CHAPTER 7

Tree Age Structure in Tropical Forests of Central Amazonia

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"How old are the trees?" is one of the first questions that come to mind while walking through a tropical rainforest. In fact, little is known about the ages of tropical trees, and even less is known about the distribution of ages across the forest landscape. The structure of tree ages provides some of the basic data needed to model population dynamics and is important for managers interested in calculating sustainable timber yields. The distribution of ages within populations also influences genetic diversity and population stability. Old trees can reproduce with trees many years younger and prevent the loss of genetic traits with the passing of generations. At an entirely different scale, the global carbon cycle is the focus of considerable international attention because potentially disastrous climatic changes are predicted to result from increases in atmospheric CO_2 and other trace gases (Kattenberg et al. 1996). For tropical rainforests, the residence time of carbon in wood is an important and yet essentially unknown parameter of climate change models.

The lack of information on tropical tree ages persists in large part because dating tropical trees is difficult. In extratropical regions, dating is facilitated by the existence of annual growth rings, but in tropical forests the lack of consistent annual variation in cambial activity results in either no ring structure or a ring structure whose annual formation is uncertain (Fahn et al. 1981). To take advantage of rings to age trees, annual rings must first be validated by other studies. In the absence of such validation, the only way to directly age a tree, in lieu of tracking a tree for its entire life, is by radiocarbon (^{14}C) dating. Here we present radiocarbon dates for forty-four large central Amazon trees and discuss the implications for forest management and conservation.

Methods

Trees were selected from a logging operation near the city of Itacoatiara, about 250 km east of Manaus, Brazil. Here, the Swiss-owned Precious Woods has established a sustainable timber harvesting operation called Mil Madeireira in 80,000 hectares of primary forest, where they have identified sixty-fix species as commercially valuable. Our samples were either selected at the log yard, where boles were stacked prior to processing, or through use of a geographic information system that precisely located stumps from all harvested trees in 2,000 ha

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Fig. 7.1. Collecting tree-ring data and wood samples from the Mil Madeireira log yard. Photo by Christopher Dick.

blocks (fig. 7.1). The vegetation is dense tropical evergreen forest (terra firme, or not seasonally inundated) similar to that of the Biological Dynamics of Forest Fragments Project. The climate is similar to that in Manaus, where mean annual rainfall is about 2,200 mm and mean average temperature is 26.7° C, with a distinct dry season from June to September (see fig. 5.1). Soil type varies gradually with elevation, comprising Oxisols on plateaus (about 80 percent clay), Utisols on slopes, and Spodosols (2 to 5 percent clay) in valleys associated with small streams (Bravard and Righi 1989). Nearly 1,200 tree species have been identified in nearby Ducke reserve (Ribeiro et al. 1999), and the total for the BDFFP sites is expected to at least equal this (Chapter 5). Each hectare contains about 350 different tree species (more than 10 cm DBH) many of which occur at densities of less than one tree per hectare.

The centermost wood (first ring) from the base of the tree provides a date commensurate with the sapling stage of a tree. In all species sampled, a ring structure was evident, and this made identifying the center relatively easy. However, some boles were hollow, and samples had to be taken either at the upper end of the base section (typically 5–6 meters above the ground), or if the hollow was continuous along the stem, from the periphery of the hollow (typically less than 5 cm diameter) at the base. Trees were chosen according to size with approximately 100 cm the minimum base diameter. From a survey of 18 ha from BDFFP permanent inventory plots, trees larger than 100 cm DBH represent just 0.08 percent of stems larger than 10 cm DBH, or about one meter-sized tree every two hectares. The samples collected at Mil Madeireira are representative of the largest and presumably oldest trees from 4,000 ha that were selectively logged.

Forty-four trees from fifteen species were radiocarbon dated by Accelerator Mass Spectrometry (AMS) at Lawrence Livermore National Laboratory (see Taylor, Long, and Kra 1992 for a review of AMS techniques). Living wood is in equilibrium with atmospheric ^{14}C, but when the wood dies, the ^{14}C content gradually declines by radioactive decay. By comparing the current radiocarbon content from the centermost wood with the atmospheric value at the time of death (Stuiver and Becker 1986), the age of the tree can be determined. The accuracy of radiocarbon dating varies with the age of the organic material because atmospheric ^{14}C concentrations respond to production rate changes caused by natural variation in cosmic radiation. As a result, there are fluctuations in the calibration curve of radiocarbon age versus true (calendar) age (Stuiver and Becker 1986). Because of these fluctuations, radiocarbon analysis can only unambiguously date organic material that is more than about 350 years old. Radiocarbon dates on younger material typically correspond to several possible calibrated age ranges between 1650 and 1950 A.D., unless other evidence allows discrimination between these possibilities. Standard errors of calendar dates for trees more than 350 years old are approximately ±50 years, and for trees less than 350 years old are approximately ±100–150 years.

Results

Radiocarbon ages, partially presented in Chambers (1998), demonstrated that large trees of the central Amazon can be very old, with some trees living more than 1,000 years (table 7.1). The oldest tree was a *Cariniana micrantha* with a calendar age of almost 1,400 years. Tree age was positively correlated with tree diameter, but the relationship was weak ($r^2 = 0.25$). The weak correlation between size and age was not simply due to differences between species. For example, two individuals of *Cariniana micrantha* with a base diameter of 180 cm differed in age by about 900 years. There were also differences among species. The largest trees from *Dinizia excelsa*, for example, were never more than about 300 years old, and the distribution of ages was much less variable. Age variation between species was related to life history strategy. Shade-tolerant, slow-growing species were older and exhibited more variability in age than did shade-intolerant fast-growing species.

Discussion

The largest trees in the central Amazon are not necessarily the oldest, conforming with temperate studies that also show poor correlations between size and age (White 1980). The growth rates of tropical tree species, including canopy emergents, vary considerably (Clark and Clark 1992), and a weak correlation between age and size, and a strong correlation between age and average growth rate age is not surprising. The oldest trees in any size class are those that grew the slowest. Previous maximum age estimates for rainforest trees centered around 500–700 years (e.g., Lieberman and Lieberman 1987; Clark and Clark 1992), although Condit, Hubbell, and Foster (1995) predicted trees older than 1,000 years based on mortality rate extrapolations.

These results suggests that for shade-tolerant, slow-growing species, there are a variety of pathways to reach the canopy. This pathway may comprise periods of fast growth in illuminated gaps, and periods of protracted slow growth beneath the canopy, comprising a number of growth and suppression events as transitory gaps periodically appear and close, with relatively few individuals attaining a canopy position. Demonstrating the prevalence of growth suppression, Clark and Clark (1992) studied six species representing a range of life history strategies in a Costa Rican rainforest and showed that about 20 percent of all individuals showed no measurable growth. Ashton (1981) suggested that suppressed trees are destined to die and that only individuals experiencing optimum growth rates will reach the canopy. For shade-intolerant species this is may be true, but what constitutes optimum growth for shade-tolerant species is quite variable.

POPULATION DYNAMICS AND CONSERVATION

Because trees are long lived, it is difficult to study the long-term dynamics of populations. Given an estimated minimum average life span of 150 years (see below) for a central Amazon tree in dense terra firme forest, population studies that last for years, or perhaps for decades, capture only a small fraction of the life span of most trees. Some commercial tree species are being exploited at high rates, and understanding age structure for these species is important for making sound management decisions.

With "roundwood" selling for about US$700 per cubic meter (Veríssmo et al. 1995), big-leaved mahogany (*Swietenia macrophylla*) is the most valuable tree species in the Amazon. As reviewed by Snook (1996), mahogany regenerates after large-scale disturbance, which results in essentially even-aged stands with few juveniles. Supporting this theory, Gullison et al. (1996) in the Bolivian Amazon found that mahogany was regenerating only in one out of five stands studied, and regeneration was due to hydrological disturbances. In the eastern Amazon, disturbances differ in scale from those discussed by Snook (1996), and regeneration in large gaps would not be inconsistent with published studies. Also, fire may play a more important role in the long-term disturbance history in eastern Amazonia than the hurricanes and flooding reported by Gullison et al. (1996, e.g.) in the western reaches of the basin.

Meggers (1994b) has compiled evidence suggesting that extensive drought, and perhaps widespread fires, linked to mega-ENSO (El Niño Southern Oscillation) events occurred in Amazonia 450, 700, 1,000, and 1,500 years ago. Existing populations of mahogany in terra firme forests of the Brazilian Amazon could be relics of such a catastrophic historical disturbance. However, regeneration of mahogany in large treefall gaps, or blowdowns (e.g., Nelson et al. 1994), would not be inconsistent with existing studies. If mahogany is regenerating in large gaps, the largest and presumably oldest trees act as an important source of seeds (Gullison et al. 1996), and their complete removal would halt regeneration. Mapping out age distributions for populations of mahogany can shed light on its regeneration strategy and distribution history and help make informed management decisions possible.

Regardless of the regeneration dynamics of mahogany, because of its high value, loggers will often explore large tracts of forest to find and harvest this single species (see Chapter 26). Mahogany can thus act as catalyst, opening up the remaining forest to logging and agricultural uses that have a much greater impact than the removal of mahogany alone (Fearnside 1997e). Because mahogany appears to be a shade-intolerant, fast-growing species (Nelson et al. 1994; Gullison et al. 1996), suggesting that the largest trees are probably relatively young (less than 300 years), enrichment planting of mahogany in selectively logged forests may be a rational alternative to exploiting large tracts of primary forests.

Tropical timber markets need to become less fixated on a few species and to realize that many Amazon tree species produce valuable timber. The Mil Madeireira logging operation, for example, has identified sixty-six species with valuable properties, although few have commercial markets. Understanding age distributions will help determine which of these species are most amenable to sustainable exploitation once they have become established on national and international markets.

GENETIC DIVERSITY

"The life of a tree is long compared to the evolutionary time scale of its major enemies" (Harper 1977, p. 635), and in a tropical forests pests, pathogens, and decomposers constitute a large, active, and diverse community of organisms. Such natural events as large-scale blowdowns (Nelson,

TABLE 7.1. Ages for Large Central Amazon Trees as Determined by Radiocarbon Dating at Lawrence Livermore National Laboratory's Center for Accelerator Mass Spectroscopy

Species	Common name	Family	Radiocarbon date	1997 age	Base diam. (cm)	Ave. growth (cm/year)
Bagassa guiananensis	Tatajuba	Moraceae	300	350	110	0.31
Brosimum parinarioides	Amapá	Moraceae	280	350	100	0.29
Cariniana micrantha	Tauari vermelha	Lecythidaceae	1440	1370	180	0.13
Cariniana micrantha	Tauari vermelha	Lecythidaceae	780	720	140	0.19
Cariniana micrantha	Tauari vermelha	Lecythidaceae	650	660	140	0.21
Cariniana micrantha	Tauari vermelha	Lecythidaceae	470	560	150	0.27
Cariniana micrantha	Tauari vermelha	Lecythidaceae	440	550	150	0.27
Cariniana micrantha	Tauari vermelha	Lecythidaceae	360	460	180	0.39
Caryocar glabrum	Piquiarana	Caryocaraceae	180	250	120	0.48
Caryocar villosum	Piquiá	Caryocaraceae	90	230	130	0.57
Caryocar villosum	Piquiá	Caryocaraceae	390	510	100	0.20
Dinizia excelsa	Angelim vermelha	Leguminosae	180	250	120	0.48
Dinizia excelsa	Angelim vermelha	Leguminosae	140	250	102	0.41
Dinizia excelsa	Angelim vermelha	Leguminosae	110	170	100	0.59
Dinizia excelsa	Angelim vermelha	Leguminosae	70	100	150	1.50
Dinizia excelsa	Angelim vermelha	Leguminosae	−20	80	100	1.25
Dipteryx odorata	Cumarú	Leguminosae	1220	1170	120	0.10
Dipteryx odorata	Cumarú	Leguminosae	730	710	100	0.14
Dipteryx odorata	Cumarú	Leguminosae	290	360	110	0.31
Hymenolobium spp (2)	Angelim pedra	Leguminosae	380	510	120	0.24
Hymenolobium spp (2)	Angelim pedra	Leguminosae	540	580	140	0.24
Hymenolobium spp (2)	Angelim pedra	Leguminosae	900	840	230	0.27
Hymenolobium spp (2)	Angelim pedra	Leguminosae	490	560	110	0.20
Hymenolobium spp (2)	Angelim pedra	Leguminosae	430	550	100	0.18
Hymenolobium spp (2)	Angelim pedra	Leguminosae	420	550	100	0.18
Hymenolobium spp (2)	Angelim pedra	Leguminosae	450	550	100	0.18
Hymenolobium spp (2)	Angelim pedra	Leguminosae	320	400	100	0.25
Iryanthera grandis	Arurá vermelha	Myristicaceae	480	560	110	0.20
Lecythis poiteaui	Jaraná	Lecythidaceae	940	900	100	0.11
Manilkara huberi	Massaranduba	Sapotaceae	380	510	140	0.27
Manilkara huberi	Massaranduba	Sapotaceae	220	270	110	0.41

TABLE 7.1. (continued) Ages for Large Central Amazon Trees as Determined by Radiocarbon Dating at Lawrence Livermore National Laboratory's Center for Accelerator Mass Spectroscopy

Species	Common name	Family	Radiocarbon date	1997 age	Base diam. (cm)	Ave. growth (cm/year)
Ocotea rubra	Louro gamela	Lauraceae	410	530	120	0.23
Ocotea rubra	Louro gamela	Lauraceae	390	510	100	0.20
Ocotea rubra	Louro gamela	Lauraceae	380	500	100	0.20
Ocotea rubra	Louro gamela	Lauraceae	280	350	110	0.31
Ocotea rubra	Louro gamela	Lauraceae	270	340	110	0.32
Parkia pendula	Angelim fava	Leguminosae	60	170	110	0.65
Peltogyne catingae	Violeta	Leguminosae	180	250	80	0.32
Schlerolobium spp (2)	Tachí	Leguminosae	100	230	100	0.43
Tabebuia serratifolia	Ipê	Bignoniaceae	650	660	80	0.12
Tabebuia serratifolia	Ipê	Bignoniaceae	650	660	80	0.12
Tabebuia serratifolia	Ipê	Bignoniaceae	540	580	90	0.16
Tabebuia serratifolia	Ipê	Bignoniaceae	440	550	80	0.15
Tabebuia serratifolia	Ipê	Bignoniaceae	300	350	90	0.26

Note: Average growth rate was calculated by dividing the diameter of the tree by its age; 1997 age is the measured age of the tree when it was harvested.

Kapos, et al. 1994) and perhaps widespread fires (Meggers 1994b) provide other agents of mortality in Amazonia. Given such an environment, a thousand-year-old tree has demonstrated impressive persistence, some of which may be the result of genetic factors. Functional differences within populations often reflect genetic differences and are not simply the result of environmental variation (Harper 1977, p. 601). Thus, ancient trees may harbor valuable genetic traits useful for developing commercial silvicultural strains (e.g., fast growth and resistance to pests), and their harvest would represent a loss well beyond their function as an individual.

CARBON CYCLING

Wood represents a long-term storage for atmospheric carbon whose residence time can exceed a millennium for wood stored in the center of a large canopy-emergent tree. A more important parameter for global carbon cycling models is the mean residence time of carbon in wood, which is a function of stand mass and tree mortality rates. Global models, such as the Frankfurt Biosphere Model (Kohlmaier et al. 1997), use a number of untested assumptions to estimate the residence time for woody tissues in tropical evergreen forests at about forty years. Based on BDFFP forest inventory data for an 18 ha plot, the standing stock of above-ground woody tissues in central Amazon terra firme forests is about 330 Mg ha^{-1} (SE = 10); according to Chambers et al. (in press) the production of woody detritus is about 4.2 Mg ha^{-1} yr^{-1}. Assuming that stand mass is not changing dramatically over time (Phillips et al. 1998), the mean residence time of carbon in woody tissues is given by standing stocks divided by production (Olson 1963), or about eighty years, twice the estimate of Kohlmaier et al. (1997). In forest fragments, because mortality rates are considerably higher (Laurance, Ferreira, et al. 1998a; Chapter 9 and 13), the mean residence time of carbon will be substantially less, and average tree age lower, than the primary forest.

The mean residence time is not the same as the average age of a tree because only the centermost wood is the same age as the tree. An object-oriented model was developed using the BDFFP permanent inventory data for trees with a DBH greater than 10 cm, which simulates forest stand and carbon cycling dynamics based on tree growth and mortality rates (Chambers 1998). The model predicted that the median tree age in a 100 ha plot was 165 years, and on average, approximately every 40 ha harbored a tree more than 1,000 years old. The model assumed that growth rates up to 10 cm DBH were equivalent to the growth rate of a 10 cm tree. Because growth rates for larger trees are often higher than for small, often suppressed, trees (Hartshorn 1980; Clark and Clark 1992), the average age at death is probably even older. Based on median growth rates through all size classes, Clark and Clark (1992) estimated that the average time required for five emergent species to reach 30 cm DBH was 260 years in Costa Rican forests.

Another important component of global carbon cycling models, and hence climate change predictions, is recovery rate for deforested areas. Because growth rates in secondary and logged forests are measurably higher than in the primary forests (N. Higuchi, unpublished data), recovery times should be shorter than suggested using long-term average growth rates from primary forest. The dynamics of regrowing forests are complex, however, and cannot be based on growth rates alone. Nepstad, Uhl, and Serrão (1991), for example, found that accumulation of stand mass and species in secondary forests of the eastern Amazon is inversely related to the intensity of use prior to abandonment. Moreover, Fearnside and Guimarães (1996) calculate that clearing and burning of secondary forests almost completely offset carbon taken up by regrowing forests in the Brazilian Amazon.

The distribution of tree size classes can also influence recovery times, because large trees, although rare, represent a large portion of forest mass (Brown, Mehlman, and Stevens 1995). At the BDFFP permanent plots, 50 percent of the above-ground stand mass is contained in the largest 8 percent of the trees. Saldarriaga et al. (1988), using a chronosequence of secondary forests recovering for up to 80 years (the oldest reported study), estimated that it takes about 200 years for secondary forests to attain mature forest mass values. Some species, however, may not yet have reached maximum size distributions even after 200 years. The average age for the largest trees of the species *Cariniana micrantha*, for example, is 720 years (table 7.1), suggesting that some emergent species will not be represented in the largest size classes for many centuries. To test whether the absence of some species in the largest size classes affects stand mass recovery times, studies in secondary forests older than 200 years need to be carried out. Considering that Neotropical evergreen forests account for about 25 percent of total global terrestrial net primary production (Mellilo et al. 1993; Potter et al. 1993), age and size distributions in these forests can have a large impact on global carbon cycling rates.

SUSTAINABLE FORESTRY

Sustainable timber production is not usually considered when logging tropical forests (see Chapter 26). Even for logging companies that do consider sustainability a criterion, allowable volume extractions do not account for different life history strategies among commercially valuable species. This is not surprising because very little practical information is available to managers of high-diversity forests. The average growth rate is not even available for most commercial tree species.

Clark and Clark (1996) found that the mean growth rate among a number of emergent tree species differed, although in most cases these differences were not statistically significant. Ages and average growth rates of commercially valuable trees from the central Amazon also vary considerably (table 7.1). However, there are some distinct differences among commercially valuable species. *Dinizia excelsa*, for example, was the fastest-growing species radiocarbon dated, with a mean age and 95 percent confidence interval of 170 ± 35 years. In contrast, mean ages and 95 percent confidence intervals for *Cariniana micrantha* and *Tabebuia serratifolia* were 720 ± 135 years and 560 ± 55 years, respectively. If commercial-sized trees of some species are typically much older than other species, sustainable harvest cycles should reflect these differences.

Once a forest is selectively logged, the increase in light and other resources allows for increased growth for trees left in the gaps. The successional sequence in these gaps is a function not simply of the size structure of populations but also of the growth-rate response. Because the spatial extent and size of canopy gaps is larger in a partially logged forest, by the second harvest the floristic and size structure will differ from the original forest (see also Chapter 27). Selective logging is likely to increase the abundance of fast-growing light-demanding species and reduce the abundance of more shade-tolerant species. Fast-growing light-demanding emergents (e.g., *Dinizia excelsa*, and perhaps *Swietenia macrophylla*) may thrive in a landscape modified by selective logging (see also Chapter 13). If the extraction of timber is deemed more valuable than maintaining an intact forest, the overall strategy should be to develop low-cost management practices that take into account differences in life history strategies and tilt competitive interactions in favor of the most valuable species. Strategies should also focus on ways of increasing the efficiency of land use to limit conversion of old-growth forest for commercial interests.

Tree Rings in Tropical Forests

Radiocarbon dating is expensive (more than US$500 per sample) and not readily available to most ecologists and forest managers. Contrary to conventional beliefs, many tropical rainforest trees exhibit a ring structure, and if these rings are annual, dating tropical trees would be facilitated. Rings are formed due to a reduction in cambial activity related to environmental stress, and tropical trees that grow in regions that experience flooding, or drought, for example, invariably produce rings. If stress occurs more than once a year, however, or if the stress is mild, rings may not be annual, or may vary from year to year (Fahn et al. 1981). Phenological events, such as leaf flush or flowering, can also cause ring formation.

Although tree rings are common in many tropical regions, in most cases it is not known whether the rings are formed on a consistently annual basis. One method used to confirm annual ring formation exploits the rapid increase in atmospheric ^{14}C caused by atmospheric nuclear testing in the late 1950s and early 1960s (Nydal and Lövseth 1970). Radiocarbon concentrations reached twice normal atmospheric levels in about 1964 and have gradually declined because the above-ground test ban went into effect. This "bomb spike" can be used as a tracer to date biotic carbon of recent (past forty years) origin. By measuring the ^{14}C content of rings produced since the late 1950s, and then comparing those values to the known atmospheric content, it can be precisely determined whether rings are annual (Worbes and Junk 1989).

Using this method Worbes and Junk have demonstrated that the rings of trees in flooded forests of the Amazon are annual. Rings in these forests are caused by the yearly stress induced by inundation during the high-water season. Preliminary results using the same method show that the rings from a pioneer species (*Pourouma* sp.) at a BDFFP upland site are also annual. Contrary to these results, Vetter (1995), using a cambial scarring method, found that *Scleronema micranthum* can produce more than one ring per year. Overall, the mechanisms of ring formation for tropical forests are complex and may result from a combination of processes. By employing a variety of methods to study ring structures for a number of species, those that consistently produce annual rings can be identified, and ages can be determined from cores of living trees. This would allow age structures to be determined at a regional scale, which is important for evolutionary and other historical studies.

Annual rings would not only promote demographic studies but would also provide a means to trace climate, or other environmental conditions, for hundreds to thousands of years. D'Arrigo, Jacoby, and Krusic (1994), for example, have generated a tree ring width chronology using *Tectonis grandis* ("teak") from Indonesia that dates back to 1565. The data were compared with ring chronologies from the United States and Mexico, and with ENSO records, demonstrating that ring chronologies from rainforests are capable of recording ENSO events. The Amazon basin is subject to prolonged drought during ENSO years, and reconstructing a climate history from tree rings can demonstrate how forests have responded historically. To obtain the longest climate records, the oldest individuals are typically selected, and, fortunately, these oldest trees often have the highest quality records (Fritts 1991). If it can be determined that the ring structures found in the trees from table 7.1 are annual, promising studies into the environmental history of the Amazon would be possible.

By measuring how ages are distributed within tree populations, a new dimension can be given to relatively short-term population studies, shedding light on historical events, as well as on the future trajectory of a community. A reconstruction of past events based on ring chronologies and other ancillary data for an old-growth forest in New Hampshire, for example, demonstrated that the forest was destroyed by a fire in 1665 and a hurricane in 1938 (Henry and Swan 1974). If the annual rings can be verified for a number of tropical forest species in the Amazon, tree cores can be used to reconstruct community history.

Even if Amazon terra firme trees with annual rings are discovered, it is a time-consuming and difficult process to measure the age structure of an entire tree community. It is important to note that detailed information on tree age structure is not critical for making many informed management decisions. Information on size distributions, a much more manageable task, may be more useful for making predictions about future population structure (Harper 1977, p. 603). However, age structure is the only way to trace the history of the forest, and this information may be critical for making evolutionary studies, understanding forest disturbances, and making some important management decisions about the sustainable harvest of timber.

Conservation Lessons

1. The central Amazon harbors giant trees, some of which are more than 1,000 years old.
2. Fast-growing, light-demanding species (e.g., *Dinizia excelsa, Swietenia macrophylla*) may thrive in a selectively logged landscape and be ideal candidates for enrichment planting.
3. Thousand-year-old trees can reproduce with trees that are many generations younger and prevent the loss of genetic diversity. The oldest individuals may also harbor genetic traits like fast growth rates or resistance to pests that may be useful for selective breeding programs.
4. Sustainable harvesting programs should consider the life history strategies and average growth rates of commercial species when determining allowable volume schedules and harvest cycles. Fast-growing, light-demanding species are probably more amenable to sustainable harvesting than are slow-growing, shade-tolerant species.
5. Growth rings, where consistently annual, will be a valuable tool for determining long-term growth rates of commercial species and for elucidating historical patterns of disturbance in tropical forests.
6. It will take hundreds of years for a deforested area to accumulate the carbon that was lost to the atmosphere after burning. When calculating forest recovery times, the size, age, and species composition of the recovering forests are important factors.
7. The residence time for carbon in woody tissues in central Amazon terra firme forests is about eighty years, and the average tree with a DBH of more than 10 cm is at least 150 years old.

8. Forest managers and ecologists should collaborate toward understanding forest function and structure in an applied context.

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