



The Potential of Tree Rings for the Study of Forest Succession in Southern Mexico

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ABSTRACT

Studies of tropical secondary forest succession face strong limitations due to the slow pace of succession and the time-consuming task of monitoring processes. The occurrence of tree rings in secondary forest trees may help expand our knowledge on succession in these systems and may be useful for fallow dating in chronosequence studies. We examine here the potential of tree rings to study forest succession by sampling 70 species along chronosequences of dry and wet forests in southern Mexico. Based on wood anatomical features, we estimated that about 37 percent of the species presented distinct growth rings useful for ring studies. Overall, maximum number of rings matched well the interview-based fallow ages but, at some sites, trees had consistently higher numbers of rings, probably due to errors in fallow ages derived from interviews. Best fallow age estimations were obtained by examining rings in both pioneer and nonpioneer species. Reconstruction of species' establishment dates revealed that pioneer and nonpioneer species establish early during succession, and that species of both groups continue to recruit after many years. Our study clearly shows that tree ring analysis is a promising tool for studies on secondary forest succession in the tropics.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: chronosequences; dendrochronology; secondary forest succession; tree age; tropical dry forest; tropical wet forest; wood anatomy.

THE EXTENT OF TROPICAL SECONDARY FOREST is increasing rapidly (Wright 2005, Wright & Muller-Landau 2006) and, in many regions, secondary forest is now the main forest type (FAO 2006). Understanding the structure and dynamics of successional forests is of paramount importance, as they are important for global carbon cycles (Archard *et al.* 2002) and may have a large conservation value (Wright 2005). Tropical forest succession is usually a slow process that may take a century (*e.g.*, Saldarriaga *et al.* 1988, Worbes *et al.* 1992, Sheil 2001) or longer (Gemerden *et al.* 2003). Real-time monitoring from earliest to the latest succession stages is therefore hardly feasible. For this reason, chronosequences are frequently used (*e.g.*, Saldarriaga *et al.* 1988, Aide *et al.* 2000, Chazdon *et al.* 2007) as they make succession studies over long time intervals (*e.g.*, decades) possible, assuming a space-for-time substitution (Pickett 1989). This approach requires data on the abandonment ages of the selected secondary forest stands, which may be difficult to gather. Presently, fallow ages may be inferred from personal accounts of local landowners and/or by use of aerial photographs or remote sensing. Both methods have their limitations as information from local people cannot always be obtained and aerial photographs or remote sensing may only work where such material is available at frequent and short intervals (*cf.* Aide *et al.* 2000, Ruiz *et al.* 2005).

The occurrence of tree rings in secondary forest trees represents an alternative or complementary dating possibility as it may accurately reveal ages of forest stands (Henry & Swan 1974, Glitzenstein

et al. 1986, Abrams *et al.* 1995). Particularly, ages of pioneer species that are expected to establish immediately after abandonment may be good indicators of stand ages. Besides, tree rings can be used to explore successional patterns of species replacement, as the rings contain retrospective information on historical growth rates and give the exact recruitment dates (Henry & Swan 1974). In temperate regions, tree ring analysis has improved our understanding of forest succession without the time-consuming task of long-term monitoring succession (Henry & Swan 1974, Foster *et al.* 1996). Even the presence of annual rings in a few species may allow us to gain insight on population and community mechanisms leading toward succession. For example, we can examine whether species establish differentially along succession according to their life history attributes (*cf.* Clements 1916), or alternatively whether species from different functional groups colonize open spaces synchronously (*cf.* Initial Floristic Composition hypothesis, IFC; Egler 1954).

To date, relatively few studies in the tropics have used tree rings to determine stand age or study historical growth patterns (Worbes *et al.* 2003, Baker *et al.* 2005, Brienen & Zuidema 2006), and none have used tree rings in the context of secondary forests (but see Worbes *et al.* 1992 for applications in primary succession of flood plains). This is largely due to the widely held assumption among tropical ecologists that most tropical trees do not form annual rings (Lieberman *et al.* 1985, Chambers *et al.* 1998, Martínez-Ramos & Alvarez-Buylla 1998, Whitmore 1998). However, this assumption may not be further supported, as the body of evidence on the presence of rings in tropical species is growing rapidly (Worbes 2002 and references therein). Annual formation of tree rings in

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the tropics has now been demonstrated in all continents (Ogden 1981; Worbes *et al.* 2003; Schöngart *et al.* 2004, 2006; Baker *et al.* 2005; Brienen & Zuidema 2005; Heinrich & Banks 2005), for a wide variety of species, and under a wide range of rainfall regimes, namely from 370 mm (Maingi 2006) to 4000 mm of annual rainfall (Fichtler *et al.* 2003; for a complete overview see Worbes 2002). The most common trigger behind ring formation in the tropics is the occurrence of a dry season (Worbes 1995). Water limitation during the annual dry season causes reduced cambial growth or cambial dormancy (Borchert 1999), often combined with leaf abscission, and results in the formation of a distinct growth layer in the wood (Worbes 1995).

In this pilot study, we examine the potential of tree rings in studies of tropical secondary forest succession. We analyze discs and increment core samples of 70 tree species obtained from two chronosequences of secondary forests of varying ages (up to 60 yr) in a dry (Lebrija-Trejos *et al.* 2008) and a wet area (Breugel *et al.* 2007) in southern Mexico. Specific objectives were to: (1) examine the occurrence of tree rings in dry and wet tropical secondary forests and to identify promising species with annual ring formation; and (2) explore potential applications of tree rings in studies on secondary forest succession. To our knowledge, this is the first study to assess the potential of tree rings for studies of tropical secondary forest succession.

METHODS

STUDY AREA.—This study was conducted in two lowland tropical areas in southern Mexico; a wet area near the Guatemala border and a dry area on the Pacific watershed of the Isthmus of Tehuantepec. The wet site is located in the Marqués de Comillas region (Chiapas State), nearby the community Loma Bonita (16°04' N, 90°45' W). The region's mean annual temperature is 23°C and total annual rainfall is 2800 mm. Rainfall is not evenly distributed throughout the year and a dry season is distinguished from January to April with < 100 mm monthly. The original vegetation was lowland tropical rain and semideciduous forests (Ibarra-Manríquez & Martínez-Ramos 2002) and nowadays is a mosaic of agriculture, pastures, young secondary forests, and remnants of old-growth forests. Our research sites are secondary forests derived from abandoned cornfields (Breugel 2007).

The dry site is located in Oaxaca State, in the Isthmus of Tehuantepec, nearby the village of Nizanda (16°39' N, 95°00' W). Mean annual temperature is 26°C and total annual rainfall is 930 mm. Rainfall is very seasonal with 6 mo having < 20 mm each, and a short rainy period (May–Oct) accounting for 90 percent of the total annual precipitation. The prevailing natural vegetation is deciduous tropical forest (Pérez-García *et al.* 2001) and our research sites comprise secondary stands derived from abandoned agricultural cornfields (Lebrija-Trejos *et al.* 2008).

In the dry area, nearly all (95%) studied species are strictly deciduous and in the wet area 35 percent of the studied species are deciduous (see Table S1; E. Pérez-García, J. Meave & M. Martínez-Ramos, pers. obs.).

SAMPLE COLLECTION AND TREATMENT.—Between November 2006 and March 2007 we collected entire stem discs ($N = 350$) or increment cores ($N = 115$) of 70 species, 21 from the dry and 51 from the wet area. Discs were mostly collected from secondary forests that were recently (< 2 mo) cleared for crop cultivation, but in a few cases we felled individual trees. Increment cores were taken with 5- and 12-mm increment borers in one or two directions. Samples were taken as low as possible above ground level (80% < 75 cm), and always < 130 cm.

In the wet locality (Chiapas), we collected samples from nine different fallows 4- to 24-yr old. Stand ages were obtained through semistructured informal interviews with local landowners or relatives (Breugel *et al.* 2006). For every new species encountered in recently felled stands we collected one disc (objective 1), and for species that seemed promising for ring studies after first inspection, we collected various discs. In these cases, we tried to include the biggest tree of the stand, but also included smaller individuals to capture as far as possible existing size differences (objective 2).

In the dry locality (Oaxaca), we collected discs from a variety of species from recently felled forest stands of known and unknown ages (objective 1). For one common pioneer, *Mimosa acantholoba*, and a few others, we took discs ($N = 51$) and increment cores ($N = 42$) along a chronosequence of 14 fallows 4–60 yr old. Ages were obtained by repeated semistructured interviews (Lebrija-Trejos *et al.* 2008).

All samples were air- or oven-dried and grained mechanically with sandpaper of a progressively finer grain (up to grid 600), until wood structure was clearly visible.

GROWTH ZONES AND POTENTIAL FOR RING STUDIES.—Wood anatomy and ring structure was studied by naked eye and by using a stereomicroscope (up to 40×). We classified growth boundaries according to Worbes (1995) into four different types: (1) density variations (DV); (2) terminal parenchyma bands (TP); (3) a repeated pattern of alternating fiber and parenchyma bands (AP); and (4) variation in vessel distribution and/or vessel size (VD, VS, VSD). Growth boundaries were often a combination of different types. Having at least one disc for each species allowed us to evaluate carefully the distinctiveness of growth zones over the entire stem surface and to detect irregularities across the stem, such as intra-annual density fluctuations (ID), poorly defined or vague rings (VR) and wedging rings (WR). All relevant features and ring anomalies were recorded, following terminology of the Multilingual Glossary of Dendrochronology (Kaennel & Schweingruber 1995).

For each species, we assessed the potential for ring studies and accurate age determinations. These assessments were carefully based on the following criteria according to whether: (1) growth zones were unambiguously distinguishable and present in all examined samples by naked eye or stereomicroscope; (2) rings were circuit uniform; and (3) ring irregularities did not prevent reliable age determinations using complete discs.

For *M. acantholoba*, we had enough samples to perform cross-datings among several individuals as a means to confirm the annual nature of the growth rings. Crossdating is a procedure that matches

variations in ring width patterns among trees (Fritts 1976). Good matching of wide and narrow growth bands between trees and correlations of these patterns to external controlling factors such as rainfall provides strong evidence on the rings' annual nature (Stahle 1999). We measured ring widths to the nearest 0.001 mm using a computer-compatible tree ring measuring system (Velmex Inc. Bloomfield, NY, U.S.A.) and a 40× stereomicroscope. We calculated inter-tree correlation as the mean Pearson correlation coefficient for all pairwise combinations of trees using unstandardized ring widths (*i.e.*, raw data). Mean ring widths were correlated to annual rainfall for the period 1980–2003. Rainfall data were obtained from the Servicio Meteorológico Nacional (SMN) of the Comisión Nacional del Agua (CONAGUA, Mexico) for the nearest weather station of Ciudad Ixtepec, 14 km from the study site. Unfortunately, we could not perform the same analysis for other species due to low sample size and short length of the time series.

RING COUNTS, FALLOW AGE, AND SPECIES ESTABLISHMENT PATTERNS.—For species with clear growth rings that met our criteria for accurate age determinations (see above), we compared ring counts and fallow ages. Sample sizes of trees and number of stands for which we could make such comparison varied per species. For some common species like *Schizolobium parabyba*, *Zanthoxylum caribaeum*, *Zanthoxylum kellermanii*, and *Cordia alliodora* in the wet locality, and *M. acantholoba* in the dry locality, we were able to compare rings and fallow ages for several samples from different stands, whereas for many species we had only one single sample.

When rings were lacking in the tree center (*i.e.*, hollow trees or missed pith in cores), we estimated the pith distance and the average number of rings of other samples of that species to estimate the missing number of rings.

If there were strong reasons to question fallow age estimates of the local landowners, *e.g.*, if multiple tree samples were giving the same amount of rings exceeding that of fallow ages, we revisited the landowners and double checked the abandonment year (without disclosing the ring-ages to landowners). If these second age estimates matched ring counts, we concluded that the landowners' initial age estimations were probably inaccurate.

For a small set of species from the wet locality, we assessed the extent to which tree rings could reveal historical establishment patterns. To this end, we estimated time between site abandonment and tree establishment in the fallow by subtracting the number of rings from the best estimate of fallow age, *i.e.*, corrected for suspected dating errors (see Table 1). We classified species into pioneers (short-lived, fast-growing species only establishing in open spaces) and nonpioneers (including relatively fast-growing, intermediate species and late successional species; Swaine & Whitmore 1988), using data and observations from long-term studies in the same region (M. Martínez-Ramos, unpubl. data). We tested for differences in median time of establishment after abandonment using the nonparametric Kruskal–Wallis tests and Dunn's tests for group and species' contrasts.

TABLE 1. Number of rings encountered in trees in secondary forest study sites in a wet locality (Chajul, Chiapas) and a dry locality (Nizanda, Oaxaca) in southern Mexico.

Fallow age from interview	Max # rings		Best estimate of fallow age (year)	Observations
	Pioneers	Others		
<i>Wet locality (Chiapas)</i>				
4	–	6	6	Fallow probably 2 yr older
7	8	–	8	Fallow probably 1 yr older
8	9	8	8	
11	10	11	11	
10	7	10	10	
15	10	14	15	
17	19	23	19	Fallow probably 2 yr older; LC & PR probably survived last clearing/burning, LC with fire mark at 3rd ring (<i>i.e.</i> , 19 yr ago)
21	21	–	21	
24	22	19	24	
<i>Dry locality (Oaxaca)</i>				
4	4	–	4	
6	4	–	6	
8	9	7	9	Fallow probably 1 yr older
10	10	–	10	
13	12	–	13	
17	11	–	17	
21	21	–	21	
25	18	–	18	Unreliable fallow age, as site is communal property.
27	12	–	13	Second interview revealed age 13 yr
30	20	25	30	
35	22	32	32	
39	40	39	–	
43	20	–	–	
≈53	–	57	57	Fallow age probably <i>ca.</i> 57
64	34	30	–	

LC = *Lonchocarpus cruentus*; PR = *Pterocarpus rohrii*.

RESULTS

DISTINCTIVENESS AND STRUCTURE OF GROWTH ZONES.—All four types of growth zones (*cf.* Worbes 1995) were encountered and species often showed a combination of several types (Table S1). Density variations (DV), caused by variation in fiber wall thickness or size (Worbes 1995), were the most commonly observed growth

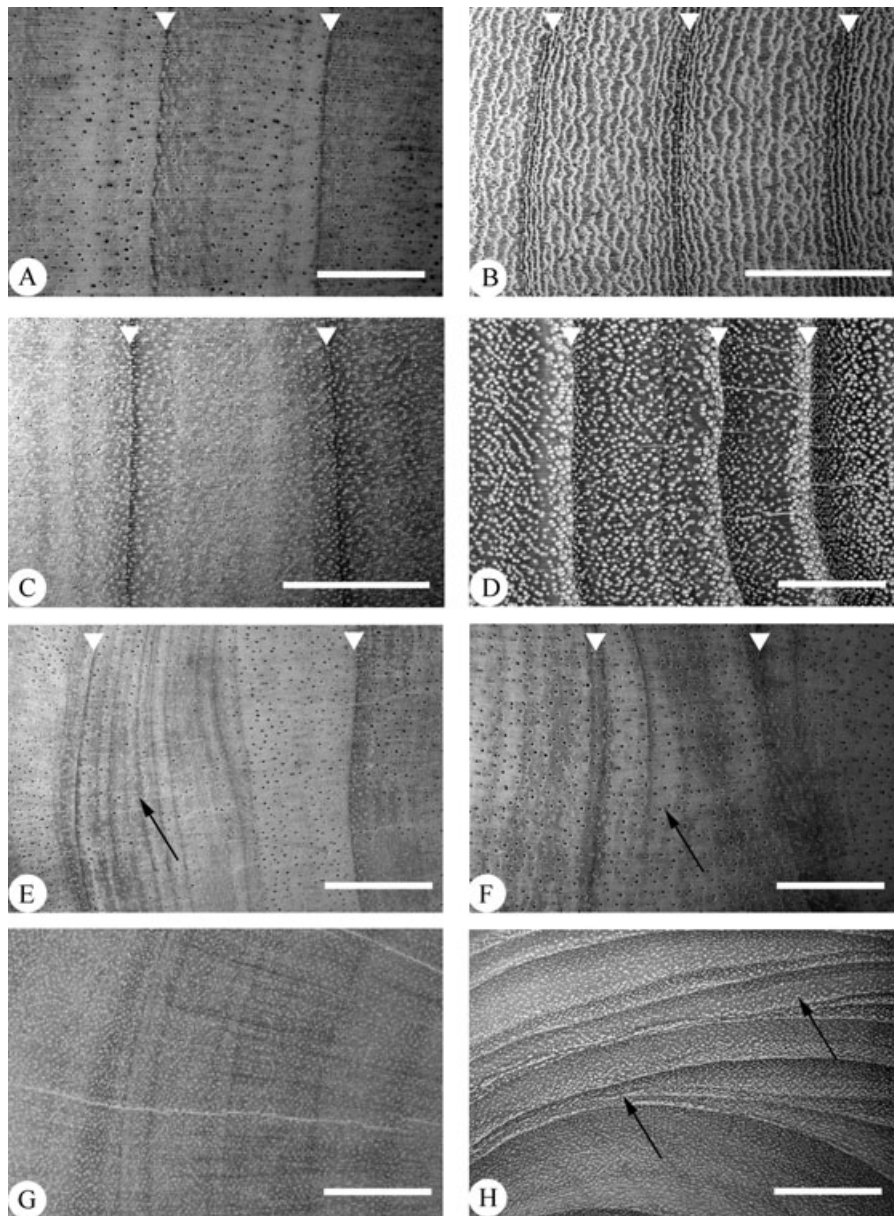


FIGURE 1. General anatomical aspects of growth zones in some of the studied tropical tree species. (A) *Schizolobium parahyba* density variation, (B) *Zanthoxylum kellermanii* alternating parenchyma bands and terminal parenchyma bands, (C) *Zanthoxylum caribaeum* density variation, (D) *Mimosa acantholoba* variation in vessel density and size, (E) *Alchornea latifolia*, multiple intra-annual density fluctuations, (F) *Cecropia peltata*, discontinuous, intra-annual rings, (G) Vague, indistinct growth boundaries in *Bursera simaruba*, (H) *Cordia alliodora*, wedging rings. Scale bars = 1 cm, excepting D and G where bars = 0.5 cm. Growth direction is from right to left (A–F) and from bottom to top (H).

boundary (66% of species). These growth boundaries were best detected by the naked eye and consisted of darker colored wood toward the end of the ring often forming a sharp edge with the lighter wood of each new ring (Figs. 1A, C). About 27 percent of the species showed alternating parenchyma bands (AP; Fig. 1B), which are marked by differences in spacing of parenchyma bands between the beginning and end of a ring. Depending on spacing between growth zones, these structures were also best detected by the naked eye. Terminal parenchyma bands (TP) often concurred

with alternating parenchyma bands (Fig. 1B), and were found in 29 percent of the species. Differences in vessel density and/or vessel size (VD/VS) were found in 23 percent of the species, but in only one species were these features alone clear enough to distinguish (annual) growth zones (*i.e.*, *M. acantholoba*; Fig. 1D).

The degree of growth zone's distinctiveness varied from complete absence of growth zones to poorly distinguishable zones in some species (Fig. 1G), and clear rings in others (*cf.* Figs. 1A–D, H). A considerable portion of species (57%) showed clear to very

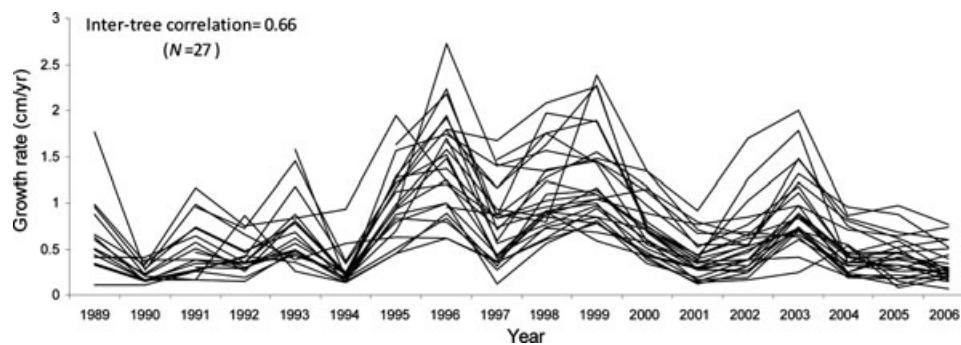


FIGURE 2. Interannual ringwidth patterns for 27 *Mimosa acantholoba* trees from Oaxaca for the period 1989–2006. Mean inter-tree correlation is calculated as the mean Pearson correlation coefficient for all pairwise combinations of the 27 trees.

clear growth zones (Table S1), but several of these species presented irregularities that restrict using its rings for accurate age-estimations. Observed irregularities include intra-annual density fluctuations (ID), varying ring distinctiveness between and/or within samples, and wedging rings (WR) (*cf.* terminology in Kaennel & Schweingruber 1995). Intra-annual density fluctuations are growth zones that can be distinguished morphologically from true annual rings by their discontinuous character (*i.e.*, circuit nonuniform growth zones; Fig. 1F) or by a less defined, diffuse structure (Fig. 1E). They often occurred in wider growth zones and were the most common problem encountered. Another common problem was that growth zones might have varying distinctiveness. This occurred within a single sample with, for example, clear rings in the outer part of stems, but vague rings (VR) in the center, or, in asymmetric stems, among different growth directions of the stem (*i.e.*, circuit nonuniform rings that become vague or disappear completely in one or more directions). Varying distinctiveness between samples occurred in various species, and it was found that rings were well defined in some samples, but absent in others. Wedging rings (Fig. 1H; synonyms 'discontinuous, partial or incomplete rings'; Kaennel & Schweingruber 1995) constituted another kind of irregularity. These rings gradually join others and become completely absent in one or more directions, due to cambial failure. By examining entire stem surfaces, wedging rings could be detected very well and be accounted for in age determinations.

POTENTIAL SPECIES FOR RING ANALYSIS.—Based on the distinctiveness of growth zones, their circuit uniformity, and the occurrence of irregularities, we estimated that 26 of the 70 studied species (37%) had good potential for use in tree ring studies (Table S1). As expected, this fraction was higher in the dry locality than in the wet area (48% vs. 33%). Promising pioneer species in the wet locality that showed good potential for ring studies are *S. parahyba* (Fig. 1B), *Z. kellermani* (Fig. 1B), *Z. caribaeum* (Fig. 1C), and two *Miconia* species. Some common, nonpioneer species with clear rings are *C. alliodora* (Fig. 1H), *Lonchocarpus cruentus*, *Pterocarpus robrii*, and *Ficus maxima* (see Table S1 for full list). Several pioneers that are dominant across the secondary forests of the Chiapas region (Breugel 2007) such as *Cecropia peltata*, *Trema micrantha*, and

Trichospermum mexicanum, proved not useful for ring analyses due to various problems. *Ochroma pyramidale* did show some potential, as we observed distinct growth boundaries in some samples, but not in all of them.

Common and promising species in the dry locality are *M. acantholoba* (Fig. 1D). *Lonchocarpus emarginatus*, *Lonchocarpus torresiorum*, *Acacia cochliacantha*, *Ceiba parvifolia*, and *Euphorbia schlechtendalii* (full list in Table S1).

Crossdating of ring width between trees of *M. acantholoba* revealed a highly similar pattern of small and wide rings between different years (Fig. 2) and a high inter-tree correlation of 0.66. Average ring width of these 27 trees correlated strongly to total annual rainfall (Pearson $r = 0.83$, $P < 0.001$) for the period 1980–2003.

FALLOW AGES VERSUS RING COUNTS.—The maximum number of rings found per site in the wet locality matched fallow ages closely (Table 1; Figs. 3A, B). At most sites at least one individual had numbers of rings close to the fallow age, although at each site there were species and trees showing lower numbers of rings than the corresponding age. The relation between the maximum number of rings and fallow age was stronger for pioneers than for nonpioneer species (*cf.* Figs. 3A, B). At one site only, the absolute maximum number of rings differed more than two years from fallow age (Chiapas-17; Table 1); in this stand, two pioneer species showed two rings more than the supposed age, while two nonpioneer species (*L. cruentus* and *P. robrii*, Table 1) had five and six rings more. One of these nonpioneer trees had a fire mark in the third ring (19 yr ago) and these are probably remnant trees that survived previous clearing and burning. For three other sites (Chiapas-4, 7, 8), we found one to two rings more than the fallow ages. Two of these fallows (4, 7) were probably older as multiple samples showed exactly the same (higher) number of rings.

In the dry locality, the (maximum) number of rings matched less well with fallow ages, and especially in some of the older fallows, we observed much lower numbers of rings in *M. acantholoba* than expected for such a pioneer species (Table 1; Fig. 3C). The largest difference between fallow age and rings were observed in the oldest stand (60 yr) in which we only counted 34 rings for the largest,

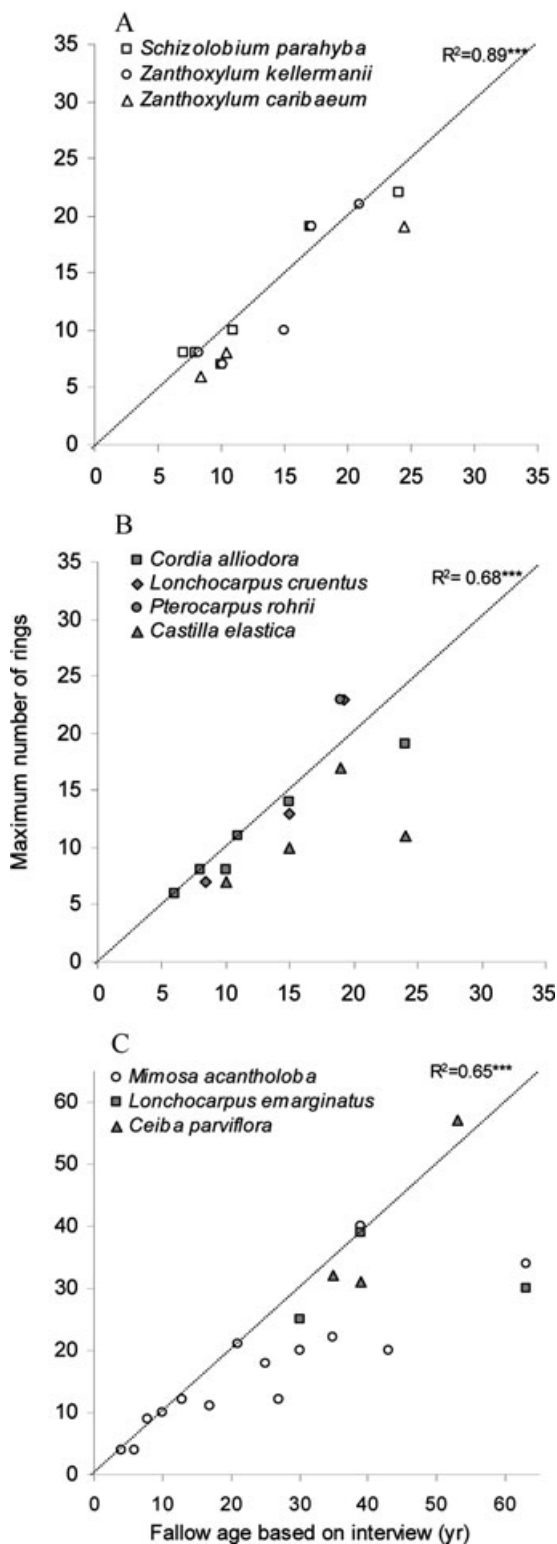


FIGURE 3. Relationship between fallow ages based on interviews and the maximum number of rings in different species for the studied wet (A = pioneer species, B = nonpioneer species) and dry site (C). Open symbols are pioneer species (*sensu* Swaine & Whitmore 1988) and filled symbols nonpioneer species. The broken lines indicate $Y = X$, where ages match exactly.

living *Mimosa*. At three sites we found an exact match between fallow age and number of rings, at two other sites we observed a higher number of rings (1 and 4 yr difference), but more often (eight times) the number of rings was lower. For two intermediate-aged fallows (estimated to have 27 and 25 yr) where we found consistently less rings, we have strong evidence that the initial interview-based ages were wrong. In one of these sites (27 yr) ownership changed since field abandonment and the former landowner (who cleared the site for cultivation) confirmed that the ages initially provided by the current landowner were wrong. The new age indications of 13 yr of the former landowner corresponded closely to the numbers of rings found (12 rings). At another site (25 yr) that was not privately but communally owned, fallow age proved inaccurate as different people provided different age estimations.

By careful evaluation of the differences between rings and fallow ages, and considering the reliability of the interviews with the landowners, we suspected that six of the 24 investigated fallows had initial dating errors, of which two were relatively large errors (7 and 14 yr difference; details in Table 1).

ESTABLISHMENT OF SPECIES AFTER ABANDONMENT.—By using tree rings, we could determine for several species of the wet locality, the time elapsed between field abandonment and tree establishment (Fig. 4). This showed that at least one tree of each species appeared in one of the sites immediately after abandonment, except for *Zanthoxylum caribaeum*, which first appeared two years after abandonment. We did not find significant differences in median times of establishment between pioneer and nonpioneer species ($P = 0.48$). Among species, we found only significant differences between *S. parahyba* and *Z. caribaeum* ($P < 0.05$).

DISCUSSION

RING FORMATION IN TROPICAL SECONDARY FORESTS.—We identified a substantial number of species (26) with clear and circuit uniform growth boundaries that may be used for tree ring analysis. For *M. acantholoba* we could confirm the true annual nature of rings (Stahle 1999) by crossdating interannual ring width patterns and relating these to an external controlling factor, rainfall. Unfortunately, we could not perform such crossdatings for other species, but we think that rings in all potential species are annual. In the dry locality, there is little doubt concerning the annual nature of rings given the prolonged dry season of 6 mo and the strict deciduous phenology of nearly all ring-forming species. Leaf abscission usually induces cambial dormancy, which is resumed soon after leaf flushing (Borchert 1999). It is this cambial rhythm what determines the formation of an anatomically distinct growth layer in the tree's xylem (Borchert 1999, Worbes 2002). Also for those species in the wet locality that exhibit a strictly deciduous leaf habit once a year, such as *S. parahyba* and *Z. kellermani*, the rings' annual nature is beyond reasonable doubt. Yet, short dry spells during the rainy season may induce intra-annual, false rings (Priya & Bhat 1998, Borchert *et al.* 2002). In the wet locality, we did observe false, intra-annual bands in various species, but when such bands were frequent and difficult

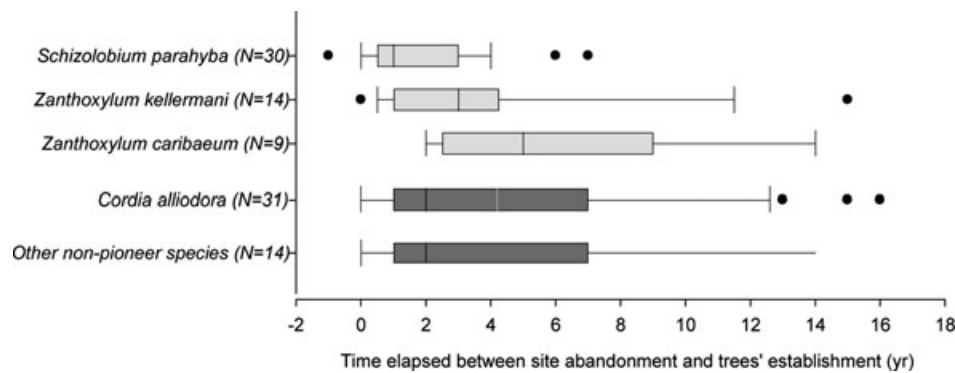


FIGURE 4. Time elapsed between field abandonment and species' establishment, calculated as the difference between fallow age and number of rings of each tree. Bars indicate 90%, 75%, median, 25% and 10% percentiles, separate points are outliers. Light gray bars are pioneer species (*sensu* Swaine & Whitmore 1988) and dark gray bars are nonpioneer species. The group of 'Other non-pioneer species' include *Lonchocarpus cruentus* (3), *Pterocarpus robrii* (6), *Dalbergia brownei* (1), *Dialium guianense* (1), *Rollinia jimenezii* (1), and *Casearia sylvestris* (2). Note that the two trees of *L. cruentus* and *P. robrii* which exceeded fallow age (*cf.* Table 1, site 17) were omitted from this analysis.

to distinguish from truly annual bands, species were disregarded for analysis. For the 26 species identified as promising for ring analysis, we are confident that we discriminated successfully between false and truly annual rings. In the wet locality, this assertion is further supported by the good match between ages of *C. alliodora*, a species with proven annual ring formation (Devall *et al.* 1995) that establishes early in succession (Breugel 2007; Fig. 4B), and the number of rings of other species in the same stands.

The use of entire discs may hold the key to success in studies on tropical tree rings as it facilitates the visual detection of ring boundaries, allows discrimination between true and (intra-annual) false rings, and to account for wedging rings (Worbes 2002, Brienen & Zuidema 2005). Ideally, one should use increment cores as this method is considerably less destructive and may also be applied in existing plots, but only few species included in this study (*e.g.*, *S. parahyba*, *L. cruentus*, and *M. acantholoba*) presented growth zones that were clear enough to distinguish annual rings unambiguously on cores.

The observed proportions of species with tree rings (37%) in our secondary plots match those observed in the Yucatan Peninsula, Mexico (Roig *et al.* 2005; 40%), and the Amazon basin in Brazil (Alves & Angyalossy-Alfonse 2000, Roig 2000, Worbes 2002; 25–50%). Hence, more species than often thought are useful for ring analysis, including some well-known pioneers such as *S. parahyba* and *Z. kellermani*. Unfortunately, *Cecropia*, the most typical Neotropical pioneer taxon, presented too many problems to be easily used in ring studies, even though annual rings in *Cecropia* have been observed in more seasonal climates in the Bolivian Amazon (R.J.W. Brienen, pers. obs.), and in floodplain forests (*várzea*) in Brazil (Worbes 2002). More advanced techniques such as image analysis (Worbes 2004), X-ray densitometry (Polge 1978), synchrotron X-ray fluorescence (Poussart *et al.* 2006), and high resolution isotope analysis (Evans & Schrag 2004, Poussart *et al.* 2004, Verheyden *et al.* 2004) may be promising to distinguish annual ring boundaries in species with poorly defined and ambiguous rings.

Although these techniques are laborious and expensive for use in large-scale ecological studies, their applications may yield clues as to how to discriminate between annual and intra-annual, anomalous growth zones using simple wood anatomical features.

DATING FALLOW AGES USING TREE RINGS.—The potential of tree rings as a reliable proxy for fallow ages varied among species and sites. No single species revealed fallow ages precisely, but by examining simultaneously pioneer and nonpioneer species, we could often precisely determine fallow ages. This was true at least for stands in the wet locality, where succession starts with a multitude of pioneer and nonpioneer species (Breugel 2007). However, in the dry locality older fallows (> 20 yr), tree rings were often not a good indication of fallow ages and even the oldest *Mimosa* trees were much younger than fallow ages. This was surprising as this species establishes nearly immediately at the beginning of succession (Lebrija-Trejos *et al.* 2008), and as maximum tree ages in the younger sites (< 20 yr) did match well with fallow ages. The unexpected discrepancy may be attributed to the early death of older trees that established since the beginning of succession, which would imply that the sampled *Mimosa* trees are relatively recent newcomers. This concurs with observations that many *Mimosa* trees showed clear signs of senescence after 20 yr and that this species may establish successfully several years after the onset of succession (E.E. Lebrija-Trejos, pers. comm.). An important implication of these findings is that tree rings' potential to accurately determine fallow ages depends on the species' longevity and on successional mechanisms. In the wet area, where long-lived pioneers are common from the moment of field abandonment, tree rings may be used successfully to date fallows. In the dry area, however, the long-lived pioneer phase is lacking, and succession proceeds through replacements of species' groups so that early stages are dominated by short-lived pioneers and establishment of longer-lived species occurs only at later stages (Ewel 1980, Lebrija-Trejos *et al.* 2008). In the absence of long-lived pioneers in dry forests, focusing on resprouts of long-lived nonpioneer

species may be a good alternative in determining fallow ages, as resprouting is a very common regeneration method in dry forests and resprouts develop mostly soon after abandonment (Swaine & Hall 1983, Kennard *et al.* 2002, Vieira & Scariot 2006). Ages of resprouts of *L. emarginatus* and *C. parvifolia* included in this study closely matched older fallows' ages (39 and 57 yr; Table 1).

The occurrence of annual rings allowed us to verify interview-based estimates of fallow ages, something not done before. Overall, interview-based age estimations were accurate or contained only smaller errors of 1–2 yr. In two cases, however, the ages indicated in the first interviews had errors of 7 and 14 yr. These large errors had specific (social) causes: in one case sites' ownership changed after its abandonment, whereas in the other the area was not privately but communally owned and people were unable to assert the exact age. In such specific cases tree rings may be especially useful as they allow the detecting and correcting of dating errors.

This study shows that tree rings are in general a good tool to independently verify fallow ages and that this may be best achieved by using multiple species instead of seeking an ideal species. Nonetheless, our results also show that relying on tree rings as the sole source of fallow age information can be unsafe in the absence of some knowledge of site-specific successional mechanisms and on individual species' longevities. Successional mechanisms may differ largely between areas (Lebrija-Trejos *et al.* 2008) and longevity varies widely among species (Lieberman *et al.* 1985, Finegan 1996, Martínez-Ramos & Alvarez-Buylla 1998, Brienen & Zuidema 2006), affecting the potential and accuracy of rings to determine fallow ages. Therefore, relying uniquely on tree rings may lead to dating errors as much as relying blindly on interviews. The combined application of both methods results in a more accurate dating of secondary forest stands, and we suggest that this approach should be used whenever possible.

USING TREE RINGS TO STUDY SECONDARY FOREST SUCCESSION.—How can tree rings further understanding of secondary forest succession in the tropics? Tree rings have successfully been used in temperate forests to reconstruct stand histories (Henry & Swan 1974, Glitzenstein *et al.* 1986, Abrams *et al.* 1995), but species diversity in these systems is typically much lower and nearly all species present annual rings (Cook & Kairiukstis 1990). In our study, reconstruction of species' establishment patterns was limited to the wet locality, to the few species that had annual rings and to few individuals. This was partly due to the sampling method (*i.e.*, we did not know beforehand which species would have reliable rings), and partly to low species' abundances in these diverse systems (Breugel 2007).

Notwithstanding, our reconstruction of establishment dates for the few species that were included revealed some interesting patterns. First, all species but one recruited very early during succession. They were present immediately after abandonment with at least one individual in one site and this did not vary between regeneration groups. Even nonpioneer species recruited at the beginning of succession, in some stands even before the pioneers included in our comparison. Second, pioneers' recruitment appeared not to be limited to the first successional years, but may continue during many

years (15–16) after succession has started. These results, crucial for the evaluation of successional theories on the invasion, recruitment, and replacement of species (Egler 1954, Finegan 1996), match those obtained by permanent plot studies in the study area (Breugel *et al.* 2007).

Our pilot study provides an idea of the potential of tree rings to accurately reconstruct historical colonization patterns. We may gather retrospective insight on historical establishment dates of specific species, without the need to perform long-term monitoring of species' recruitment patterns. Such information can obviously not be gathered from static observations of plots along different points of chronosequences, as such static data do not necessarily reflect real time processes (Bakker *et al.* 1996, Chazdon *et al.* 2007, Johnson & Miyanishi 2008). Tree rings, however, only provide information on surviving trees and, in older stands, we risk missing the first successional phases, typically dominated by short-lived pioneers that do not live longer than 10–30 yr (Finegan 1996, Martínez-Ramos & Alvarez-Buylla 1998). In our study, we clearly missed the earliest establishment data of the short-lived pioneer species in the dry area's oldest fallows.

We envision other promising applications of tree rings. For example, it is possible to assess the influence of soil variables and land-use history (*e.g.*, Ruffner & Abrams 1998) on the long-term growth of tree species, and to estimate rates of tree biomass gains (*e.g.*, Bascietto *et al.* 2004) in tropical secondary forests. Also, tree rings may be used to estimate the influence of climate on secondary succession. Our crossdating of *Mimosa* trees showed that tree responses to annual variation in climate may be highly similar among trees and that variation in climate may be very important to tree growth, even significantly influencing successional stands. Finally, the occurrence of annual rings in common Neotropical pioneer species, such as *S. parahyba*, may be used to determine ages of natural gaps in primary forests and estimate gap rate formation. Thus, tree rings cannot replace real-time observations of permanent monitoring (Bakker *et al.* 1996, Finegan 1996, Breugel *et al.* 2007, Johnson & Miyanishi 2008), but they will certainly prove a valuable addition to existing techniques of studies on tropical forest succession and should be included in the portfolio of methods applied in these systems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. *Species with their types and distinctiveness of growth zones, encountered problems, and potential for tree ring studies.*

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LITERATURE CITED

- ABRAMS, M. D., D. A. ORWIG, AND T. E. DEMEO. 1995. Dendroecological analysis of successional dynamics for a presettlement-origin white pine-mixed oak forest in the southern Appalachians, USA. *J. Ecol.* 83: 123–133.
- ACHARD, F., H. D. EVA, H. J. STIBIG, P. MAYAUX, J. GALLEGO, T. RICHARDS, AND J. P. MALINGREAU. 2002. Determination of deforestation rates of the world's humid tropical forests. *Science* 297: 999–1002.
- AIDE, T. M., J. K. ZIMMERMAN, J. B. PASCARELLA, L. RIVERA, AND M. H. VEGA. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: Implications for restoration ecology. *Rest. Ecol.* 8: 328–338.
- ALVES, E. S., AND V. ANGYALOSSY-ALFONSO. 2000. Ecological trends in the wood anatomy of some Brazilian species. 1. Growth rings and vessels. *IAWA J.* 21: 3–30.
- BAKER, P. J., S. BUNYAVEJCHEWIN, C. D. OLIVER, AND P. S. ASHTON. 2005. Disturbance history and historical stand dynamics of a seasonal tropical forest in western Thailand. *Ecol. Monogr.* 75: 317–343.
- BAKKER, J. P., H. OLFF, J. H. WILLEMS, AND M. ZOBEL. 1996. Why do we need permanent plots in the study of long-term vegetation dynamics? *J. Veg. Sci.* 7: 147–156.
- BASCIETTO, M., P. CHERUBINI, AND G. SCARASCIA-MUGNOZZA. 2004. Tree rings from a European beech forest chronosequence are useful for detecting growth trends and carbon sequestration. *Can. J. For. Res.* 34: 481–492.
- BORCHERT, R. 1999. Climatic periodicity, phenology, and cambium activity in tropical dry forest trees. *IAWA J.* 20: 239–247.
- BORCHERT, R., G. RIVERA, AND W. HAGNAUER. 2002. Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. *Biotropica* 34: 27–39.
- BREUGEL, M. VAN. 2007. Dynamics of secondary forests. PhD Dissertation, Wageningen University, Wageningen, The Netherlands.
- BREUGEL, M. VAN, M. MARTÍNEZ RAMOS, AND F. BONGERS. 2006. Community dynamics during early secondary succession in Mexican tropical rain forests. *J. Trop. Ecol.* 22: 663–674.
- BREUGEL, M. VAN, M. MARTÍNEZ RAMOS, AND F. BONGERS. 2007. Species dynamics during early secondary forest succession: Recruitment, mortality and species turnover. *Biotropica* 35: 610–619.
- BRIENEN, R. J. W., AND P. A. ZUIDEMA. 2005. Relating tree growth to rainfall in Bolivian rain forest: a test for six species using tree ring analysis. *Oecologia* 146: 1–12.
- BRIENEN, R. J. W., AND P. A. ZUIDEMA. 2006. Lifetime growth patterns and ages of trees in a tropical forest in Bolivia based on tree ring analysis. *J. Ecol.* 94: 481–493.
- CHAMBERS, J. Q., N. HIGUCHI, AND J. P. SCHIMEL. 1998. Ancient trees in Amazonia. *Nature* 39: 135–136.
- CHAZDON, R. L., S. G. LETCHER, M. VAN BREUGEL, M. MARTÍNEZ-RAMOS, F. BONGERS, AND B. FINEGAN. 2007. Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philos. Trans. R. Soc. Lond. B.* 362: 273–289.
- CLEMENTS, F. E. 1916. Plant succession: An analysis of the development of the vegetation. Cargenie Institute. Publication no 242, Washington, DC.
- COOK, E. R., AND L. A. KAIRIUKSTIS (Eds.). 1990. Methods of dendrochronology. Kluwer Academic, Dordrecht, The Netherlands.
- DEVALL, M. S., B. R. PARRÉSOL, AND S. J. WRIGHT. 1995. Dendroecological analysis of *Cordia alliodora*, *Pseudobombax septenatum* and *Annona spraguei* in central Panama. *IAWA J.* 16: 411–424.
- EGLER, F. E. 1954. Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. *Vegetatio* 4: 412–417.
- EVANS, M. N., AND D. P. SCHRAG. 2004. A stable isotope-based approach to tropical dendroclimatology. *Geochim. Cosmochim. Acta* 68: 3295–3305.
- EWEL, J. 1980. Tropical succession: manifold routes to maturity. *Biotropica* 12: 2–7.
- FAO. 2006. Global Forest Resources Assessment 2005: Progress towards sustainable forest management, Rep. No. 147. United Nations Food and Agricultural Organization, Rome, Italy.
- FICHTLER, E., D. A. CLARK, AND M. WORBES. 2003. Age and long-term growth of trees in an old-growth tropical rain forest, based on analyses of tree rings and ¹⁴C. *Biotropica* 35: 306–317.
- FINEGAN, B. 1996. Pattern and process in Neotropical secondary rain forests: the first 100 years of succession. *Trends Ecol. Evol.* 11: 119–124.
- FOSTER, D. R., D. A. ORWIG, AND J. S. MCLACHLAN. 1996. Ecological and conservation insights from reconstructive studies of temperate old-growth forests. *Trends Ecol. Evol.* 11: 419–424.
- FRITTS, H. C. 1976. Tree rings and climate. The Blackburn Press, New Jersey.
- GEMERDEN, B. S. VAN, H. OLFF, M. P. E. PARRÉN, AND F. BONGERS. 2003. The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity. *J. Biogeogr.* 30: 1381–1390.
- GLITZENSTEIN, J. S., P. A. HARCOTBE, AND D. R. STRENG. 1986. Disturbance, succession, and maintenance of species diversity in an east Texas forest. *Ecol. Monogr.* 56: 243–258.
- HEINRICH, I., AND J. C. G. BANKS. 2005. Dendroclimatic potential of the Australian red cedar. *Austr. J. Bot.* 53: 21–32.
- HENRY, J. D., AND J. M. A. SWAN. 1974. Reconstructing forest history from live and dead plant material: An approach to the study of forest succession in southwest New Hampshire. *Ecology* 55: 772–783.
- IBARRA-MANRÍQUEZ, G., AND M. MARTÍNEZ RAMOS. 2002. Landscape variation of liana communities in a Neotropical rain forest. *Plant Ecol.* 160: 91–112.
- JOHNSON, E. A., AND K. MIYANISHI. 2008. Testing the assumptions of chronosequences in succession. *Ecol. Lett.* 11: 419–431.
- KAENNEL, M., AND F. H. SCHWEINGRUBER. 1995. Multilingual glossary of dendrochronology. Terms and definitions in English, German, French, Spanish, Italian, Portuguese, and Russian. Birmensdorf, Swiss Federal Institute for Forest, Snow and Landscape Research. Berne, Switzerland, Stuttgart, Germany, Vienna, Austria.
- KENNARD, D. K., K. GOULD, F. E. PUTZ, T. S. FREDERICKSEN, AND F. MORALES. 2002. Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. *For. Ecol. Manage.* 162: 197–208.
- LEBRIJA-TREJOS, E., F. BONGERS, E. A. PÉREZ-GARCÍA, AND J. A. MEAVE. 2008. Successional change and resilience of a very dry tropical deciduous forest following shifting agriculture. *Biotropica* 40: 422–431.
- LIEBERMAN, D., M. LIEBERMAN, G. S. HARTSHORN, AND R. PERALTA. 1985. Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. *J. Trop. Ecol.* 1: 97–109.
- MAINGI, J. K. 2006. Growth rings in tree species from the Tana river floodplain, Kenya. *J. East Afr. Nat. Hist.* 9: 181–211.
- MARTÍNEZ-RAMOS, M., AND E. R. ÁLVAREZ-BUYLLA. 1998. How old are tropical rain forest trees? *Trends Plant Sci.* 3: 400–405.
- OGDEN, J. 1981. Dendrochronological studies and the determination of tree ages in the Australian Tropics. *J. Biogeogr.* 8: 405–420.
- PÉREZ-GARCÍA, E. A., J. A. MEAVE, AND C. GALLARDO. 2001. Vegetación y flora de la región de Nizanda, Istmo de Tehuantepec, Oaxaca, México. *Acta Botanica Mexicana* 56: 19–88.

- POUSSART, P. F., M. N. EVANS, AND D. P. SCHRAG. 2004. Resolving seasonality in tropical trees: Multi-decade, high-resolution oxygen and carbon isotope records from Indonesia and Thailand. *Earth Planet. Sci. Lett.* 218: 301–316.
- POUSSART, P. M., S. C. B. MYNENI, AND A. LANZIROTTI. 2006. Tropical dendrochemistry: A novel approach to estimate age and growth from ringless trees. *Geophys. Res. Lett.* 33: L17711.1–L17711.5.
- POLGE, H. 1978. Fifteen years of wood radiation densitometry. *Wood Sci. Technol.* 12: 187–196.
- PRIYA, P. B., AND K. M. BHAT. 1998. False ring formation in teak (*Tectona grandis* L.f.) and the influence of environmental factors. *For. Ecol. Manage.* 108: 215–222.
- PICKET, S. T. A. 1989. Space for time substitution as an alternative to long-term studies. In G. E. Likens. (Ed.). *Long-term studies in ecology: Approaches and alternatives*, pp. 110–135. Springer, New York, New York.
- ROIG, F. A. 2000. Dendrocronología en los bosques del neotrópico: Revisión y proyección futura. In F. A. Roig (Ed.). *Dendrocronología en América Latina* pp. 307–357. EDIUNC, Mendoza, Argentina.
- ROIG, F. A., J. J. JIMÉNEZ-OSORNIO, J. VILLANUEVA-DÍAZ, B. LUCKMAN, H. THIESSEN, A. MEDINA, AND E. J. NOELLEMAYER. 2005. Anatomy of growth rings at the Yucatán Peninsula. *Dendrochronologia* 22: 187–193.
- RUFFNER, C. M., AND M. D. ABRAMS. 1998. Relating land-use history and climate to the dendroecology of a 326-year-old *Quercus prinus* talus slope forest. *Can. J. For. Res.* 28: 347–358.
- RUIZ, J., M. C. FANDINO, AND R. L. CHAZDON. 2005. Vegetation structure, composition, and species richness across a 56-year chronosequence of dry tropical forest on Providencia Island, Colombia. *Biotropica* 37: 520–530.
- SALDARRIAGA, J. G., D. C. WEST, M. L. THARP, AND C. UHL. 1988. Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. *J. Ecol.* 76: 938–958.
- SCHÖNGART, J., W. J. JUNK, M. T. F. PIEDADE, J. M. AYRES, A. HUTTERMANN, AND M. WORBES. 2004. Teleconnection between tree growth in the Amazonian floodplains and the El Niño-Southern Oscillation effect. *Glob. Change Biol.* 10: 683–692.
- SCHÖNGART, J., B. ORTHMANN, K. HENNENBERG, S. POREMBSKI, AND M. WORBES. 2006. Climate-growth relationships of tropical tree species in West Africa and their potential for climate reconstruction. *Glob. Change Biol.* 12: 1139–1150.
- SHEIL, D. 2001. Long-term observations of rain forest succession, tree diversity and responses to disturbance. *Plant Ecol.* 155: 183–199.
- STAHL, D. W. 1999. Useful strategies for the development of tropical tree-ring chronologies. *IAWA J.* 20: 249–253.
- SWAINE, M. D., AND J. B. HALL. 1983. Early succession on cleared forest land in Ghana. *J. Ecol.* 71: 601–628.
- SWAINE, M. D., AND T. C. WHITMORE. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81–86.
- VIEIRA, D. L. M., AND A. SCARIOT. 2006. Principles of natural regeneration of tropical dry forests for restoration. *Rest. Ecol.* 14: 11–20.
- VERHEYDEN, A., G. HELLE, G. H. SCHLESER, F. DEHAIRS, H. BEECKMAN, AND N. KOEDAM. 2004. Annual cyclicity in high-resolution stable carbon and oxygen isotope ratios in the wood of mangrove tree *Rhizophora mucronata*. *Plant Cell Environ.* 27: 1525–1536.
- WHITMORE, T. C. 1998. *An introduction to tropical rain forests*. Oxford University Press, New York, New York.
- WORBES, M. 1995. How to measure growth dynamics in tropical trees: A review. *IAWA J.* 16: 337–351.
- WORBES, M. 2002. One hundred years of tree-ring research in the tropics – a brief history and an outlook to future challenges. *Dendrochronologia* 20: 217–231.
- WORBES, M. 2004. Tree-ring analysis. In J. Burley, J. Evans, and J. A. Youngquist (Eds.), *Encyclopedia of forest sciences*, pp. 586–599. Elsevier, Oxford, UK.
- WORBES, M., H. KLINGE, J. D. REVILLA, AND C. MARTIUS. 1992. On the dynamics, floristic subdivision and geographical distribution of várzea forests in Central Amazonia. *J. Veg. Sci.* 3: 553–564.
- WORBES, M., R. STASCHEL, A. ROLOFF, AND W. J. JUNK. 2003. Tree ring analysis reveals age structure, dynamics and wood production of a natural forest stand in Cameroon. *For. Ecol. Manage.* 173: 105–123.
- WRIGHT, S. J. 2005. Tropical forests in a changing environment. *Trends Ecol. Evol.* 20: 553–560.
- WRIGHT, S. J., AND H. C. MULLER-LANDAU. 2006. The future of tropical forest species. *Biotropica* 38: 287–301.