

# Can a fast-growing early-successional tree (*Ochroma pyramidale*, Malvaceae) accelerate forest succession?

Ivar Vleut\*<sup>1</sup>, Samuel Israel Levy-Tacher\*, Willem Frederik de Boer†, Jorge Galindo-González‡ and Neptalí Ramírez-Marcial\*

\* El Colegio De La Frontera Sur (ECOSUR), Carretera Panamericana y Periférico Sur s/n, Barrio de María Auxiliadora, San Cristóbal de Las Casas, C.P. 29290, Chiapas, Mexico

† Resource Ecology Group, Wageningen University, P.O. Box 47, 6400 AA, Wageningen, the Netherlands

‡ Instituto de Biotecnología y Ecología Aplicada (INBIOTECA), Universidad Veracruzana, Av. Culturas Veracruzanas #101, Colonia E. Zapata, C.P. 91090, Xalapa, Veracruz, Mexico

(Received 10 October 2012; revised 11 February 2013; accepted 11 February 2013)

**Abstract:** Species-specific traits of trees affect ecosystem dynamics, defining forest structure and understorey development. *Ochroma pyramidale* is a fast-growing tree species, with life-history traits that include low wood density, short-lived large leaves and a narrow open thin crown. We evaluated forest succession in *O. pyramidale*-dominated secondary forests, diverse secondary forests, both 10–15 y since abandonment, and rain forests by comparing height, density and basal area of all trees (> 5 cm dbh). Furthermore, we compared species richness of understorey trees and shrubs, and basal area and density of trees of early- and late-successional species (< 5 cm dbh) between forest types. We found that tree basal area (mean  $\pm$  SD:  $32 \pm 0.9 \text{ m}^2 \text{ ha}^{-1}$ ) and height ( $12.4 \pm 1.8 \text{ m}$ ) of canopy trees were higher, and density ( $1450 \pm 339 \text{ ha}^{-1}$ ) lower in *O. pyramidale* forests than in diverse forests, and more similar to rain forest. Understorey shrub diversity and tree seedling density and diversity were lower in *O. pyramidale* forests than in diverse forests, but these forest types had a similar density of early- and late-successional trees. Canopy openness (> 15%) and leaf litter (> 10 cm) were both highest in *O. pyramidale* forests, which positively affected density of understorey trees and shrubs and negatively affected density of late-successional trees. In conclusion, *O. pyramidale* forests presented structural features similar to those of rain forest, but this constrained the establishment of understorey tree species, especially late-successional species, decreasing successional development.

**Key Words:** canopy openness, diversity, leaf litter, pioneer species, regeneration

## INTRODUCTION

Species-specific traits of trees control ecosystem dynamics, define the process of forest succession, and differences in traits are at the basis of temporal changes in forest structural characteristics (Guariguata *et al.* 1995, Parrotta 1995, Powers *et al.* 1997). Monocultures permit the study of the impact of specific traits of individual tree species and their role in the successional development of secondary forests. In contrast, in a natural, more diverse, forest, the variation in successional changes cannot be directly attributed to the myriad of species' traits. Species-specific traits of a dominant plant species, usually a fast-growing early-successional tree species, have proven to be

important in the establishment of seedlings, driving forest succession (Cusack & Montagnini 2004, Guariguata *et al.* 1995, Lugo 1997, Parrotta *et al.* 1997).

*Ochroma pyramidale* is known as a very fast-growing pioneer tree species, with the lightest wood density produced in commercial plantations ( $0.17 \text{ g cm}^{-3}$ ), with a fast turnover of some of the largest leaves among neotropical trees, able to create a thick leaf-litter biomass cover, and has a narrow, thin crown, and a short life cycle (15–20 y; Coley 1983, Dalling *et al.* 1999, Francis 1991, Park & Cameron 2008, Selaya *et al.* 2008). Early-successional tree species are typically characterized by bursts of accelerated growth, rapid early height and basal area growth (Aide *et al.* 2001, Cusack & Montagnini 2004, Denslow & Guzman 2000, Finegan 1996, Park & Cameron 2008, Saldarriaga *et al.* 1988). The relative open crown in *O. pyramidale* forests allows some light

<sup>1</sup> Corresponding author. Email: ivar82@yahoo.com

to reach the understorey, and is expected to promote establishment and growth of tree seedlings (Poorter 1999, Whitmore 1978). However, the rapid leaf growth, leaf turnover and large leaf size ( $13 \times 13$  to  $35 \times 35$  cm) of *O. pyramidale* creates a thick litter layer, which could impede seeds reaching the soil layer, thereby creating an obstacle for the colonization of early-successional plant species (Carson & Peterson 1990, Sayer 2006, Vázquez-Yanes & Orozco-Segovia 1992). Larger seeds of late-successional tree species are probably favoured by the thick litter layer, as they have enough reserves to survive (Seiwa & Kikuzawa 1996, Tao *et al.* 1987).

We evaluated the potential of this fast-growing early-successional tree species *O. pyramidale* to accelerate structural growth by comparing height, density and basal area of canopy trees in *O. pyramidale* dominated forests with diverse secondary forests and rain forests. Furthermore, we tested whether *O. pyramidale* is able to facilitate succession by comparing diversity and density of established seedlings (trees and shrubs), and basal area and density of tree seedlings of early- and late-successional species among forest types. Finally, we tested whether the leaf-litter thickness and canopy openness were correlated with the diversity and density of shrubs and tree seedlings of especially early and late-successional tree seedlings.

We hypothesized that: (1) the secondary forests dominated by *O. pyramidale* have similar canopy structural attributes (basal area, height and density) relative to rain forest; (2) *Ochroma pyramidale* forests have a lower density of early-successional tree seedlings and a higher density of late-successional tree seedlings compared with diverse forests; (3) the leaf-litter-layer thickness increases the density of late-successional trees, and (4) canopy openness is positively correlated with the density of early-successional tree seedlings.

## METHODS

The study was carried out on the margin of Montes Azules Biosphere reserve, Chiapas, Mexico ( $16^{\circ}46'08''\text{N}$ ,  $91^{\circ}08'12''\text{W}$ ) in the Mayan community named Lacanhá Chansayab, with an altitude of 350 m asl. The climate is humid and warm with a mean annual temperature of  $25^{\circ}\text{C}$  and a mean annual precipitation  $> 2000$  mm (INEGI 1988, Pennington & Sarukhán 2005). The farmers of this community manage the natural resources using a traditional slash-and-burn system (Nations & Nigh 1980). The predominant vegetation consists of evergreen rain forest with dominant species such as *Dialium guianense*, *Brosimum alicastrum*, *Swietenia macrophylla*, *Ficus* spp. and *Spondias mombin* (Miranda & Hernández X 1963). *Ochroma pyramidale* is often preferred by farmers in Lacanhá, and they sow these seeds in high densities starting several months before the initiation of

the fallow period to facilitate their rapid establishment and dominance (Douterlungne *et al.* 2010).

## Study sites

A total of 12 sites were selected (Figure 1), eight covered with secondary forest with an area of 0.5–1.0 ha, that were last cultivated 10–15 y previously, which were divided into four patches of secondary forest dominated by *O. pyramidale* (referred to as *O. pyramidale* forests), and four secondary forest patches without *O. pyramidale* (referred to as diverse forests). Four rain-forest sites were included as control sites.

## Data collection

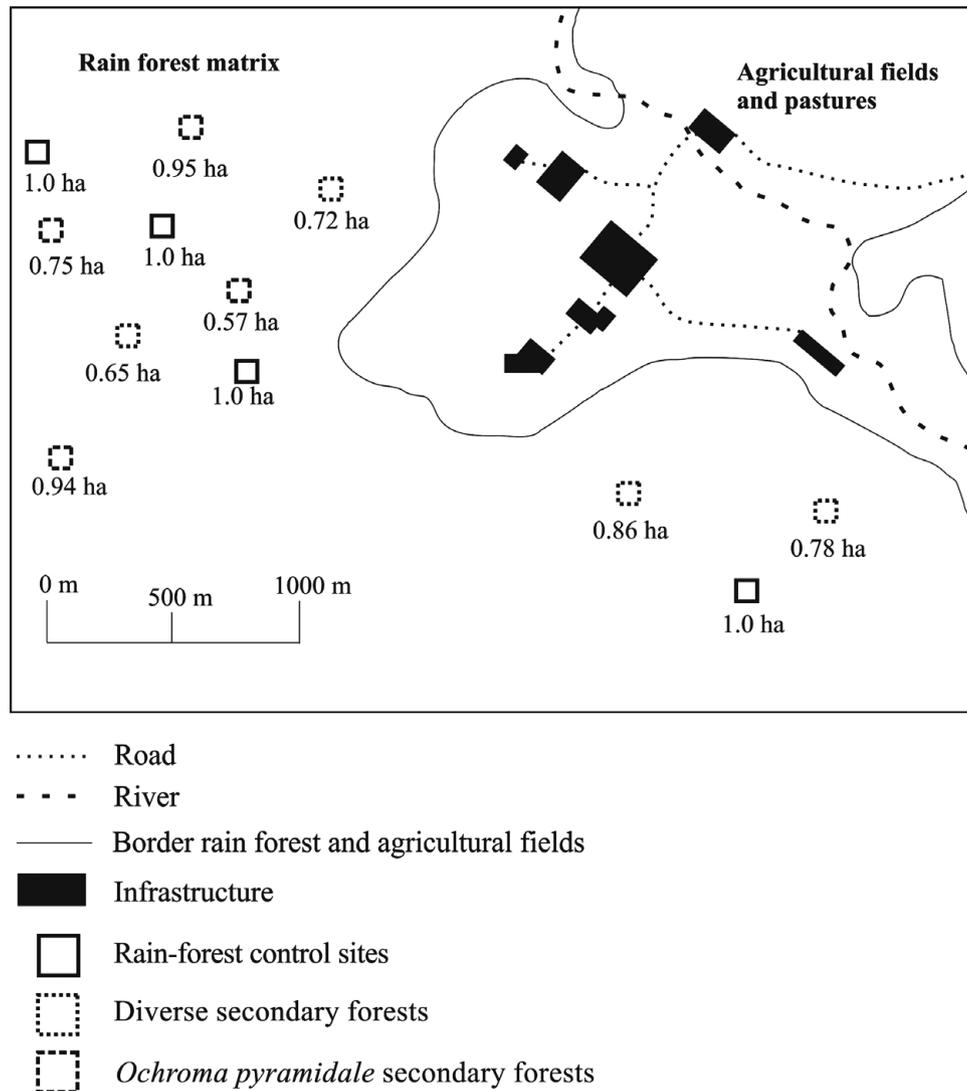
Canopy trees were measured in six quadrats of  $10 \times 10$  m per site in which dbh and height of all trees  $\geq 5$  cm dbh were measured and identified. Tree density, height and basal area were determined per species per site.

Vegetation in the understorey was measured in  $2 \times 2$ -m plots per site in which plant species  $< 5$  cm dbh were categorized into trees and shrub seedlings. Tree and shrub seedling height and diameter at base were measured, and density and diversity (Shannon–Wiener  $H'$ ) were calculated per site. Tree individuals were distinguished from shrubs by their monopodial growth form (Pennington & Sarukhán 2005). Tree seedlings were classified as early- or late-successional species based on their tolerance to shade, seed size, growth rates and maximum height based on information gathered from previous studies in the area (Levy-Tacher 2000, Levy-Tacher & Aguirre-Rivera 2005, Román-Dañobeytia *et al.* 2012).

We estimated the percentage of canopy openness at 15 random points for each site using a hemispherical crown densiometer (Forestry Suppliers, Inc, Jackson, MS, USA). The litter-layer thickness was measured by estimating the distance from the top mineral-soil layer until the top of the litter layer in five random positions with the use of a ruler, in each of the sites.

## Data analysis

Plant species diversity (Shannon–Wiener  $H'$  index) was calculated per site using EstimateS (Version 7.0.0: <http://viceroy.eeb.uconn.edu/estimates>). All variables were tested for normality using Kolmogorov–Smirnov normality tests. Non-normal data were normalized using logarithm transformations. Data were analysed for differences among forest types with an ANOVA, followed by Tukey post hoc tests and a Kruskal–Wallis test, followed by Bonferroni-corrected Mann–Whitney  $U$  post hoc tests



**Fig. 1.** Location and size (ha) of each site per forest type (*Ochroma pyramidale* secondary-forests, diverse secondary-forests and rain forests) in the community of Lacanhá, Chansayab, Chiapas, Mexico.

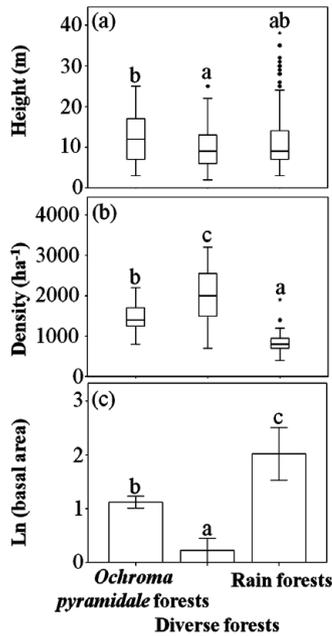
for data that could not be transformed to follow a normal distribution. Analyses were conducted in SPSS 17 (SPSS, Inc). GLMs with backward elimination were used, by discarding the least significant predictor variables one by one until all remaining ones were significant ( $P < 0.05$ ). Basal area, density and tree height of canopy trees, leaf litter, canopy openness and forest type were used as predictors. The response variables were tree and shrub diversity and density, and density of early- and late-successional tree seedlings in the understorey.

## RESULTS

Tree height of canopy trees was lowest in diverse forests (mean  $\pm$  SD:  $9.8 \pm 1.7$  m), followed by rain forest ( $12.8 \pm 2.9$  m) and *O. pyramidale* forests ( $12.4 \pm 1.8$  m;

$\chi^2_{2,1076} = 24.3$ ,  $P < 0.001$ ; Figure 2a). Tree density of canopy trees was highest in diverse forests ( $1988 \pm 685$  ha $^{-1}$ ), followed by *O. pyramidale* forests ( $1450 \pm 339$  ha $^{-1}$ ) and lowest density in rain forests ( $875 \pm 307$  ha $^{-1}$ ;  $\chi^2_{2,69} = 36.3$ ,  $P < 0.001$ ; Figure 2b). Basal area of canopy trees was similar between rain forest ( $14.2 \pm 17.6$  m $^2$  ha $^{-1}$ ) and *O. pyramidale* secondary forests ( $3.2 \pm 0.9$  m $^2$  ha $^{-1}$ ), and lowest in diverse forests ( $1.4 \pm 0.8$  m $^2$  ha $^{-1}$ ; ln-transformed;  $F_{2,69} = 34.3$ ,  $P < 0.001$ ; Figure 2c). The basal area of *O. pyramidale* trees compromised 59% of the total basal area in *O. pyramidale* sites, while in diverse forests the tree species with the highest densities (*Belotia mexicana*, *Heliocarpus appendiculatus* and *Astronium graveolens*) did not surpass 25% of the total basal area per site.

We recorded a total of 241 tree species in the understorey, of which 90 species occurred in *O. pyramidale*

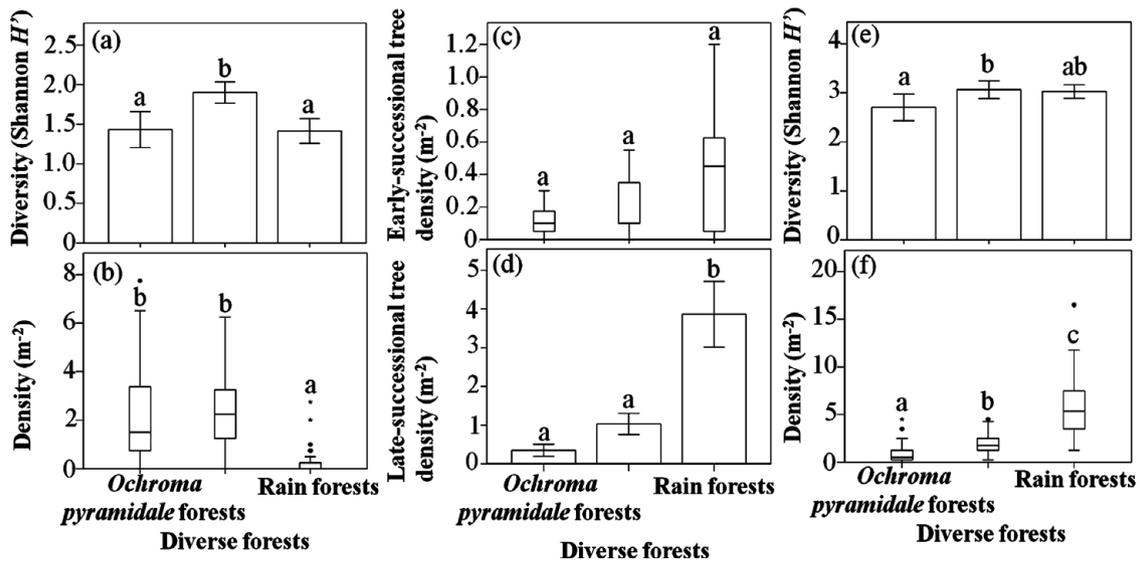


**Fig. 2.** Box plots and bars comparing tree height (a), tree density (ha<sup>-1</sup>) (b) and bars with natural logarithm of basal area (m<sup>2</sup> ha<sup>-1</sup>) (c) from canopy trees (> 5 cm) measured in six quadrats of 10 × 10 m among *Ochroma pyramidale* secondary-forest, diverse secondary-forests and rain forests in the community of Lacanhá, Chiapas, Mexico. Box plots with the same letters are not significantly different; based on a Kruskal–Wallis and a post hoc Mann–Whitney *U* test with Bonferroni correction. Bars with the same letters are not significantly different; based on an ANOVA test and post hoc Tukey test. Black dots represent outliers, and asterisks extreme cases of outliers.

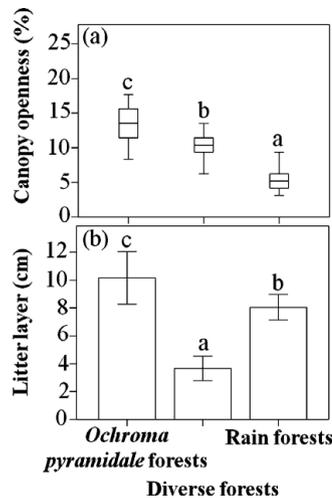
forests, 111 in diverse forests and 120 in rain forest. The tree seedling diversity was lowest in *O. pyramidale* secondary forest and highest in diverse forests ( $F_{2,45} = 4.28, P = 0.02$ ; Figure 3a). Total tree seedling density was also lowest in *O. pyramidale* secondary forests ( $\chi^2_{2,237} = 148, P < 0.001$ ; Figure 3b).

We were not able to classify all measured tree species in early- or late-successional species, and therefore only tree species with a total density of 10 or more individuals were considered in the classification, resulting in 79% (33 species) of the total species richness (Appendix 1). The density of early-successional tree seedlings in the understorey was lowest in *O. pyramidale* forests (Appendix 1), but not significantly different from the other two forest types ( $\chi^2_{2,45} = 5.17, P = 0.075$ ; Figure 3c). The density of late-successional tree seedlings was highest in the rain forest, and similar between *O. pyramidale* and diverse forests ( $F_{2,45} = 46.3, P < 0.001$ ; Figure 3d). The basal area of early-successional tree seedlings ( $\chi^2_{2,45} = 2.41, P = 0.300$ ) and late-successional tree seedlings ( $\chi^2_{2,45} = 5.20, P = 0.074$ ) was similar in all three forest types. The diversity of shrubs was highest in diverse forests ( $F_{2,45} = 11.1, P < 0.001$ ; Figure 3e) and lowest in rain forest and *O. pyramidale* forests. The density of shrubs was highest in rain forest, and lowest in *O. pyramidale* forests ( $\chi^2_{2,237} = 119, P < 0.001$ ; Figure 3f).

Canopy openness was lowest in rain forests (5.3% ± 1.2%), followed by diverse forests (10.2% ± 1.8%), with highest values in *O. pyramidale* forests (mean 13.5% ±



**Fig. 3.** Box plots and bars that represent the comparison of understorey tree diversity (Shannon  $H'$ ) (a), tree density (m<sup>-2</sup>) (b), early- (c) and late-successional tree density (m<sup>-2</sup>) (d), shrub diversity (Shannon  $H'$ ) (e) and shrub density (m<sup>-2</sup>) (f) among *Ochroma pyramidale* secondary-forests, diverse secondary-forests and rain forests in the community of Lacanhá, Chiapas, Mexico, including individuals < 5 cm in dbh from 20 2 × 2-m plots. Bars with equal letters are not significantly different; based on an ANOVA test and post hoc Tukey test. Box plots with equal letters are not significantly different; based on a Kruskal–Wallis and a post hoc Mann–Whitney *U* test with Bonferroni correction. Black dots represent outliers, and asterisks extreme cases of outliers.



**Fig. 4.** Box plots and bars that represent the comparison of canopy openness (%) (a), measured at 15 random points for each site using a hemispherical crown densitometer and litter layer thickness (cm) (b), measured by estimating the distance from the top soil layer until the top of the litter layer in five random positions with the use of a ruler and among *Ochroma pyramidale* secondary-forests, diverse secondary-forests and rain forests, in the community of Lacanhá, Chiapas, Mexico. Bars with equal letters are not significantly different; based on an ANOVA test and post hoc Tukey test. Box plots with equal letters are not significantly different; based on a Kruskal–Wallis and a post hoc Mann–Whitney *U* test with Bonferroni correction.

2.6%;  $\chi^2_{2,178} = 135$ ,  $P < 0.001$ ; Figure 4a). The litter layer was thickest in *O. pyramidale* forests ( $10.2 \pm 4.0$  cm), followed by rain forests ( $8.0 \pm 2.0$  cm), with lowest thickness ( $3.7 \pm 1.9$  cm) reported from diverse forests ( $\chi^2_{2,178} = 27.9$ ,  $P < 0.001$ ; Figure 4b).

The diversity of both tree seedlings and shrubs in the understorey could not be explained by any of the predictor variables. Tree ( $F_{1,11} = 66.9$ ,  $R^2 = 0.87$ ,  $P < 0.001$ ) density in the understorey decreased with canopy openness and shrub density ( $F_{1,11} = 11.3$ ,  $R^2 = 0.53$ ,  $P = 0.007$ ) increased with increasing canopy openness. The density of late-successional tree seedlings ( $F_{1,11} = 79.1$ ,  $R^2 = 0.89$ ,  $P < 0.001$ ) increased with decreasing canopy openness. Early-successional tree seedling density and basal area, as well as late-successional tree seedling basal area in the understorey were not correlated to any of the predictor variables.

## DISCUSSION

Our results show that forests with *O. pyramidale* as the dominant tree present higher basal area and height of canopy trees, compared with diverse forests. Density of canopy trees was lowest in rain forests, but a lower density of canopy trees was observed in *O. pyramidale* forests than in diverse forests. The vegetation in the

understorey had a lower tree density, tree diversity and shrub diversity in *O. pyramidale* forests than in diverse forests. Canopy openness proved an important variable in explaining the density of shrubs and tree seedlings in the understorey as well as late-successional tree seedling density. Height, density and basal area measurements of canopy trees in *O. pyramidale* forests were different from the values reported in rain forests but differences were smaller between rain forest and *O. pyramidale* than between rain forest and diverse forests, implying a structural acceleration of trees in the canopy of *O. pyramidale* forests. The sowing of *O. pyramidale* seeds before the fallow period results in high light competition between recruited individuals, stimulating vertical growth. Similar management strategies have been used as an inexpensive and effective method for restoring degraded areas dominated by the invasive fern *Pteridium aquilinum* (Douterlungne *et al.* 2010) or to compensate for high predation risks and to improve growth form in monoculture plantations (Chapman & Chapman 1999). The weeding of undesired plant species before the end of the cultivation period allows *O. pyramidale* individuals a head start on other plant species, decreasing total tree density and ensuring a dominance of *O. pyramidale* in the canopy (Douterlungne *et al.* 2010). The high density, rapid tree growth and closed canopy cover created by the large leaves, during initial early stages of growth of *O. pyramidale*, increases opportunities to compete among other plants, even out-shading the invasive fern *Pteridium aquilinum* (Douterlungne *et al.* 2010). Vertical growth is increased due to crown competition between *O. pyramidale* individuals, while stem diameter growth is developed after optimal height is reached, and does not necessarily decline with tree density due to accelerated growth of surviving trees (Laurance *et al.* 2004). The dominance of *O. pyramidale* permits the advanced basal area and height of trees in secondary forest, which could facilitate the restoration process, creating a higher basal area as well as an average height, but due to its fast leaf turnover, also increases the soil organic matter accumulation (Diemont *et al.* 2006, Douterlungne *et al.* 2010, Levy-Tacher & Golicher 2004), and a structural barrier for seedling establishment.

Forests dominated by *O. pyramidale* have a lower overall density of seedlings in the understorey layer. The lower tree density in the canopy as well as lower total density of tree seedlings facilitates the removal of the vegetation before the cultivation period after 5 y of fallow period, with little effort to clear the area for another agricultural cycle, especially because *O. pyramidale* individuals have a relatively soft wood density ( $0.16 \text{ g cm}^{-3}$ ; Byrne & Nagle 1997) compared with other early successional tree species such as *Cecropia* spp. ( $0.30 \text{ g cm}^{-3}$ ) or *Lonchocarpus* spp. ( $0.69 \text{ g cm}^{-3}$ ; Fearnside 1997). A lower tree density in *O. pyramidale* forests could increase

occupation of biological space and therefore positively affect seedling establishment (Ross & Harper 1972), however, we expected that leaf-litter thickness could play an important role in reducing seedling establishment and form a barrier for emerging seedlings (Carson & Peterson 1990, Vázquez-Yanes & Orozco-Segovia 1992). In contrast, leaf litter-layer thickness was not correlated with density of early- or late-successional tree seedlings in the understorey, and hence, does not seem to function as a barrier for seedling growth. However, early-successional tree seedlings only contributed 8.5% of the total tree seedling density, implying that seedling establishment for early-successional tree species was relatively low. It was probably due to this low density that we did not find a relation between the density of early-successional tree seedlings and litter layer thickness in these secondary forests of 10–15 y of age, where canopy trees are slowly replaced by mid- to late-successional tree species (Finegan 1996). Neither did we find a relation between leaf-litter thickness and late-successional tree seedling density; canopy openness was a better predictor in explaining their density.

While canopy openness was considerably higher in *O. pyramidale* forests, which could negatively affect late-successional tree seedling density in the understorey (Molofsky & Fischer 1993), also favouring the establishment of early-successional species, the density of both late- and early-successional tree seedlings was similar between the two secondary forest types.

Guariguata *et al.* (1995) studied a tree monoculture plantation (*Jacaranda copaia*) with high canopy openness in comparison to other tree species. They reported a higher understorey shrub density in areas with higher canopy openness, similar to our results, where *O. pyramidale* forests were associated with a higher shrub density. The higher density of shrubs in the understorey could attract a larger diversity and abundance of bats and birds which are known for their preference of fruits from shrubs (Galindo-González *et al.* 2000). This indicates the importance of the species-specific functional traits of canopy trees, which can influence seed dispersers and hence the establishment of certain plant species (Powers *et al.* 1997). Tree species that have a thin crown can be important for the initial stages of succession, creating an ideal environment for light-demanding plant species in the understorey, and in turn, provide shade for the establishment of mid- to late-successional tree species (Parrotta 1995, Powers *et al.* 1997). Even though late-successional tree density in the understorey was similar between secondary forest types, the low density of overall plant species in the understorey, as found in this study, is unlikely to cast sufficient shade to favour the establishment of mid- to late-successional tree species. Moreover, the thin crown of *O. pyramidale*, could negatively affect establishment and growth of these mid- to late-successional tree species over time. We therefore

recommend monitoring establishment and growth of late-successional tree species in both secondary forest types, to be able to understand the consequences of species-specific traits of canopy trees on secondary forest succession.

Due to its fast growth *O. pyramidale* can enhance growth of secondary forest in terms of structural attributes towards late-successional stage forest, and has the capacity to suppress overall seedling establishment. Density of late-successional trees was similar between *O. pyramidale* and diverse forests, but our sites were partly encompassed by rain forest, which can function as seed sources for late-successional tree species. In a study where seed sources were limited, a fast-growing tree species facilitated native tree species recruitment (Otsamo 2000). We therefore hypothesize that *O. pyramidale* can facilitate late-successional seedling establishment and stimulate structural growth in degraded areas with low seed source availability, but this should be tested further in the future.

#### ACKNOWLEDGEMENTS

This research was funded by Etnobiología para la Conservación A.C. and by a doctoral scholarship awarded to the first author by CONACyT-Mexico (Reg. 239503). We are grateful to M. Castellano and E. Chankin for allowing us to work on their lands. Furthermore, we would like to thank J. Chankin, A. Chankin, C. Peñaloza Guerrero, R. van Toor, V. Hommersen, M. Wulms and A. Sanchez for their help in the fieldwork. We would also like to thank Dr L. B. Vázquez for useful comments during the writing of the manuscript.

#### LITERATURE CITED

- AIDE, T. M., ZIMMERMAN, J. K., PASCARELLA, J. B., RIVERA, L. & MARCANO-VEGA, H. 2001. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. *Restoration Ecology* 8:328–338.
- BYRNE, C. E. & NAGLE, D. C. 1997. Carbonization of wood for advanced materials applications. *Carbon* 35:259–266.
- CARSON, W. P. & PETERSON, C. J. 1990. The role of litter in an old-field community: impact of litter quantity in different seasons on plant species richness and abundance. *Oecologia* 85:8–13.
- CHAPMAN, C. A. & CHAPMAN, L. J. 1999. Forest restoration in abandoned agricultural land: a case study from East Africa. *Conservation Biology* 13:1301–1311.
- COLEY, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* 53:209–233.
- CUSACK, D. & MONTAGNINI, F. 2004. The role of native species plantations in recovery of understorey woody diversity in degraded pasturelands of Costa Rica. *Forest Ecology and Management* 188:1–15.

- DALLING, J. W., LOVELOCK, C. E. & HUBBELL, S.P. 1999. Growth responses of seedlings of two neotropical pioneer species to simulated forest gap environments. *Journal of Tropical Ecology* 15:827–839.
- DENSLOW, J. S. & GUZMAN, G. S. 2000. Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. *Journal of Vegetation Science* 11:201–212.
- DIEMONT, S. A. W., MARTIN, J. F., LEVY-TACHER, S. I., NIGH, R. B., RAMIREZ LOPEZ, P. & GOLICHER, J. D. 2006. Lacandon Maya forest management: restoration of soil fertility using native tree species. *Ecological Engineering* 28:205–212.
- DOUTERLUNGNE, D., LEVY-TACHER, S. I., GOLICHER, J. D. & ROMÁN DAÑOBEYTIA, F. 2010. Applying indigenous knowledge to the restoration of degraded tropical rain forest dominated by bracken. *Restoration Ecology* 18:322–329.
- FEARNSIDE, P. M. 1997. Wood density for estimating forest biomass in Brazilian Amazonia. *Forest Ecology and Management* 90:59–87.
- FINEGAN, B. 1996. Pattern and process in neotropical secondary rainforests: the first 100 years of succession. *Trees* 11:119–124.
- FRANCIS, J. K. 1991. *Ochroma pyramidale Cav. Balsa – Bombacaceae*. SO. Institute of Tropical Forestry, USDA, SM-41. Río Piedras. 6 pp.
- GALINDO-GONZÁLEZ, J., GUEVARA, S. & SOSA, V. J. 2000. Bat- and bird-generated seed rains at isolated trees in pastures in tropical rain forest. *Conservation Biology* 14:1693–1703.
- GUARIGUATA, M. R., RHEINGANS, R. & MONTAGNINI, F. 1995. Early woody invasion under tree plantation in Costa Rica: implications for forest restoration. *Restoration Ecology* 3:252–260.
- INEGI (Instituto Nacional de Estadística Geografía e Informática). 1988. Las Margaritas (E15-12, D15-3). Carta climática. Esc.: 1:250,000. México DF, México.
- LAURANCE, W. F., OLIVEIRA, A. A., LAURANCE, S. G., CONDIT, R., NASCIMENTO, H. E. M., SANCHEZ-THORIN, A. C., LOVEJOY, T. E., ANDRADE, A., D'angelo, S., RIBEIRO, J. E. & DICK, C. W. 2004. Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature* 428:171–175.
- LEVY-TACHER, S. I. 2000. *Sucesión causada por roza-tumba-quema en las selvas de Lacanhá, Chiapas*. Dissertation. Colegio de Posgraduados. Montecillo, Texcoco, Estado de México, México. 165 p.
- LEVY-TACHER, S. I. & GOLICHER, J. D. 2004. How predictive is traditional ecological knowledge? The case of the Lacandon Maya fallow enrichment system. *Interciencia* 29:496–503.
- LEVY-TACHER, S. I. & AGUIRRE-RIVERA, J. R. 2005. Successional pathways derived from different vegetation use patterns by Lacandon Mayan Indians. *Journal of Sustainable Agriculture* 26:49–82.
- LUGO, A. E. 1997. The apparent paradox of reestablishing species richness on degraded lands with tree monocultures. *Forest Ecology and Management* 99:9–19.
- MIRANDA, F. & HERNÁNDEZ X, E. 1963. Los tipos de vegetación de México y su clasificación. *Boletín de la Sociedad Botánica de México* 28:29–179.
- Molofsky, J. & Fischer, B. L. 1993. Habitat and predation effects on seedling survival and growth in shade-tolerant tropical trees. *Ecology* 74:261–265.
- Nations, J. & Nigh, R. 1980. The evolutionary potential of Lacandon Maya sustained-yield tropical forest agriculture. *Journal of Anthropological Research* 36:1–30.
- OTSAMO, R. 2000. Secondary forest regeneration under fast-growing forest plantations on degraded *Imperata cylindrica* grasslands. *New Forests* 19:69–93.
- PARK, A. & CAMERON, J. L. 2008. The influence of canopy traits on throughfall and stemflow in five tropical trees growing in a Panamanian plantation. *Forest Ecology and Management* 255:1915–1925.
- PARROTTA, J. A. 1995. Influence of overstory composition on understory colonization by native species in plantations on a degraded tropical site. *Journal of Vegetation Science* 6:627–636.
- PARROTTA, J. A., KNOWLES, O. & WUNDERLE, J. M. 1997. Floristic diversity development in a 10-year-old restoration forest on a bauxite mined site in Amazonia. *Forest Ecology and Management* 99:21–42.
- PENNINGTON, T.D. & SARUKHÁN, J. 2005. *Árboles tropicales de México*. (Third edition). Universidad Nacional Autónoma de México y Fondo de Cultura Económica, México, D.F. 534 pp.
- POORTER, L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology* 13:396–410.
- POWERS, J. S., HAGGAR, J. P. & FISHER, R. F. 1997. The effect of overstory composition on understory woody regeneration and species richness in 7-year-old plantations in Costa Rica. *Forest Ecology and Management* 99:43–54.
- ROMÁN-DAÑOBEYTIA, F. J., LEVY-TACHER, S. I., ARONSON, J., RODRIGUES, R. R. & CASTELLANOS-ALBORES, J. 2012. Testing the performance of fourteen native tropical tree species in two abandoned pastures of the Lacandon Rainforest Region of Chiapas, Mexico. *Restoration Ecology* 20:378–386.
- ROSS, M. A. & HARPER, J. L. 1972. Occupation of biological space during seedling establishment. *Journal of Ecology* 60:77–88.
- SALDARRIAGA, J. G., DARREL, C. W., THARP, M. L. & UHL, C. 1988. Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. *Journal of Ecology* 76:938–958.
- SAYER, E. J. 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological Reviews* 81:1–31.
- SEIWA, K. & KIKUZAWA, K. 1996. Importance of seed size for the establishment of seedlings in relation to seed size. *Canadian Journal of Botany* 69:532–538.
- SELAYA, N. G., OOMEN, R. J., NETTEN, J. J. C., WERGER, M. J. A. & ANTEN, N. P. R. 2008. Biomass allocation and leaf life span in relation to light interception by tropical forest plants during the first years of secondary succession. *Journal of Ecology* 96:1211–1221.
- TAO, D. L., XU, Z. B. & LI, X. 1987. Effect of litter layer on natural regeneration of companion tree species in the Korean pine forest. *Environmental and Experimental Botany* 27:53–65.
- VÁZQUEZ-YANES, C. & OROZCO-SEGOVIA, A. 1992. Effects of litter from a tropical rainforest on tree seed germination and establishment under controlled conditions. *Tree Physiology* 11:391–400.
- WHITMORE, T. C. 1978. Gaps in the forest canopy. Pp. 639–655 in Tomlinson, P. B. & Zimmermann, M. H. (eds.). *Tropical trees as living systems*. Cambridge University Press, Cambridge.

**Appendix 1.** Density ( $m^{-2}$ ) of tree species and family per early- (E) or late-successional species (L) in the understorey (< 5 cm dbh) of *Ochroma pyramidale* secondary-forests, diverse secondary-forests and rain forests, in the community of Lacanhá, Chiapas, Mexico. Species nomenclature follows Miranda & Hernández X (1963) and Pennington & Sarukhán (2005).

Family	Species	FG	<i>O. pyramidale</i> forests	Diverse forests	Rain forests
Anacardiaceae	<i>Spondias mombin</i>	L	7	7	0
Annonaceae	<i>Cymbopetalum penduliflorum</i>	L	0	0	6
Araliaceae	<i>Dendropanax arboreus</i>	L	1	5	5
Boraginaceae	<i>Cordia alliodora</i>	E	0	2	3
Burseraceae	<i>Protium copal</i>	L	2	2	15
Calophyllaceae	<i>Calophyllum brasiliense</i>	L	2	20	2
Chrysobalanaceae	<i>Licania arborea</i>	L	0	0	7
Chrysobalanaceae	<i>Licania</i> sp.	L	3	0	11
Connaraceae	<i>Rourea glabra</i>	E	3	6	1
Fabaceae	<i>Acacia mayana</i>	E	0	0	7
Fabaceae	<i>Inga punctata</i>	E	0	5	7
Fabaceae	<i>Inga</i> sp. 1	E	0	4	1
Fabaceae	<i>Inga</i> sp. 2	E	1	1	6
Fabaceae	<i>Lonchocarpus guatemalensis</i>	E	6	3	0
Fabaceae	<i>Pterocarpus rohrii</i>	L	0	6	26
Fabaceae	<i>Vatairea lundellii</i>	L	3	2	2
Fabaceae	<i>Platymiscium dimorphandrum</i>	L	1	5	0
Lauraceae	<i>Ocotea cernua</i>	L	0	9	3
Malvaceae	<i>Ceiba pentandra</i>	L	0	3	1
Meliaceae	<i>Guarea glabra</i>	L	0	3	14
Moraceae	<i>Brosimum alicastrum</i>	L	5	13	83
Moraceae	<i>Castilla elastica</i>	L	2	3	13
Moraceae	<i>Poulsenia armata</i>	L	1	4	56
Moraceae	<i>Pseudolmedia oxyphyllaria</i>	L	0	2	7
Rubiaceae	<i>Blepharidium mexicanum</i>	L	4	0	13
Rubiaceae	<i>Psychotria flava</i>	L	6	6	3
Rubiaceae	<i>Rondeletia capitellata</i>	L	0	1	3
Salicaceae	<i>Pleuranthodendron lindenii</i>	L	3	2	10
Sapindaceae	<i>Cupania dentata</i>	L	4	4	0
Sapotaceae	<i>Manilkara zapota</i>	L	0	2	3
Ulmaceae	<i>Ampelocera hottlei</i>	L	0	0	86
Ulmaceae	<i>Ulmus mexicana</i>	L	0	11	6
Violaceae	<i>Rinorea hummelii</i>	L	2	1	64
Number of species			18	27	29
Total			56	132	463