Distance effect from cloud forest fragments on plant community structure in abandoned pastures in Veracruz, Mexico

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Abstract: Secondary succession was studied in a Mexican cloud forest region along a chronosequence of 15 abandoned pastures (0.25–80 y). Our objective was to determine the effects of distance from the forest border on successional vegetation structure and woody species richness along the chronosequence. Vegetation structure similar to that of mature forests recovered over 40–50 y, both close to (0–10 m) and away from (40–50 m) the border. Total woody species richness was similar for both distances but species composition differed significantly. When primary forest species were analysed separately, basal area, height, abundance and richness were all significantly higher close to the forest border. Primary species such as *Quercus* spp. (barochorous-synzoochorous) and *Carpinus caroliniana* (anemochorous) had lower basal area, density and height away from the border than close to it. Secondary species such as *Lippia myriocephala* (anemochorous) and *Myrsine coriacea* (endozoochorous) did not differ in their rate of colonization between distances. The limitation of seed dispersal and establishment for primary woody species away from forest borders suggests that propagules need to be introduced to accelerate forest restoration.

Key Words: chronosequence, functional type, richness, secondary succession, seed dispersal syndrome, tropical montane forest

INTRODUCTION

Regeneration of natural forest or passive restoration occurs when agricultural lands are abandoned owing to environmental and socio-economic factors such as low productivity, low minimum crop price and rural emigration (Guariguata & Ostertag 2001, Stonich & DeWalt 1996, Thomlinson *et al.* 1996). Forest remnants that punctuate landscapes characterized by large areas of agricultural and pasture land may play an important role as a source of propagules for the colonization of abandoned fields. In tropical forests the abundance and diversity of seeds dispersed into open old fields is inversely proportional to the distance between secondary successional sites and mature forest fragments or isolated remnant trees (Cubiña & Aide 2001, González-Montagut 1996, Guevara *et al.* 1992, Holl 1999). However, all previous studies of secondary succession in Mexico have

been carried out mainly in tropical lowland rain forests (Gómez-Pompa & Vázquez-Yanes 1981, Martínez-Ramos 1985, Purata 1986), and little is known about the recovery of tropical montane cloud forests and in particular, about the potential impact of remnant forest patches on forest recovery.

It has been suggested that a major factor preventing the recovery of tropical forests in abandoned pastures is seed dispersal limitation (Aide & Cavelier 1994, Nepstad *et al.* 1990, Zimmerman *et al.* 2000). Dispersal is much reduced at distances greater than 5–10 m from forest borders, but the small seeds of some wind- and animal-dispersed species can travel greater distances (Cubiña & Aide 2001, Finegan & Delgado 2000, Holl 1999). The seedlings developing from these small seeds are, however, often outcompeted by the tall, dense, herbaceous vegetation that dominates abandoned pastures (Duncan & Duncan 2000, Holl *et al.* 2000). In the Neotropics, this competition effect is more prominent in abandoned pastures that were sown with tall non-native African grass species. Besides competition with the herbaceous vegetation, seedling establishment can be limited by other factors such as a short viability period and the low germination rate of

seeds, high seed and seedling predation, water stress, soil infertility, and the absence of mycorrhizas (Aide & Cavalier 1994, Holl *et al.* 2000, Nepstad *et al.* 1990).

Our main objective in this study was to investigate the effects of distance from the forest border on vegetation structure and floristic composition through time using a chronosequence of 15 pastures that had been abandoned for 0.25–80 y. Specifically, we asked: what are the effects of distance to forest fragment and time since abandonment on (1) the regeneration of the overall vegetation structure, (2) the regeneration of functional types defined according to seed dispersal syndrome, and (3) the species richness of woody species, particularly those that are unique to primary cloud forest. The working hypotheses were: (1) forest structure can regenerate both at short (0–10 m) and long distances (40–50 m) from the forest remnant owing to the long distance dispersal of ane-mochorous and endozoochorous small-seeded woody species; however, (2) the regeneration of the community composition will be different at different distances from the forest border because of the limited dispersal capabilities of primary forest woody species. We expect that, overall, the greater the elapsed time since pasture abandonment and the shorter the distance to the forest border, the more similar the vegetation structure and community composition will be to that of mature forests.

STUDY AREA

The study area was located in the tropical montane cloud forest region near Xalapa, Veracruz, Mexico (19°29′–19°36′ N, 96°56′–97°0′ W). The climate is mild and humid (Williams-Linera 2002). The most common soil in the region is humic andosol (Rossignol 1987). Domi-nant canopy tree species have temperate affinities (*Quercus xalapensis, Q. germana, Q. leiophylla, Liquidambar styraciflua* var. *mexicana, Carpinus caroliniana, Clethra mexicana*) whereas understorey trees (*Turpinia insignis, Cinnamomum effusum, Oreopanax xalapensis*) and shrubs (*Palicourea padifolia, Eugenia xalapensis, Miconia glab-errima, Ocotea psychotrioides*) have tropical affinities (Williams-Linera 2002). Nomenclature follows Flora of Veracruz (Sosa & Gómez-Pompa 1994).

Study sites

We selected 15 abandoned pastures ranging in age from 0.25 to 80 y old (0.25, 0.75, 1.5, 2.5, 5, 5.5, 8, 9, 12, 14, 15, 17, 23, 35 and 80 y old). Age of abandonment was determined through interviews with the owners, and cross interviews with the neighbours. Most of our study sites had an abrupt land-use change when they were sold to new private owners interested in land uses other

than raising cattle, such as recovering the original cloud forest, or government creation of forest reserves. The altitude ranged between 1300 and 1580 m asl, annual precipitation was 1500–1650 mm, and mean annual temperature ranged between 14 and 16 °C. All the fields had a minimum area of 1 ha, and were adjacent to a mature forest fragment with a linear border of at least 100 m. Field size and shape were different but all samp-ling plots were located at least 50 m away from any other forest remnant. The slope of the terrain ranged from 4° to 26°. The orientation was northwards for eight sites and southwards for the others. The recently abandoned pastures (< 3 y old) were dominated by native short grasses such as *Axonopus compressus, Paspalum conjugatum, P. notatum, P. variabile, P. laxiflorum*, and herbs such as *Melampodium divaricatum, Borreria laevis, Hyptis atrorubens, Desmodium* sp. and *Eupatorium* sp. An exotic tall grass dominated one of these abandoned pastures (*Cynodon plectostachyus*).

METHODS

Sampling design

To assess distance effects, in each old field 100×10-m parallel bands were located at 0–10 m and 40–50 m from the forest border. Four 10×10-m plots were randomly located in each band to sample trees ≥ 5 cm dbh (diameter at 1.3 m height). At the centre of each 10×10-m plot, one 4×4-m plot was established to sample woody plants < 5 cm dbh and > 1.3 m height (saplings, shrubs and lianas), and one 2×2-m plot was set up for seedlings < 1.3 m height. We measured dbh and height, and counted the number of individuals per species in the 10×10-m and 4×4-m plots. In the 2×2-m plots, the number of individuals and basal diameter of tree species were measured. All plants in the plots were identified to the species level, and herbarium specimens were collected and deposited in the XAL herbarium, Instituto de Ecología, A.C. After they are first mentioned, species will be referred by their generic name only.

In each stand, and for the two distances from the forest border, structural variables such as basal area (m^2 ha^{-1}), density (individuals ha^{-1}), mean height (m) and mean maximum height (m) were calculated for trees ≥ 5 cm dbh, shrubs (woody plants ramified at the base) and lianas. For saplings and seedlings we calculated density and basal area only.

Tree species were classified as barochorous-synzoo-chorous, i.e. trees with large seeds dispersed by gravity and animals (e.g. *Cinnamomum, Quercus*), endozoochor-ous, i.e. trees with small seeds dispersed mainly by birds (e.g. *Meliosma, Myrsine, Trema*) or anemochorous, i.e. trees with small seeds dispersed by wind (e.g.

Table 1. ANCOVA for structure variables of selected tree species $\geq$ 5 cm dbh along the chronosequence of abandoned pastures in central Veracruz, Mexico. Results are for basal area, density, mean height, and maximum height. R^2 is the proportion of variance explained by each source of variation. * = P < 0.05, ** = P < 0.01.

	Basal area (m^2 ha^{-1})		Density (stems ha^{-1})		Mean height (m)		Maximum height (m)	
	F	R^2	F	R^2	F	R^2	F	R^2
Total of trees $\geq$ 5 cm dbh								
Distance	0.2	0.00	1.2	0.04	1.1	0.01	8.8*	0.06
Age	51.3**	0.73	10.4**	0.34	63.9**	0.73	109**	0.80
Age^2	–	–	–	–	5.1*	0.06	–	–
Residuals		0.27		0.62		0.20		0.14
Quercus spp.								
Distance	37.6**	0.64	61**	0.68	16.4**	0.40	19.5**	0.52
Age	6.2*	0.11	7.3*	0.08	9.8**	0.24	3.0	0.08
Dist × age	–	–	7.0*	0.08	–	–	–	–
Residuals		0.25		0.16		0.36		0.40
Carpinus caroliniana								
Distance	8.8*	0.33	8.8*	0.37	5.9*	0.16	4.8*	0.19
Age	4.8*	0.18	2.2	0.09	13.9*	0.37	7.8*	0.30
Dist × age	–	–	–	–	6.1*	0.16	–	–
Residuals		0.49		0.54		0.32		0.51
Myrsine coriacea								
Distance	0.0	0.0	0.0	0.00	0.0	0.00	0.1	0.01
Age	0.0	0.0	0.0	0.0	8.8**	0.32	0.4	0.02
Residuals		1		1		0.68		0.97
Lippia myriocephala								
Distance	1.7	0.09	0.0	0.00	0.0	0.00	0.1	0.01
Age	2.6	0.13	0.0	0.0	0.4	0.02	0.4	0.02
Residuals		0.78		1		0.98		0.97

Carpinus, *Lippia*, *Liquidambar*) (terminology follows van der Pijl 1972). Also, tree species were classified as primary and secondary following Sosa & Gómez-Pompa (1994), experts' opinions and personal experience (see Appendix).

Additionally, the structural variables were calculated for trees pooled by seed dispersal syndrome (barochorous-synzoochorous, endozoochorous and anemochorous), and for selected tree species. The selected species were *Carpinus caroliniana* (medium-sized seed, anemochorous), *Lippia myriocephala* (small seed, anemochorous), *Quercus* (*Q. xalapensis, Q. germana, Q. leiophylla, Q. salicifolia* and *Q. acutifolia*; large seed, barochorous-synzoochorous), and *Myrsine coriacea* (small seed, endozoochorous). These species were selected based on their abundance and representation of different seral stages and seed dispersal mechanisms.

The number of species (richness, S) was estimated for all trees $\geq$ 5 cm dbh, primary and secondary trees, saplings, seedlings, shrubs and lianas.

Data analysis

To examine the effect of distance from a forest border and time since abandonment on the response variables (basal area, density, mean and maximum height and S), we used analysis of covariance (ANCOVA) with the age

of the old field as the continuous explanatory variable (covariate), and distance as a categorical explanatory variable. A quadratic age term was also included in the ANCOVA model since we expected a non-linear, quadratic relationship between pasture age and some of the response variables. Since the 80-y-old site covers more than half of the range of the x-axis, it was omitted from the ANCOVA, but was not omitted from the data presented. Data were Box-Cox transformed when there was a significant deviation from normality. Simplification of the ANCOVA models followed the protocol of Crawley (2002), removing non-significant terms sequentially to obtain the minimal adequate model (principle of parsimony). All the statistical analyses were carried out with the statistical package S-PLUS 4.6 professional 2000, MathSoft, Inc. (Crawley 2002). Reported values are mean $\pm$ 1 SE.

RESULTS

Age and distance effect on vegetation structure

Results from the ANCOVA indicated that for trees $\geq$ 5 cm dbh, the age of the old-field significantly explained differences in basal area, density, mean height and maximum height along the chronosequence of abandoned pastures (Table 1). The ANCOVA models indicated a relatively fast recovery during the first stages
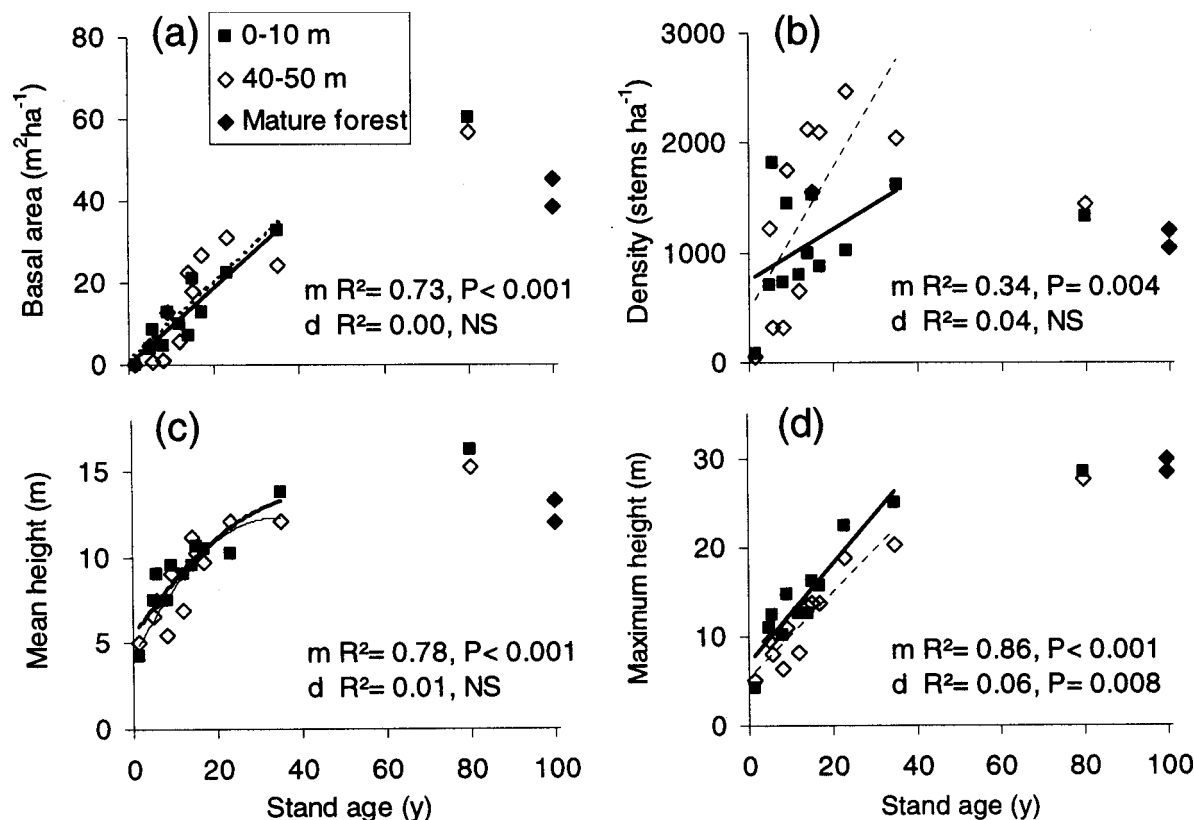
Figure 1. Differences in the vegetation structure variables for trees ≥ 5 cm dbh along a chronosequence of 15 abandoned pastures in central Veracruz, Mexico, at two distances from a forest border: 0–10 m (solid line) and 40–50 m (dashed line). The lines are derived from the minimal adequate model of ANCOVA; a quadratic term was used in the ANCOVA, when it is significant the relationship is represented by a unimodal curve, when it is non-significant the relationship is linear. Data from mature forest are shown for comparison (diamond). (a) Basal area, (b) density, (c) mean height and (d) maximum height. Multiple R^2 (m R^2) is the variance explained by the minimal adequate model, and distance effect R^2 (d R^2) is the variance explained by the effect of the factor distance. NS = not significant (P > 0.05).

of this chronosequence (Figure 1a-d). The values of the structural variables at the two distances from the forest border were similar except for maximum height (F = 8.8, R^2 = 0.06, P = 0.008), which was greater at 0–10 m (15.4 ± 2 m) than at 40–50 m (12.0 ± 2 m) from the forest border (Figure 1d). ANCOVAs for saplings, seedlings, shrubs and lianas indicated no significant age effect on the structural variables. Similarly, there were no differences between distances from the border except for seedling basal area (F = 5.0, R^2 = 0.16, P = 0.034), which was significantly higher close to the border $(0.25 \pm 0.057 \, m^2 \, ha^{-1})$ than in the interior of the old field $(0.12 \pm 0.035 \, m^2 \, ha^{-1})$.

Seed dispersal syndrome

Results from the ANCOVAs for barochorous-synzoochorous, endozoochorous and anemochorous tree species showed that the age of the old field accounted for significant differences in the four structural response variables within these groups (Figure 2). The effect of

distance was significant for the barochorous-synzoochorous group only. Values for basal area (F = 49.9, R^2 = 0.58, P < 0.001), density (F = 54.4, R^2 = 0.63, P < 0.001), mean height (F = 32, R^2 = 0.42, P < 0.001) and maximum height (F = 26, R^2 = 0.47, P < 0.001) were greater close to the forest border than inside the old field (Figure 2a-c). In contrast, ANCOVA results for both endozoochorous and anemochorous trees indicated no significant differences for any of the structural variables (Figure 2d-h); the exception was mean height of anemochorous trees which was higher close to the border during the first stages of the chronosequence (F = 4.9, R^2 = 0.06, P = 0.04, Figure 2i).

Age significantly affected all of the structural variables for *Quercus*, except maximum height. Age also affected basal area, mean and maximum height of *Carpinus* (Table 1). All structural variables of *Quercus* and *Carpinus* were significantly higher closer to the forest border. Differences between the two distances were greater during the early stages of the chronosequence (up to 35 y) while in the later stage (80 y old) there was no difference. There were no differences between distances for the four
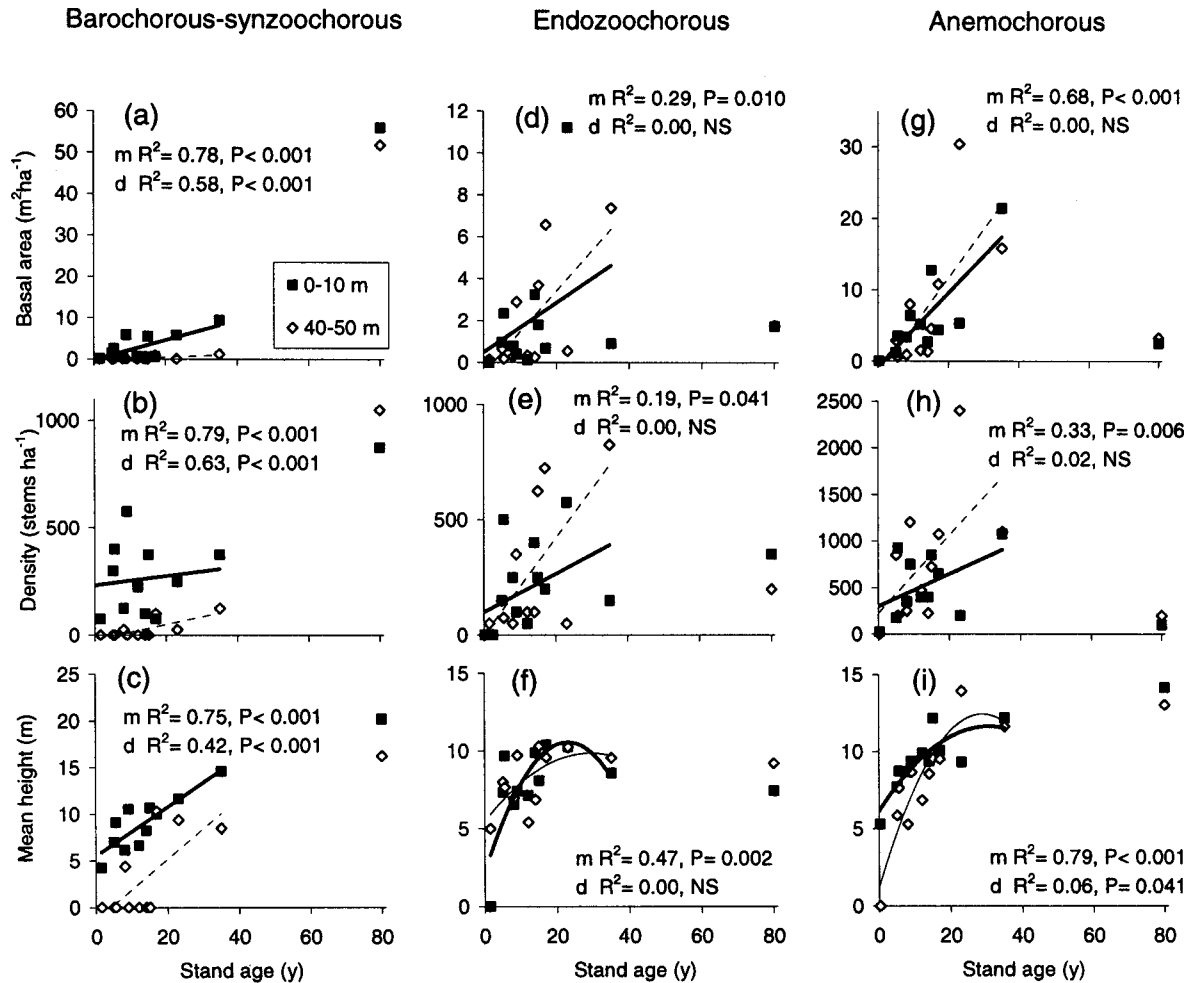
Figure 2. Differences in the vegetation structure variables for trees ≥ 5 cm dbh along a chronosequence of 15 abandoned pastures in central Veracruz, Mexico, at two distances from a forest border: 0–10 m (solid line) and 40–50 m (dashed line). The lines are derived from the minimal adequate model of ANCOVA; a quadratic term was used in the ANCOVA, when it is significant the relationship is represented by a unimodal curve, when it is non-significant the relationship is linear. Tree species are classified into three seed dispersal mechanisms: (a), (b) and (c) barochorous–synzoochorous, (d), (e) and (f) endozoochorous, and (g), (h) and (i) anemochorous. NS = not significant (P > 0.05).

structural variables in species with long-distance seed dispersal such as *Myrsine* and *Lippia* (Table 1).

Species richness

Overall, a total of 164 woody species was recorded in the 15 abandoned pastures: 71 species were trees, 49 were shrubs and 44 vines. We recorded 63 tree, 40 shrub and 36 vine species at 0–10 m from the border; and 49 tree, 38 shrub and 29 vine species for the interior of the old field.

The age of the old field significantly affected tree species richness (S) along the chronosequence. S of trees ≥ 5 cm dbh and seedlings increased with time of pasture abandonment, and decreased towards the final stage of the chronosequence (Figure 3a, c). Sapling richness

increased linearly with age until the last stage of the chronosequence (Figure 3b). Shrubs and lianas did not display any significant trend along the chronosequence. S was similar at the two distances from the forest border for trees ≥ 5 cm dbh, saplings, shrubs and lianas. Only tree seedlings displayed higher S values close to the border (Figure 3c).

Interestingly, S of primary species was higher close to the border for trees ≥ 5 cm dbh (F = 9.8, R^2 = 0.18, P = 0.020), saplings (F = 15.9, R^2 = 0.33, P < 0.001) and seedlings (F = 14.6, R^2 = 0.27, P = 0.002) (Figure 3d-f) whereas S of secondary species was similar for the two distances for those groups. Primary species richness increased in the chronosequence for trees ≥ 5 cm and for saplings, whereas S of secondary species significantly increased until the 35-y-old site and then decreased towards the 80-y-old site.
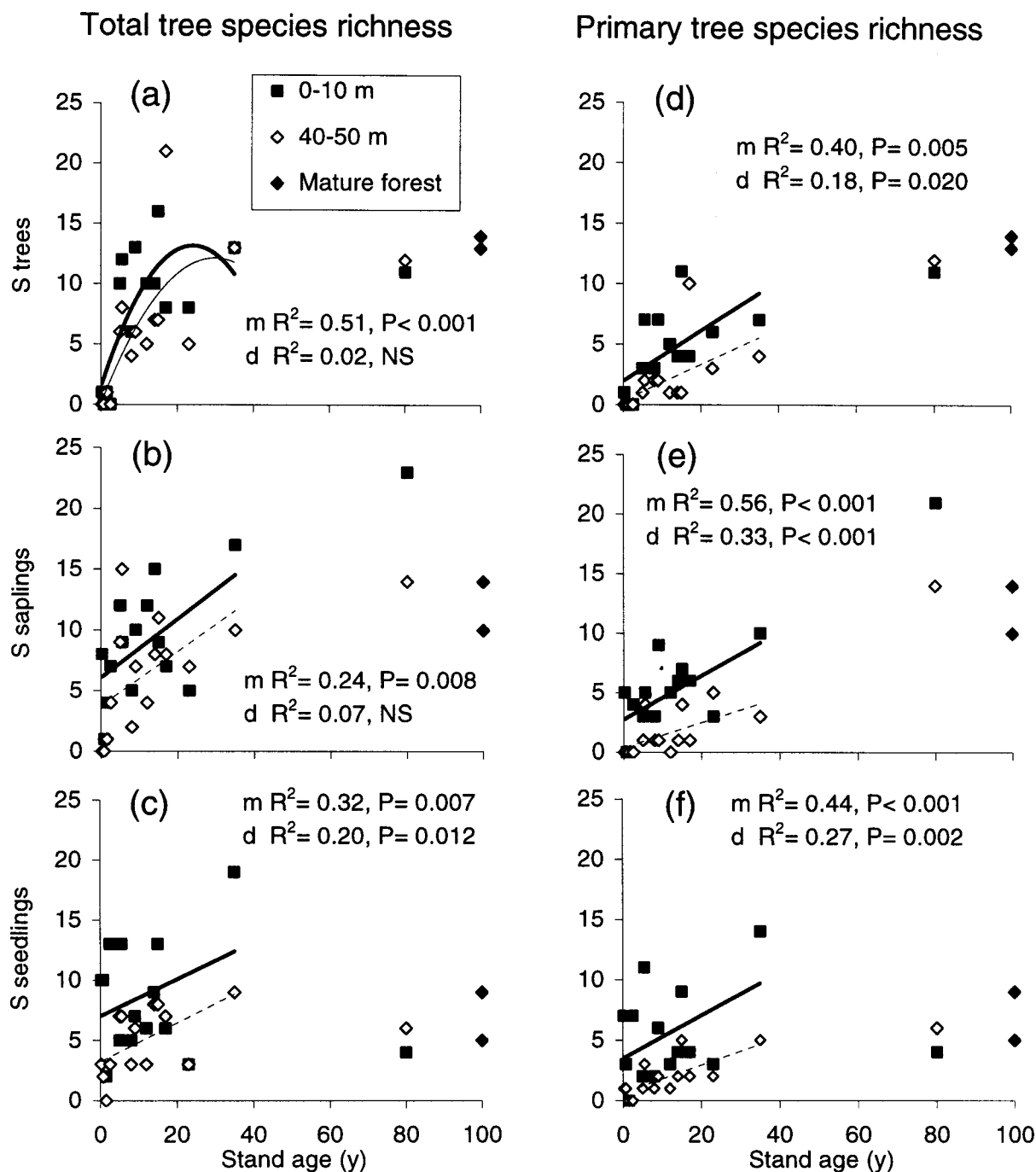
Figure 3. Distance to the forest border and age effects on tree species richness (S) along a chronosequence of abandoned pastures in central Veracruz, Mexico. Data from mature forest are shown for comparison (diamond). a, b and c are total tree species; d, e, f are primary tree species. Distances are 0–10 m (solid line) and 40–50 m (dashed line). The lines are derived from the minimal adequate model of ANCOVA; a quadratic term was used in the ANCOVA, when it is significant the relationship is represented by a unimodal curve, when it is non-significant the relationship is linear. S was determined in $400 \, \text{m}^2$ for trees, $64 \, \text{m}^2$ for saplings and $16 \, \text{m}^2$ for seedlings. NS = not significant ($P > 0.05$).

DISCUSSION

This study investigated the effects of time since abandonment and distance to the forest border on the regeneration of cloud forest in old fields. Most tree establishment has occurred right after pasture abandonment. However, an individual of *Carpinus* $\geq$ 5 cm dbh growing in the 0.25-y-old site indicates that some pre-abandonment tree regeneration had happened at the forest margin. Nevertheless, we believe that 1.5 y was

enough time for very fast-growing tree species (e.g. *Cnidoscolus multilobus*) to establish and reach ≥ 5 cm dbh. Overall, the longer a pasture had been abandoned, the greater the similarity of the vegetation structure and community composition to that of mature forest (Figure 1). However, the effects of distance to the forest border were primarily related to the dispersal syndrome and functional type of the species involved.

Age and distance effects on vegetation structure

In the study region, after 40–50 y of pasture abandonment, structural variables such as canopy height and tree basal area reach values that are characteristic of an 80-y-old cloud forest, and similar to those of the primary forest vegetation structure (Figure 1, Williams-Linera 2002). The relatively fast recuperation of basal area over a period of *c*. 50 y is in accordance with the rank of values observed in another successional chronosequence in a lowland tropical forest (Guariguata & Ostertag 2001). However, it is faster than in Costa Rican high-elevation montane forests (Kappelle *et al.* 1996).

Along the chronosequence, trees, shrubs and lianas have similar basal area, density and mean height values at the two distances from the forest border. This suggests that, at this level of analysis, there is no barrier to the arrival and establishment of propagules in abandoned pastures. Thus, in our old fields the regeneration of vegetation is not limited by the lack of seed dispersal or grass competition as has been widely reported for other tropical sites (Aide & Cavalier 1994, Cubiña & Aide 2001, Holl *et al.* 2000). Along an altitudinal gradient of abandoned Puerto Rican pastures with short grass species, there was no distance effect on forest recovery between 50 and 200 m from forest fragments (Aide *et al.* 1996). The authors argued that just a few long-distance dispersal events during the first 10–15 y may be sufficient to initiate forest recovery. In central Veracruz, short native grasses compose most pastures, but tall African grasses dominate a few pastures. In one of our sites (1.5 y old), the tall grass *Cynodon plectostachyus* prevented the establishment of woody plants, except very close to the forest border. This is in accord with the inhibition of woody plant establishment by non-native tall grasses reported for montane Costa Rican pastures (Holl *et al.* 2000).

Seed dispersal syndrome

The values for basal area, density and height of barochorous-synzoochorous tree species similar to those of the mature forest were reached at the end of the chronosequence (80 y old). Also, those values were higher close to the border than away from it. In contrast, fast regeneration both close to (0–10 m) and away from (40–50 m) the forest border was related to the arrival and establishment of anemochorous and endozoochorous tree species, which exhibited a peak of basal area, density and height between 23 and 35 y. Along the chronosequence, values for the structural variables of tree species with relatively large seeds (*Quercus* and *Carpinus*) increased whereas for species with small seeds (*Myrsine* and *Lippia*) values increased and then decreased.

An effect of distance was clearly observed in *Quercus* spp. and *Carpinus*. Differences between the two distances decreased with age for trees, but persisted for saplings and seedlings along the chronosequence. This indicates that even at intermediate and older successional stages, contiguous forest remnants serve an important role as sources of primary species propagules. More than 35 y were required for *Carpinus* to reach the basal area values of mature forest (1.2–4.8 m^2 ha^{-1}, MAMC & GWL unpubl. data) at more than 40 m from the forest border, whereas it took *c*. 10 y to reach those values at 0–10 m from the forest border. The arrival and establishment of *Carpinus* at a distance greater than 40 m is believed to be limited by its relatively large seed size as compared with other anemochorous species. The same pattern of a sharp decline in the abundance of woody species with distance from forest borders has been observed in a Costa Rican upper montane cloud forest (Oosterhoorn & Kappelle 2000), and in European and North American deciduous forests in which *Quercus* and *Carpinus* are important canopy components (Dzwonko 1993, Hardt & Forman 1989, Lawson *et al.* 1999, Myster & Pickett 1992).

In contrast to primary forest species, secondary species exhibit a peak at early and intermediate ages of the chronosequence. *Myrsine* and *Lippia* are characterized by high dispersal capability to open pastures and low tolerance of competition. They attained similar structural values for both distances from the border throughout the chronosequence.

Old fields derived from short native grasses displayed a considerable initial colonization by pioneer trees and shrubs with very small wind-dispersed seeds (e.g. *Vernonia patens*, *Ageratina ligustrina*, *Verbesina turbacensis*, *Roldana sartorii*, *Lippia myriocephala*). These results are in accordance with previous studies in Costa Rican montane forests where an over-representation of wind-dispersed species in early abandoned pastures has been observed (Holl 1999). Likewise, Aide *et al.* (1996) found that two of the three most common pioneer species colonizing the recently abandoned pastures of four subtropical moist and wet forest regions in Puerto Rico are wind-dispersed. These fast-growing pioneer species may in turn act as facilitators for bird-dispersed woody species such as *Myrsine coriacea*. Similarly, isolated trees and shrubs left in pastures may increase the deposition of seeds dispersed by animals (Duncan & Chapman 1999, Guevara &

Laborde 1993, Guevara *et al.* 1992, McClanahan & Wolfe 1993, Willson & Crome 1989). Some pastures in our study did have remnant *Acacia pennatula* and *Leucaena diversifolia* trees (*c.* 30 to 144 trees ha^{-1}). However, their presence appears not to have been sufficient to favour the establishment of primary tree species with large seeds such as *Quercus* and medium-sized seeds such as *Carpinus*.

Species richness

Richness of tree species similar to those of the mature forest was achieved by earlier successional stages (*c.* 15 y). There is a balance between the linear relationships for primary species (positive) and secondary species (negative) along the chronosequence. Closer to the forest border, the richness of primary species is higher. As the forest matures, primary species outcompete secondary species.

Similarly, shrub, vine and tree seedling richness reached values similar to those of the 80-y-old secondary forest very early (first 5 y). This finding suggests the fast establishment of secondary (close and away from the border) and primary species (close to the forest border), followed by a linear decrease in secondary species richness and a simultaneous increase in primary species richness. The fast recovery of species richness in smaller size classes has been reported for other tropical regions (Denslow & Guzmán 2000, Saldarriaga *et al.* 1988). In abandoned, moderately used pastures in Costa Rica, the species richness of seedlings and saplings reached mature forest values at 16–18 y, while the richness of trees > 10 cm dbh was much lower (Guariguata *et al.* 1997).

Conclusions and implications for cloud forest restoration

Our first hypothesis that forest structure can regenerate both at short and long distances from the forest remnant is supported by the following: the chronosequence of abandoned pastures showed a relatively fast rate of recovery of vegetation structure, after 40–50 y of abandonment, and this rate was similar both near to (0–10 m) and far from (40–50 m) the forest border. Our second hypothesis that the regeneration of the community composition would be different at different distances from the forest border is supported because structural characteristics such as basal area and density, and the species richness of primary species were higher near the forest border than away from it. Our results agree with previously described patterns of forest succession where secondary, pioneer species with high colonization (dispersal and establishment) capacities are progressively replaced in space and time by primary, shade-tolerant species with low colonization but high competition capacities.

The significant limitations on the establishment of primary species at distances greater than 40 m suggest the need for active restoration (sowing and/or planting these species) to accelerate the regeneration of mature cloud forest habitats. For distances less than *c.* 20 m we propose that passive restoration be allowed to occur naturally in order to reduce reforestation costs. Future studies will need to evaluate the dispersal and natural establishment capacities of the primary species along a more detailed sequence of distances to the forest border to ascertain thresholds and assist with decisions about active vs. passive restoration procedures. In any case, the conservation of mature forest remnants is a key strategy for ensuring the regeneration of forests habitats.

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Appendix. List of tree species ≥ 5 cm dbh found in the 15 abandoned pasture chronosequence in central Veracruz, Mexico. Species were classified by main seed dispersal mechanism: barochorous-synzoochorous (large seeds dispersed by gravity and/or animals), endozoochorous (small seeds dispersed by animals), and anemochorous (wind).

Primary species	Family	Secondary species	Family
Barochorous-synzoochorous		Barochorous-synzoochorous	
Cinnamomum effussum (Meisn.) Kosterm.	Lauraceae	*Annona cherimola* Miller	Annonaceae
Magnolia schiedeana Schldl.	Magnoliaceae	*Cnidoscolus multilobus* (Pax) I. M. Johnston	Euphorbiaceae
Microtropis schiedeana Loes.	Celastraceae		
Ocotea psychotrioides Kunth	Lauraceae		
Quercus acutifolia Nee	Fagaceae		
Quercus germana Cham. & Schldl.	Fagaceae		
Quercus leiophylla A. DC.	Fagaceae		
Quercus salicifolia Nee	Fagaceae		
Quercus xalapensis Humb. & Bonpl.	Fagaceae		
Endozoochorous		Endozoochorous	
Arachnothryx capitellata Planchon	Rubiaceae	*Callicarpa acuminata* Kunth	Verbenaceae
Brunellia mexicana Standley	Brunelliaceae	*Cestrum nocturnum* L.	Solanaceae
Dendropanax arboreus (L.) Decne & Planchon	Araliaceae	*Crataegus mexicana* Mociño & Sessé	Rosaceae
Eugenia xalapensis (Kunth) DC.	Myrtaceae	*Cyphomandra hartwegii* (Miers) Dunal	Solanaceae
Gymnanthes longipes Muell Arg.	Euphorbiaceae	*Myrica cerifera* L.	Myricaceae
Hedyosmum mexicanum Cordem	Chloranthaceae	*Rapanea myricoides* (Schldl.) Lundell	Myrsinaceae
Ilex tolucana Hemsley	Aquifoliaceae	*Rhamnus capraefolia* Schldl. var. *capraefolia*	Rhamnaceae
Meliosma alba (Schldl.) Walp	Sabiaceae	*Rhamnus c.* var. *grandifolia* M. Johnston & L. A. J.	Rhamnaceae
Oreopanax echinops (Schldl. & Cham.) Decne & Planchon	Araliaceae	*Solanum schlechtendalianum* Walp	Solanaceae
		Solanum umbellatum Miller	Solanaceae
Oreopanax xalapensis (Kunth) Decne. & Planchon	Araliaceae	*Trema micrantha* (L.) Blume	Ulmaceae
		Witheringia stramonifolia Kunth	Solanaceae
Saurauia leucocarpa Schldl.	Actinidiaceae	*Leucaena diversifolia* (Schldl.) Benth	Leguminosae
Solanum aphyodendron S. Knapp	Solanaceae	*Acacia pennatula* (Cham. & Schldl.) Benth.	Leguminosae
Ternstroemia sylvatica Cham. & Schldl.	Theaceae		
Trichilia havanensis Jacq.	Meliaceae		
Turpinia insignis (Kunth) Tul.	Staphyleaceae		
Zanthoxylum melanostictum Cham. & Schldl.	Rutaceae		
Styrax glabrescens Benth.	Styracaceae		
Anemochorous		Anemochorous	
Carpinus caroliniana Walter	Betulaceae	*Ageratina ligustrina* (DC.) R. King & H. Robinson	Asteraceae
Cedrela odorata L.	Meliaceae	*Heliocarpus donnell-smithii* Rose	Tiliaceae
Clethra mexicana DC.	Clethraceae	*Lippia myriocephala* Schldl. & Cham.	Verbenaceae
Liquidambar styraciflua L. var. *mexicana* Oersted	Hamamelidaceae	not identified	Asteraceae
		Vernonia patens Kunth	Asteraceae
Ostrya virginiana (Miller) K. Koch	Betulaceae		