4), which is a common result among experimental trials that have measured understory plant communities below various crop tree species (Montagnini 2011). At the time of sampling (7 years after plantation establishment) *Tectona* crop trees were larger and more closely spaced than *Terminalia* trees (Table 2). Such features of overstory structure have been shown to influence patterns of understory regeneration (Jones et al. 2004), yet we are unable to distinguish what factors led to the divergence in understory composition between our crop species. Moreover, on a nearby plantation, *Terminalia* stands obtained higher basal area than *Tectona* stands after 20 years (Griess and Knoke 2011). Therefore, if overstory structure did affect the plant communities that we measured, then differences between *Terminalia* and *Tectona* stands are likely to change as the stands mature.

Healey and Gara (2003) found that a 10-year-old *Tectona* plantation in Costa Rica had lower densities of woody stems and species than a nearby 12-year-old abandoned pasture. The authors concluded that *Tectona* suppressed forest regeneration. However, it is likely that the manual thinning of recruits under *Tectona*, rather than *Tectona* per se, suppressed regeneration. The plantation studied by Healey and Gara (2003) cleared recruiting understory vegetation for the first 5 years of plantation establishment, creating a seven-year head start for recruitment in the abandoned pasture, which likely contributed to the higher stem density there. Similarly, Leopold and Salazar (2008) found that understory stem density and species richness were lower on a commercial *Tectona* plantation than on nearby seven-to-eight-year-old mixed-species restoration plantation sites in Costa Rica; yet they did not report management practices for the plantations, which likely differed greatly considering the divergent goals of commercial and restoration plantations. We know of no other studies that have quantified understory recruitment on *Tectona* plantations in the Neotropics.

Understory thinning is a common practice in *Tectona* plantations (Pandey and Brown 2000) and has been implicated as causing high erosion rates (Bell 1973), leading to the perception that *Tectona* suppresses understory recruitment. In our study, management actions differed slightly between the *Tectona* and *Terminalia* stands, consistent with the particular silvicultural recommendations for the crop species. *Tectona* was planted at closer spacing than *Terminalia* and its understory was not cut after the initial 2 years while rows were regularly cut in the understory of *Terminalia*. Since shading grass-dominated areas increases the rates of germination, survival, and growth of tree seedlings (Hooper et al. 2002), the management actions in *Tectona* stands likely favored forest regeneration more than the management actions in *Terminalia* stands, as they would reduce the time to canopy closure and increase the uncut area available for plants to grow >15 cm height. We

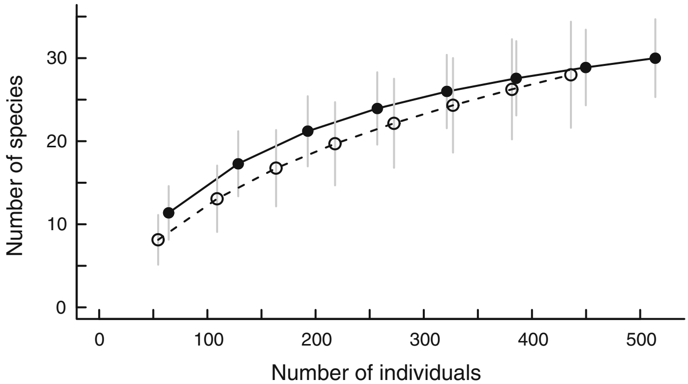
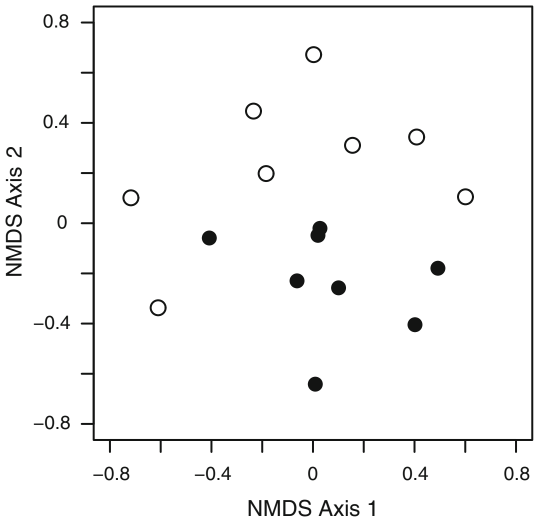


Fig. 3 Rarefaction-based species accumulation curves for woody understory vegetation in stands of *Terminalia* (*filled circles*) and *Tectona* (*open circles*). *Bars* represent the 95 % confidence intervals

Fig. 4 Non-metric multidimensional scaling (NMDS) plot of understory woody vegetation in stands of *Terminalia* (*filled circles*) and *Tectona* (*open circles*)



conclude that understory recruitment was similar under *Tectona* and *Terminalia* stands within a plantation that was managed for both biodiversity conservation and timber production, when subjected to the species' particular silvicultural practices. However, in order to better understand how *Tectona* and native tree species affect understory vegetation more rigorous experiments are needed.

Acknowledgments We thank Iliana Armién and Andreas Eke for facilitating research at the Futuro Forestal plantations, Emilio Mariscal for training, Carolina Sarmiento for help in making Fig. 1, and two anonymous reviewers for helpful comments on the manuscript. This research was undertaken as part of PRORENA, a collaborative native species reforestation research project between the School of Forestry and Environmental Studies of Yale University and the Center for Tropical Forest Science at the Smithsonian Tropical Research Institute. Financial support for PRORENA has been provided by the Frank Levinson Donor-Advised Fund at the Peninsula Community Foundation, the Levinson Family Foundation, and the Grantham Family Foundation.

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