Cultivation of Non-timber Forest Products Alters Understory Light Availability in a Humid Tropical Forest in Mexico[1]

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ABSTRACT

The planting of non-timber forest products (NTFPs) in the understory of tropical forests is promoted in many regions as a strategy to conserve forested lands and meet the economic needs of rural communities. While the forest canopy is left intact in most understory plantations, much of the midstory and understory vegetation is removed in order to increase light availability for cultivated species. We assessed the extent to which the removal of vegetation in understory plantations of *Chamaedorea hooperiana* Hodel (Arecaceae) alters understory light conditions. We also examined how any changes in light availability may be reflected by changes in the composition of canopy tree seedlings regenerating in understory plantations. We employed a blocked design consisting of four *C. hooperiana* plantation sites; each site was paired with an adjacent, unmanaged forest site. Hemispherical canopy photographs were taken and canopy tree seedlings were identified and measured within 12 3 × 2 m randomly placed plots in each site for a total of 96 plots (4 blocks × 2 sites × 12 plots). Plantation management did not affect canopy openness or direct light availability but understory plantations had a higher frequency of plots with greater total and diffuse light availability than unmanaged forest. Comparisons of canopy tree seedling composition between understory plantations and unmanaged forest sites were less conclusive but suggest that management practices have the potential to increase the proportion of shade-intolerant species of tree seedlings establishing in plantations. Given the importance of advanced regeneration in gap-phase forest dynamics, these changes may have implications for future patterns of succession in the areas of forest where NTFPs are cultivated.

RESUMEN

En muchas regiones el establecimiento de plantaciones de especies forestales no-maderables (EFNM) en el sotobosque de selvas tropicales es una estrategia para conservar areas naturales y cubrir necesidades económicas de comunidades rurales. En estos tipos de plantaciones se acostumbra dejar intacto el dosel para aprovechar su sombra, mientras que la mayor parte del sotobosque es removida para aumentar la disponibilidad de luz para las especies cultivadas. En el presente trabajo investigamos cómo la eliminación del sotobosque en plantaciones de *Chamaedorea hooperiana* Hodel, modifica las condiciones de luz en el sotobosque. Examinamos también cómo los cambios en las condiciones de luz pueden afectar la composición de plántulas de árboles del dosel que se están regenerando en plantaciones de EFNMs. Para comparar las condiciones de luz y la composición de plántulas, usamos un diseño de "bloques" en cuatro sitios con plantaciones de *C. hooperiana*, cada uno aparejado a un area de selva sin manejo. Tomamos fotografías hemisféricas del dosel e identificamos y medimos las plántulas de árboles del dosel presentes en doce lotes de 3 × 2 m, establecidos al azar en cada sitio con un total de 96 lotes seleccionados (4 bloques × 2 sitios × 12 lotes). El manejo de plantaciones no afectó la abertura del dosel o la disponibilidad de luz directa, pero las plantaciones experimentaron con más frecuencia áreas disponibles de más luz indirecta que los sitios del bosque sin manejo. Los resultados de la comparación de la composición de las plántulas entre plantaciones de EFNMs y el bosque sin manejo son menos conclusivos, pero sugieren que las formas de manejo de plantaciones usadas por los campesinos pueden aumentar la proporción de plántulas de especies pioneras que se establecen. Estos cambios pueden resultar en modificaciones en el proceso de regeneración del bosque en el futuro.

Key words: advanced regeneration; *Chamaedorea hooperiana;* enrichment planting; hemispherical photographs; Los Tuxtlas, Mexico; non-timber forest products; seedling composition.

THE GROWING ECONOMIC IMPORTANCE OF NON-TIMBER FOREST PRODUCTS (NTFPs) has led government and nongovernment agencies to promote NTFP cultivation, or enrichment planting, in the understories of tropical forests near rural communities around the world (Gunatilleke *et al.* 1993, Sugandhi & Sugandhi 1995, Ratsirarson *et al.* 1996, Carpentier *et al.* 2000, Ticktin *et al.* 2003). The forest canopy is left largely intact in most understory NTFP plantations. However, in order to decrease competition and increase light availability for cultivated species, plantation owners clear much of the understory and midstory vegetation both before and periodically after crops are planted (Trauernicht & Ticktin 2005). Although

there is evidence that the production of some NTFP species increases with greater light availability (Ticktin *et al.* 2003), to date no study that we are aware of has characterized how the understory light environment varies between understory plantations and unmanaged forest and what the ecological implications of these differences may be.

Light is a major factor that affects plant growth and survival (Augspurger 1984, Chazdon *et al.* 1996, Whitmore 1996, Kobe 1999) and influences patterns of forest regeneration (Clark & Clark 1992, Clark *et al.* 1996). Recent studies suggest that relatively small changes in light availability beneath closed forest canopy may influence community composition by shifting the competitive hierarchy among species of tree seedlings (Montgomery & Chazdon 2002) and saplings (Poorter & Arets 2003). These interactions in the forest

understory may in turn be a significant determinant of community composition during gap-phase regeneration, given that the majority of regrowth in canopy gaps consists of the advanced regeneration of seedlings and saplings that establish before the gaps occur (Uhl *et al.* 1988, Brown & Jennings 1998).

Periodic clearing of the seedlings and saplings in understory NTFP plantations essentially arrests the process of forest regeneration. While many landowners maintain that timber saplings are spared during plantation clearing, the selective management of naturally occurring species appears limited primarily to economic understory palms (Trauernicht & Tickt 2005). Thus, at present, canopy trees are left standing simply to provide shade for cultivated NTFP species. However, in the event of a treefall gap, sections of understory plantations are temporarily abandoned due to the high mortality of NTFP crops exposed to full sunlight. As regeneration proceeds in these abandoned gaps, the composition of the vegetative regrowth consists of the advanced regeneration that has established since the last time the understory plantation was cleared. Therefore, if understory plantations alter the understory light environment, they may have the potential to affect the composition of tree seedlings and the subsequent composition of vegetative regrowth that establishes with the eventual occurrence of a canopy opening.

The primary objective of this study was to examine the extent to which the removal of vegetation in understory NTFP plantations changes the light environment in the forest understory. We used hemispherical photographs to compare the light environments in areas of forest containing plantings of the economic palm, *Chamaedorea hooperiana* Hodel with neighboring areas of unmanaged forest. A secondary objective of this study was to explore how differences in light conditions may be reflected in differences in the composition of canopy and subcanopy tree seedlings regenerating in plantations versus unmanaged forest. To do so, we compared seedling species composition between plantations and unmanaged forest and examined seedling density and size class structure to determine whether plantation seedling communities appear to be establishing after the understory vegetation is cleared. To determine whether or not seedling composition simply reflects the composition of adult trees, we also examined adult composition.

MATERIALS AND METHODS

STUDY SITE.—This research was conducted in the buffer zone of the Los Tuxtlas Biosphere Reserve (LTBR) in southeastern Mexico in an area of old growth tropical high evergreen rain forest (*e.g.*, Bongers *et al.* 1988) adjacent to the community of Adolfo Lopez Mateos. Adolfo Lopez Mateos is located at 18°24′N, 94°58′W, approximately 18 km east of the city of Catemaco at an elevation of 200 m. Mean annual temperature in the area is approximately 24°C and mean annual precipitation is between 3000 mm and 4000 mm with a dry season from December to May (Soto & Gama 1997). The leaves of several species of *Chamaedorea* palms are harvested from both wild and planted populations throughout

southern Mexico and Central America and sold for export in the floriculture industry. Due to the economic importance of these palms, understory plantations of several *Chamaedorea* species have been established in the areas of old growth and secondary forests surrounding Adolfo Lopez Mateos and other communities in the buffer zone of the LTBR.

STUDY DESIGN.—To assess whether NFTP plantation management alters the understory light environment and the composition of subsequent canopy tree seedling establishment, we compared understory plantations with areas of unmanaged forest. We surveyed all of the *Chamaedorea* palm plantations in the vicinity of Adolfo Lopez Mateos, and selected four of the larger plantations of *C. hooperiana* that were most similar in size (0.5–1 ha) and age of palms (1–3 yr), and that were adjacent to an area of forest suitable for cultivation but that had not yet been cleared and planted. The experimental design, therefore, consisted of four blocks, each containing a plantation site paired with an adjacent unmanaged forest site of similar size, inclination, and slope aspect. All blocks were situated on steep slopes ranging from about 30° to 45°. Blocks 1 and 2 were located at approximately 300 m in elevation and Blocks 3 and 4 were located at approximately 500 m in elevation. Block 1 had an easterly slope aspect and Blocks 2, 3, and 4 had northerly slope aspects. The plantations in Blocks 2, 3, and 4 were established in 2001 and the herbaceous vegetation in their understories was cleared again within 1–3 mo before data sampling. The plantation in Block 1 was established in 1999 and its owner had not cleared the understory vegetation for over a year.

Hemispherical canopy photographs and seedling measurements were taken in 12 3 × 2 m randomly established plots in each forest and plantation site for a total of 96 plots across all blocks (4 blocks × 2 sites × 12 plots). A minimum distance of 10 m was maintained between adjacent plots and no plot was placed <10 m from a treefall gap edge or <5 m of a plantation edge. The latter condition was maintained in order to avoid confounding effects of plantation edges and existing treefall gaps.

Canopy photographs were taken at the center of each plot, 1 m above the ground (approximately the same height as most cultivated palm canopies) using a Nikkor 8-mm hemispherical lens mounted on a Nikon FM10 (Nikon Corporation, Tokyo, Japan) camera body at the start of the wet season (June 2003). All photographs were taken either under overcast skies or within 1 h after sunrise or before sunset to minimize the effects of light reflection off leaves. Hemispherical photographs are useful in revealing larger patterns in canopy structure and the distribution of canopy openings (Whitmore 1993, Clark *et al.* 1996, Nicotra *et al.* 1999). Because the objective of this research was to compare the general patterns of light availability and canopy openness across plantation and forest sites rather than to characterize the small-scale variation within each site, hemispherical photography provided a method of measuring light conditions that was both logistically feasible and adequate for the purpose of this study.

To assess canopy tree seedling composition and size structure, all seedlings <50 cm in height were counted and identified in each

of the 96 3 × 2 m plots for a total sampling area of 72 m² in each site. For each seedling, stem height was measured and crown area was calculated from the measurements of crown length and width. The composition of adult trees was determined by counting, identifying, and measuring the diameter at 1.3 m height (DBH) of all woody individuals ≥1 cm DBH in 10 m diameter circular plots that circumscribed each 3 × 2 m plot. This resulted in a total sampling area of 942.5 m² per site.

HEMISPHERICAL PHOTOGRAPHS.—Photographic negatives were digitized using a Hewlett-Packard scanner. We used the program Gap Light Analyzer version 2.0 (Frazer *et al.* 1999) to compute percent site openness (PSO), direct light transmittance (DRT), diffuse light transmittance (DFT), and total light transmittance (TT) for each sampling point. PSO is the percentage of open sky visible from below the forest canopy (*i.e.*, percent canopy openness). Light transmittance measurements are predictions of the average photon flux density (mol/m²/d) of solar radiation transmitted by the canopy per day based on calculations of the solar path over each sample point during the course of the year. DRT is a measurement of direct solar radiation (*i.e.*, direct site factor), DFT is a measurement of diffuse, or indirect, solar radiation (*i.e.*, indirect site factor), and TT is a measurement of combined direct and diffuse solar radiation (*i.e.*, total site factor).

The most effective method for demonstrating differences in light conditions is through analyses of frequency distribution as opposed to analyses of means of light availability (Chazdon & Fetcher 1984, Brown & Parker 1994, Nicotra *et al.* 1999). Therefore, in order to assess differences in light conditions, we examined the frequency distributions of PSO, DRT, DFT, and TT among sampling points in forest and plantation sites. Categories of light availability and canopy openness were determined by dividing the total range of values for each measurement into three equal-sized groups. For PSO the categories were: (1) 1.8–7.5 percent; (2) 7.6–13.3 percent; and (3) 13.4–19.1 percent. For DRT, the categories were: (1) 0.27–2.26 mol/m²/d; (2) 2.27–4.26 mol/m²/d; and (3) 4.27–6.26 mol/m²/d. For DFT, the categories were: (1) 0.19–1.90 mol/m²/d; (2) 1.91–3.62 mol/m²/d; and (3) 3.63–5.33 mol/m²/d. For TT, the categories were: (1) 0.5–4.0 mol/m²/d; (2) 4.1–7.5 mol/m²/d; and (3) 7.6–11.2 mol/m²/d.

We employed the log-linear model of goodness of fit, which incorporated the blocked study design, to produce a *G* statistic (Sokal & Rohlf 1995) that assessed if the distribution of plots among categories of canopy openness (for PSO) and light availability (for DRT, DFT, and TT) was independent of management type (*i.e.*, plantation vs. unmanaged forest). Despite the low accuracy of predictions of photon flux density (*e.g.*, light transmittance measurements) reported for hemispherical photographs under closed-canopy conditions (Clark *et al.* 1996; Nicotra *et al.* 1999), the use of frequency distributions in this case likely provides a robust analysis. By dividing the light levels of DRT, DFT, and TT into three categories, we were able to focus the analysis on the upper and lower limits of the ranges of light values and thus reduce the error due to the potential overlapping of inaccurate predictions in the middle range of values.

SEEDLING SIZE AND DENSITY.—We tested the independence of seedling size class distribution and management type (plantation vs. unmanaged forest) using the log-linear analysis of goodness of fit (Sokal & Rohlf 1995). We analyzed size class distributions based both on seedling stem height and on crown area. Because these analyses included many species with differing life-history traits, stem height size classes were assigned based on 5 cm increments from 0 to 50 cm and crown area size classes were based on 20 cm² increments between 0.1 cm² and 200 cm² and then by 100 cm² increments from 200.1 to >600 cm². This was due to the wide range of sizes for crown area (0.1–1335.3 cm²). Differences in seedling density between forest sites and plantation sites were assessed using randomized complete blocks ANOVA.

SEEDLING COMMUNITY COMPOSITION.—To examine patterns of seedling establishment in the context of differing light environments, we classified all canopy tree seedlings as either shade-tolerant or shade-intolerant based on the ecological characteristics outlined by Swaine and Whitmore (1988) and Whitmore (1989). Classifications for 41 of the 61 species of seedlings recorded were based on the published accounts of physiological characteristics and seed ecology as well as anecdotal references made by biologists (see Appendix). We used only sources that made references to the environment in which seedlings are capable of establishing. For the remaining 20 species not discussed in the literature, we relied on ecological descriptions made by local plant experts.

Differences between plantation and forest sites in the proportion of shade-intolerant species were compared using randomized complete blocks ANOVAs (Table 1; Sokal & Rolf 1995). Because the understory vegetation in the Block 1 plantation had not been

TABLE 1.   *Results of ANOVA to test for differences in the proportion of shade-intolerant species of seedlings (<50 cm) and adult trees (≥20 cm DBH) in forest versus plantation sites. All comparisons were made using completely randomized blocks design ANOVAs. Treatment refers to comparisons of management type (understory Chamaedorea plantations vs. unmanaged forest). Block refers to among-block differences for the four study blocks. Significant P values (<0.05) are indicated in bold type.*

Analysis		df	F value	P value
Proportion of shade-intolerant	Treatment	1	2.27	0.2287
seedling species	Block	3	0.63	0.6420
	Overall	4	1.04	0.5066
Proportion of shade-intolerant	Treatment	1	30.48	**0.0313**
seedling species excluding	Block	2	5.04	0.1656
Block 1	Overall	3	13.52	0.0697
Proportion of shade-intolerant	Treatment	1	0.07	0.4724
adult tree species	Block	3	2.63	0.2239
	Overall	4	2.14	0.2788
Proportion of shade-intolerant	Treatment	1	1.48	0.4037
spp. adult tree species	Block	2	0.09	0.7958
excluding Block 1	Overall	3	1.01	0.5314

recleared as recently as the other plantations, we also carried out these same sets of analyses excluding this block.

To investigate whether differences between plantation and forest sites in the proportion of shade-intolerant seedlings were due to differences in the composition of the overstory (*i.e.*, the available local seed sources), we performed the same set of tests described above on all adult individuals ($\geq$20 cm DBH) of the same 61 species recorded for seedlings that were sampled from the 10 m diameter plots within each site. Only adults $\geq$20 cm DBH were used in the analysis because the density of woody individuals <20 cm DBH is significantly reduced in plantation sites due to management practices (Trauernicht & Ticktin 2005).

RESULTS

LIGHT AVAILABILITY AND CANOPY OPENNESS.—Log-linear analyses showed that for TT and DFT, the distribution of light categories was dependent on management type (TT: $G = 30.7$; $P < 0.005$, df = 8; DFT: $G = 18.77$; $P < 0.05$, df = 8). For both PSO and DRT, there was no significant relationship between light category distribution and management type (PSO: $G = 8.26$, $P = 0.31$, df = 8; DRT: $G = 10.91$, $P = 0.21$, df = 8). The distributions of TT, DFT, and PSO exhibited the same pattern: A greater proportion of forest plots fell into the darker, less open categories, skewing the distribution to the left, whereas plantation plots were more normally distributed (Fig. 1). For TT, 62.5 percent of the forest plots fell into the lowest light category versus 34.4 percent of the plantation plots. For DFT, 4.2 percent of forest plots fell into the highest light category versus 25 percent of the plantation plots. For DRT, the distributions of plantation and forest plots were similar and skewed towards the darker light categories (Fig. 1).

SEEDLING SIZE CLASS AND DENSITY.—Seedling size class distributions based on seedling height (Fig. 2) and crown area showed that plantations had a higher proportion of seedlings in the smaller size classes than forest sites. Log-linear analyses of the size class frequency distributions showed that seedling size class distribution was dependent on management type (plantation vs. forest) for both seedling height ($G = 136.12$, $P < 0.0005$, df = 35) and crown area ($G = 136.73$, $P < 0.0005$, df = 42). Although average seedling density was greater in plantation sites (mean = 2.83 individuals/m^2) than in forest sites (mean = 1.91 individuals/m^2), this difference was not significant ($F = 2.21$, $P = 0.2339$, df = 1).

SEEDLING COMPOSITION.—Although the mean proportion of shade-intolerant seedling species was greater in plantation sites (0.37) than in forest sites (0.23), this difference was not significant; however, when Block 1, which contains the older and less intensively managed plantation, was removed from the analysis, the proportion of shade-intolerant seedling species was significantly greater in plantation sites than in forest sites (Fig. 3). The mean proportion of shade-intolerant species of trees $\geq$20 cm DBH did not significantly differ between forest and plantation sites, both including and excluding Block 1 (Fig. 3).

DISCUSSION

The ecological effects of NTFP cultivation in the forest understory include both direct impacts through the alteration of midstory and understory vegetation, and indirect impacts through abiotic and biotic changes brought about by the manipulation of forest structure and composition. The results of this study illustrate that management of *Chamaedorea* palm plantations alters patterns of light
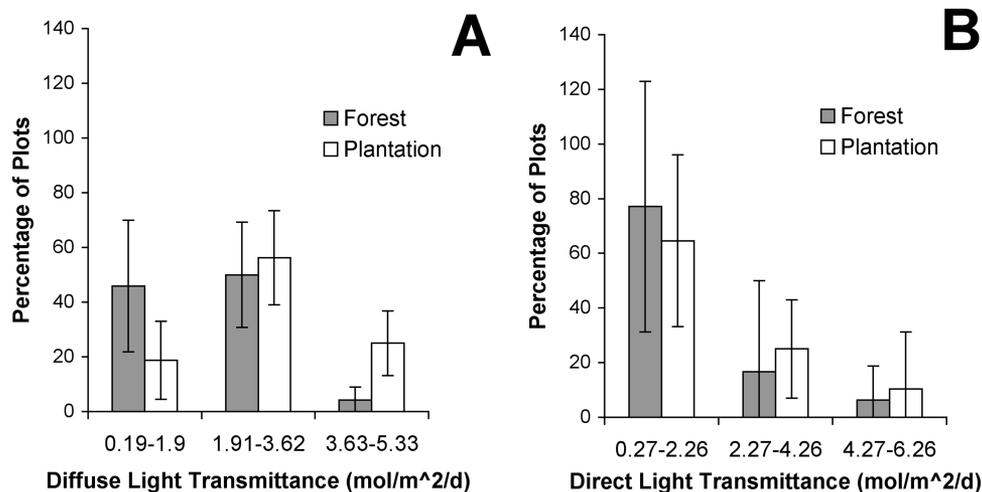

FIGURE 1.   Distributions of diffuse light (graph A) and direct light (graph B) transmitted by the canopy for unmanaged forest sites versus sites planted with *Chamaedorea hooperiana*. Log-linear analyses indicate that the distribution of plots among light categories is dependent upon management type for diffuse light transmittance (A) but not for direct light transmittance (B).
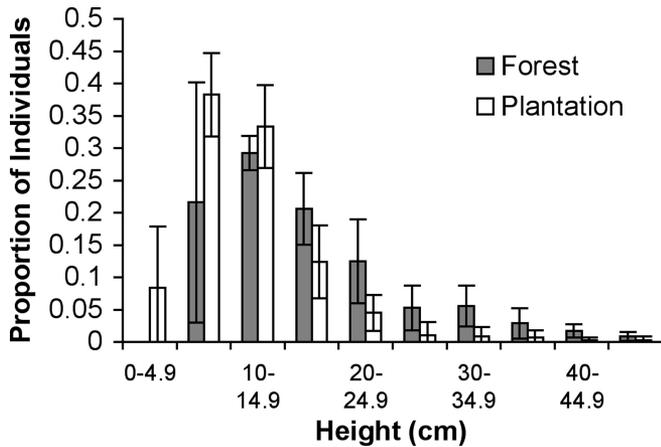
FIGURE 2.   Size class distributions of canopy and subcanopy tree seedlings for unmanaged forest sites versus *Chamaedorea* plantation sites based on seedling height. Error bars represent ±1 standard deviation.

availability and potentially the composition of tree seedling regeneration.

PATTERNS OF UNDERSTORY LIGHT DISTRIBUTION AND SEEDLING COMPOSITION.—Our analyses of PSO and light transmittance suggest that understory plantation management does not affect canopy openness or DRT. For both total and DFT, however, there was a significant relationship between management type (*i.e.*, under-
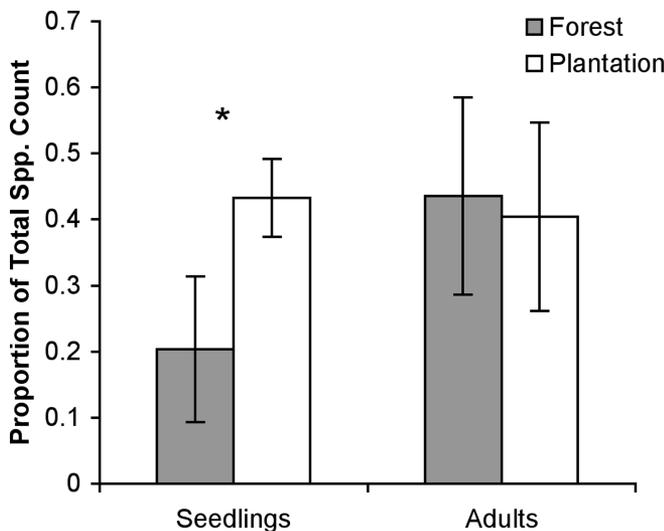

FIGURE 3.   Mean proportion of shade-intolerant species of canopy and sub-canopy tree seedlings (<50 cm in height) and adults (≥20 cm DBH) in un-managed forest sites versus *Chamaedorea* plantation sites omitting Block 1. The plantation in Block 1 was managed less intensively than the plantations in Blocks 2, 3, and 4. Proportions were calculated as the number of shade-intolerant species divided by the total species count in each site. Error bars represent ±1 standard deviation. (*$P < 0.05$)

story plantation vs. unmanaged forest) and the distribution of light availability, with a greater percentage of forest plots in lower light categories than plantation plots. Thus, by leaving the forest over-story intact, *Chamaedorea* plantation owners do not alter canopy openness or the availability of direct solar radiation. Yet the felling of smaller trees and shrubs (<20 cm DBH) below the canopy appears to increase the levels of diffuse light reaching the understory and therefore overall light availability (TT) is higher in understory plantations. While our study does not demonstrate a causal relationship between light availability and understory plant density, our results are consistent with other research that has illustrated the effects of understory vegetation on light attenuation near the forest floor (Montgomery 2004).

Some studies suggest that light availability in the forest under-story directly affects seedling growth and survival (*e.g.*, Augspurger 1984, Whitmore 1996) as well as seedling community composition due to differential responses to light gradients (Kobe 1999, Montgomery & Chazdon 2002, Hall *et al.* 2003). However, despite evidence of altered light conditions in *Chamaedorea* plantations, the ecological significance of these changes is difficult to identify. Any difference in plantation seedling composition due to light depends on the establishment of a majority of seedlings after plantation un-derstories are cleared (*i.e.*, once light patterns are different) and on the regeneration of a different assemblage of species in the altered light conditions. Our results indicate that the majority of seedlings in plantations do indeed establish after the understory is cleared. The differences in seedling size-class distributions between planta-tion and forest sites show that the frequency of larger, potentially more established seedlings is reduced in plantation sites. This pat-tern may simply reflect a tendency for plantation owners to overlook smaller seedlings and remove larger individuals while clearing the understory. However, seedling density between plantation and for-est sites was not significantly different, suggesting that recruitment sites created by plantation management are soon occupied by new seedlings.

In terms of compositional changes in the seedling community, however, we found no significant difference between plantation and forest sites in the proportion of shade-intolerant seedling species. This lack of difference may be due either to the fact that there is no difference in seedling assemblages or to the confounding effects of variation in management among plantation sites. When Block 1 is removed from the analysis, we found that the proportion of shade-intolerant seedling species was significantly greater in plantation sites than in forest sites. The owner of the plantation in Block 1 maintained that he does not clear the vegetation as often or as thoroughly as in other plantations in order to preserve soil humid-ity. By comparison, the clearing practices in the other plantations were much more intensive. Thus, it is possible that some kinds of management may, in fact, alter the composition of seedlings that regenerate in plantation understories. This type of variation in hu-man management complicates quantitative studies due to the lack of controlled replication and emphasizes the need for more experimen-tal approaches in NTFP research (*e.g.*, Ticktin *et al.* 2002; Endress *et al.* 2004). It is also indicative of the range of ecological impacts that plantation management can have and underscores the need to

collaborate with local harvesters and plantation owners to develop and implement more sustainable practices (*e.g.*, Alcorn 1995).

FURTHER CONSIDERATIONS.—We emphasize that demonstrating a causal relationship between light availability and seedling composition is beyond the scope, and was not the intention of this study. Due to the static nature of our data on seedling community structure, it is not possible to relate changes in environmental conditions to shifts in seedling survival or species abundances. The compositional changes suggested by our results have important implications for the long-term sustainability of understory plantations, however. The dichotomous species classification scheme of shade-tolerant versus shade-intolerant (although criticized for being ecologically crude; *e.g.*, Brown & Jennings 1998) provides a useful baseline from which to make preliminary analyses of the ecological impacts of forest management. Moreover, given the growing practice of NTFP cultivation for conservation and rural development, the ecological consequences of management warrant serious consideration.

Beyond differences between understory plantations and unmanaged forest, we may also need to consider the variation among plantations in the light environment experienced by tree seedlings due to differences in the density and composition of cultivated NTFPs. For example, the density of *C. hooperiana* among the four plantations in this study varied widely (mean = 2870 stems/ha, SD = 1529; Trauernicht & Ticktin 2005). In addition, the pinnate fronds of *C. hooperiana* may let more light pass than other cultivated species, such as *C. ernesti-augustii*, which has bifid leaves. Chazdon (1986) specifically suggested that the abundance of understory palms at La Selva, Costa Rica was largely responsible for reduced light levels near the forest floor. This observation is supported by recent research explicitly illustrating the positive relationship between the density of understory foliage and the degree of light attenuation near the floor across several tropical forests (Montgomery 2004). Furthermore, Denslow *et al.* (1991) found that palms and cyclanths affected the growth and survival of *Inga* seedlings at La Selva, Costa Rica, and in a temperate forest, the understory fern layer was shown to alter the composition of canopy tree seedlings (George & Bazzaz 1999a, 1999b). Thus, the extent to which NTFP management alters the understory light environment and the composition of tree seedlings may not simply be dependent on how much vegetation is removed when a plantation is cleared, but also how and which species of NTFPs are cultivated.

Although light availability in tropical forests is likely to be the most important variable determining plant growth and survival (Whitmore 1996), factors other than light may also influence differences in seedling distributions. Some studies further suggest that single factors are inadequate to explain community composition (Rees & Brown 1992, Meiners & Handel 2000). Altered patterns of seedling composition in understory NTFP plantations may be due to reduced levels of above- and below-ground competition from understory vegetation when plantations are cleared (*e.g.*, Holl 1998). There may also be different patterns of seed dispersal in plantations due to the more open midstory and understory affecting bird and mammal assemblages (*e.g.*, Gallina *et al.* 1996, Calvo & Blake 1998). In addition, the periodic disturbance of plantation clearing may favor the survival of certain species of seedlings over others, such as those capable of resprouting due to underground seed reserves (Dalling & Harms 1999).

FUTURE MANAGEMENT IMPLICATIONS.—The effects of understory NTFP plantation management on community structure and composition, light conditions, and seedling assemblages are likely to have significant implications for future patterns of forest regeneration. Specifically, as gap-phase regeneration proceeds in understory plantations, our results suggest that management practices may favor a higher percentage of shade-intolerant species in the advanced regeneration as compared to unmanaged forest. This shift in species composition may be further exacerbated once canopy gaps fill in with fast-growing pioneer trees. As management proceeds in newly closed gaps and the understory and midstory are cleared again for cultivation, shade-tolerant species that may require multiple gap events to reach maturity may not be able to complete their life cycles (*e.g.*, Clark & Clark 1992). Over the long term, this shift in successional patterns may ultimately favor a disproportionately lower percentage of the local tree species diversity due to the fact that most species in tropical forests are shade-tolerant (Brokaw & Scheiner 1989, Hubbell 1998).

The widespread adoption of NTFP cultivation is relatively recent, occurring only over the past 10 yr. Thus, it is difficult to assess and predict with certainty the long-term consequences of NTFP cultivation. Research on the composition of gap-phase regeneration in previously cultivated areas may provide a better picture of these longer-term management effects on forest composition. Given the economic dependence of many rural communities on NTFPs, the current transition from wild harvesting to NTFP cultivation is likely to continue and expand. In order to establish NTFP cultivation as a viable conservation strategy, we must consider management effects in the broader context of community succession and forest dynamics. Fortunately, human-managed systems easily lend themselves to long-term research through community-based resource monitoring in collaboration with local harvesters and landowners.

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APPENDIX. *Species classifications according to shade tolerance based on a review of available literature and discussions with local experts. 1 = shade-tolerant; capable of forming banks of seedlings beneath closed canopy, 2 = shade-intolerant; requiring light for germination.*

Family	Species	Classification	References
Actinidaceae	*Saurauia scabrida* Hemsl.	2	a
Anacardiaceae	*Spondias radlkoferi* J.D. Smith	2	c, g, h
	Tapirira mexicana Marchand	2	o
Annonaceae	*Cymbopetalum bailloni* R.E. Fries	1	b, j, y
	Cymbopetalum penduliflorum (Dunal) Baillon	1	a
	Guatteria amplifolia Triana & Planch.	2	a
	Rollinia mucosa (Jacq.) Baill.	2	a
Araliaceae	*Dendropanax arboreus* (L.) Decne. & Planchon	2	h, j, l
Bignoniaceae	*Tabebuia guayacan* (Seeman) Hemsl.	1	h
Bombacaceae	*Bernoullia flammea* Oliver	2	q
	Quararibea yunckeri Standl.	1	a
Boraginaceae	*Cordia megalantha* Blake	1	r
	Cordia stellifera I.M. Johnston	2	a
Burseraceae	*Bursera simaruba* (L.) Sarg.	2	j, p, q, s, w
Cecropiaceae	*Cecropia obtusifolia* Bertol.	2	c, h, j, k, p, q, s, t, w
Clusiaceae	*Calophyllum brasiliense* Camb.	1	f, h, m, p
	Garcinia intermedia (Pittier) Hammel	1	j, q
Ebenaceae	*Diospyrus digyna* Jacq.	1	j
Elaeocarpaceae	*Sloanea medusula* Shumann & Pittier	2	a
	Sloanea petenensis Standley	2	a

APPENDIX. *Continued.*

Family	Species	Classification	References
Euphorbiaceace	*Alchornea latifolia* Sw.	2	c
	Croton draco Schlecht.	2	j, k
Fabaceae	*Cynometra retusa* Britton & Rose	1	q
	Dialium guianense (Aublet) Sandw.	1	j, p
	Dussia mexicana (Standley) Harms	1	j, q
	Inga sp. 1	1	a
	Inga sp. 2	1	a
	Inga thibaudiana DC.	2	x
	Ormosia panamensis Benth.	2	a
	Pithecellobium macrandrium J.D. Smith	2	p
	Platymiscium pinnatum (Jacq.) Dugand	1	e
Icacinaceae	*Calatola laevigata* Standley	1	h, q
Juglandaceae	*Alfaroa sp.*	1	a
Lauraceae	*Nectandra ambigens* (Blake) Allen	1	h, q, s, w
	Ocotea luesenedi	1	a
	Persea schiedeana Nees	2	j
Malvaceae	*Hampea nutricia* Fryx.	2	q
	Robinsonella mirandae Gomez-Pompa	2	k, q
Meliaceae	*Guarea glabra* Vahl	1	h
	Trichilia moschata Sw.	1	p
	Trichilia pallida Sw.	1	q
Moraceae	*Brosimium alicastrum* Sw.	1	j, k, q, s, t
	Ficus yoponensis Desv.	2	h, g
	Poulsenia armata (Miq.) Standley	1	h, s, h, t
	Pseudolmedia oxyphyllaria J.D. Smith	1	h, j, s, t
Myristicaceae	*Virola guatamalensis* (Hemsl.) Warb.	1	a
Myrtaceae	*Eugenia acapulcensis* Steud.	1	a
	Eugenia lindeniana Berg	1	a
	Pimenta dioica (L.) Merr.	1	j, p
Nyctaginaceae	*Neea psychotroides* J.D. Smith	1	q
Polygonaceae	*Coccoloba hondurensis* Lundell	2	a
Proteaceae	*Roupala borealis* Hemsley	1	a
Rutaceae	*Zanthoxylum caribaeum* Lam.	2	j
Sapindaceae	*Cupania glabra* Sw.	2	y
	Cupania macrophylla A. Rich.	2	a
Sapotaceae	*Pouteria reticulata* (Engl.) Eyma	1	u
Staphyleaceae	*Turpinia occidentalis* (Sw.) G. Don	1	h, k
Sterculiaceae	*Sterculia apetala* (Jacq.) Karst.	1	h, n
Tiliaceae	*Heliocarpus appendiculatus* Turcz.	2	k, q, s, v
	Trichospermum galeottii (Turcz.) Kosterm.	2	a
Vochysiaceae	*Vochysia guatemalensis* J.D. Smith	1	I

(a) Ecological description by local plant expert, confirmed by G. Ibarra-Manriquez, (b) Coates-Estrada and Estrada (1988), (c) Condit *et al.* (1996), (d) Dalling and Tanner (1995), (e) Davidson *et al.* (2002), (f) Fischer and Dos Santos (2001), (g) Foster and Brokaw (1996), (h) Garwood (1983), (i) Garwood (1998), (j) Gomez-Pompa (1966), (k) Gomez-Pompa and C. Vasquez-Yanes (1985), (l) Gonzales (1991), (m) Holl (1998), (n) Janzen (1972), (o) Loik and Holl (2001), (p) Lundell (1937), (q) Martinez-Ramos (1985), (r) Popma and Bongers (1988), (s) Soriano *et al.* (1997), (t) Strauss-Debenedetti and Bazzaz (1991), (u) Tyree *et al.* (1998), (v) Vazques-Yanes and Orozco-Segovia (1992), (w) Vazques-Yanes and Sada (1985), (x) Wickers (1997), (y) Williams-Linera *et al.* (1998).