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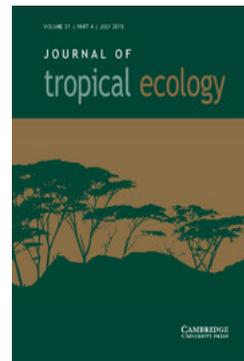
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¹⁴C dating of tree falls on Barro Colorado Island (Panama): a new method to study tropical rain forest gap dynamics

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ABSTRACT. A new method for investigating the age structure of the patch mosaic of a tropical forest by utilizing radiocarbon dating techniques on fallen trees is proposed. Aboveground nuclear explosions in the early 1960s, before the nuclear test ban treaty, created a spike in the ¹⁴C concentration content of the atmosphere. The amount of radiocarbon in the outer layers of wood collected from trunks of trees that had died in known years (1970–1989) on Barro Colorado Island (BCI) and Gigante Peninsula (Panama) was analysed to test the hypothesis that radiocarbon concentration was predictive of year of tree death. The date of tree death was negatively related to the level of ¹⁴C, following a trend similar to published data on tree rings from German and Amazonian trees. Combining our data with these data in a statistical analysis revealed a significant predictive effect of radiocarbon on year. Analysis of covariance showed that there was no significant difference among the slopes of the three groups of data, but there was significant heterogeneity among the intercepts. The differences suggest a need for site-specific calibration and refinement of field protocols. The technique shows promise and suggestions are made to improve its usefulness for future studies.

KEY WORDS: age structure of gaps, bomb peak, gap dynamics, radiocarbon dating of wood, tropical rain forest dynamics

INTRODUCTION

Tropical rain forest structure is characterized by a dynamic mosaic of patches in various stages of regeneration or succession following gap formation due to tree falls (Brokaw 1985, Denslow 1987). Understanding the dynamic structure of tropical forests is of interest in several ecological and evolutionary contexts. The dynamic structure of tropical rain forests is likely a major contributor to its characteristically high diversity (Alvarez-Buylla *et al.* 1996, Brokaw & Scheiner 1989, Dirzo *et al.* 1992). Other issues include life-history evolution of

tropical trees (Alvarez-Buylla *et al.* 1996), co-evolution between plants and their seed dispersers (Horvitz & Schemske 1986, 1994), and the impact of spatial and temporal variation on population dynamics of rain forest organisms (Martínez-Ramos & Alvarez-Buylla 1986). Successful management of tropical forest ecosystems for either conservation or sustained-yield forestry also depends upon developing an accurate model of natural regeneration processes (Hubbell & Foster 1986, Webb 1998).

Despite the importance of understanding tropical forest dynamics to many issues of tropical ecology, evolution and conservation, accurate estimates of forest gap turnover rates are very rare (Alvarez-Buylla & García-Barrios 1993, Brokaw 1985, Martínez-Ramos & Alvarez-Buylla 1986). A complete data set would include knowledge of both the rate of formation of new gaps and the dynamic age structure of the patch mosaic. By the latter, we mean both the relative abundance of patches of different ages (where age zero is the year when a tree fall gap is created at a particular patch) and the probability for the forest environment to change (become shadier or more open) with age. Several researchers have modelled such dynamic processes (Cipollini *et al.* 1994, Horvitz & Schemske 1986, Pascarella & Horvitz 1998), but few have the complete set of empirical data. Such a complete data set is simply not available for any tropical forest, although data of this nature may be forthcoming in the long term from the series of 50-ha plots that have been established across the tropics (e.g. Condit *et al.* 1995, 1996). Data that have been used to obtain rough estimates of forest dynamics include ground surveys of necessarily small (usually ≤ 50 ha) study areas in which designated areas are surveyed once or several times during relatively few years. Such ground surveys are usually logistically restricted to small areas and/or infrequent censuses. Aerial photographs have also been used in one study to measure sizes and numbers of gaps (resolution: 40 m², scale 1 : 2400 in Sanford *et al.* 1986). This method allowed an increase in the area sampled (97.2 ha) relative to ground work, but it did not reveal age structure or rate of creation of new gaps.

A complete schedule of patch dynamics including the age structure of the patch mosaic for a large tract of tropical forest has not yet been obtained. Short of a bio-indicator (Martínez-Ramos 1985) there has not yet been a method of ageing gaps except by keeping long-term records of particular trees falling. Here, we propose a new method for investigating the age structure of the patch mosaic of a tropical forest by utilizing radiocarbon dating techniques on outer layers of trunks from fallen trees.

Radiocarbon dating can be used to date tree falls and other recent events because numerous aboveground nuclear explosions in the early 1960s, before the nuclear test ban, created a spike in the ¹⁴C concentration content of the atmosphere (Worbes & Junk 1989). This spike is characterized by a sharp increase in ¹⁴C concentration during the nuclear test period (about two-fold) (Nydal & Lövseth 1970) and a sharp decrease after the ban (Nydal & Lövseth

1983). Plant biomass formed during any given year bears the ^{14}C concentration signature of the atmosphere in that year, as plants fix carbon from the atmosphere. For example, plant biomass formed in 1989 has about 1.2 greater ^{14}C concentration relative to the pre-nuclear-testing (1950) standard (Worbes & Junk 1989). Such differences are highly significant and well within the accuracy of measurement of ^{14}C concentration presently being used (Southon *et al.* 1992, Sternberg *et al.* 1985). This ^{14}C spike has created a dating window for the last 40 y. This dating technique has been previously used to investigate utilization of carbon dioxide from decomposing peat by plants (Sternberg *et al.* 1985), the ages of houses built by the Warao Indians (Tamers 1969), the ages of water samples from a series of wells (Tamers 1969) and, more recently, below-ground cycling of carbon (Trumbore *et al.* 1995) and the age of seeds in a seed bank (L. Venable, *pers. comm.*).

To accurately date samples, it is necessary to know not only the ^{14}C concentration in the outer layer of a trunk, but also whether the biomass in the outer layer of a trunk was formed previous to or following the bomb spike. Thus, for samples from an unknown year, it would be necessary to analyse sequential samples in tree trunks (outer surface and below the outer surface). If ^{14}C concentration increases as one samples toward the interior of the trunk, then the outer layer of the trunk was formed after the bomb spike; conversely if it decreases as one samples toward the interior, then the outer layer of the trunk was formed before ^{14}C reached the peak during the era of above-ground nuclear tests. If there is no difference as one samples towards the interior, then it may be that the outer layer was formed well before the onset of above-ground nuclear tests (1950s or before); this method would not be instructive for events of that time period. Cellulose is an end-product which does not break down during various metabolic processes, therefore it provides the best metabolic component for ^{14}C concentration analysis. Thus, the year that a tree fell may be determined by associating the concentration of ^{14}C in the outer layer of wood cellulose in the trunk with the concentration of ^{14}C in the atmosphere in a given year or with the concentration of ^{14}C in calibrated wood samples.

Success of this technique to age tree fall gaps depends additionally on two assumptions: (1) the outer layer of the trunk persists for several years and does not decay quickly after the tree falls and (2) most gaps result from trees that fall alive rather than from trees that die standing and fall several years later. If these assumptions hold, then samples taken from the outer layer of the fallen trunk will contain carbon that was fixed during the year that the tree fell. The validity of these assumptions may vary between tree species and forests.

The first step in investigating whether this technique could be used to study forest dynamics is to test the hypothesis that the amount of radiocarbon in the outer layer of a fallen tree is predictive of the year of its death. We investigated this hypothesis by analysing the amount of radiocarbon in the outer layers of wood collected from trunks of trees that had fallen or had died in known years.

We combined our data with published data on the amount of radiocarbon in rings of trees, each ring from a known year (Worbes & Junk 1989), to make a predictive model.

METHODS AND MATERIALS

Field protocol

To obtain data on the relationship between radiocarbon content of wood and year of tree fall, we located trunks of trees that had fallen or died in known years on Barro Colorado Island (BCI) and Gigante Peninsula. We began with many notes supplied by other researchers and we obtained many samples, but only 19 of the samples met all the criteria necessary for the study. For these samples, the methods of collection are outlined here. We used field notes and field tags supplied by other researchers and/or direct personal knowledge of persons accompanying us to the sites to locate the samples, with the exception of three samples. Two of these three samples were from stem disks previously cut and stored in the herbarium of BCI, supplied by J. Wright (*pers. comm.*). The other sample was from a tree that fell in a storm on 29 July 1989 while we were present at the field site. For the forest-collected specimens, care was taken to be sure that the trunk sampled was in fact the dead tree referred to in the notes. Only unambiguous cases are reported in the analysis. Most samples were located in the field (26–30 July 1989) while accompanied by a person familiar with the researcher's sites, including those we learned about from M. Loveless, from S. Williams (50-ha plot), and from A. Smith (his assistant G. Abrego took us to the field) (Table 1). The year of tree death for one monocarpic species, *Tachigalia versicolor* Standl. & Will., was presumed to be the same as the year of flowering, since trees of this species die soon after reproducing (Foster 1977). The flowering dates of trees of this species on BCI were well known, since this species was the subject of an intensive life history and mating system study (Loveless *et al.*, in press).

On each trunk, an area that appeared to still have the outer layer of wood intact was located. We then used a handsaw to cut out a small wedge of wood (*c.* 20 cm long by 10 cm deep), storing each sample with an identifying tag in a plastic bag. When preparing the samples, we again verified the integrity of the outer layer. Nineteen samples met all the above criteria; these samples were from trees that had fallen or died between 1970 and 1989 (Table 1).

Preparing wood samples for analysis

Samples were prepared for analysis in October 1989 at the University of Miami. For each field sample, we obtained *c.* 20 g of material from each of several different layers (defined by *c.* 0.7-cm increments measured from the outer edge) of wood. For each layer, we drilled out several small cylinders of wood (0.5 cm in diameter each), leaving an undrilled layer of *c.* 1 cm between sample layers. No oil was used on the drill bits. The cylinders from each layer were pooled and each

Table 1. Field data on each collection and name of the laboratory where samples were analysed. BCI is Barro Colorado Island; Gigante is the Gigante Peninsula. Plot references are to the 20-m \times 20-m grid coordinate system on the 50-ha plot; ML: = M. Loveless; SW = S. Williams; AS = A. Smith; JW = J. Wright; NB = N. Brokaw; CH = C. Horvitz; Beta = Beta Analytic, Inc, Miami, FL; AZ = Department of Geosciences, University of Arizona.

Year of death	Species	Location	Trail	Source of data on tree death	Lab. for ^{14}C	Reference No.
1970	<i>Tachigalia versicolor</i>	BCI	Wheeler 5	ML	Beta	2
1970		BCI	Plot(3,20)	ML	AZ	13
1970		BCI	Plot(15,18)	ML	AZ	14
1974		BCI	Drayton 0	ML	AZ	4B
1974		BCI	Standley 2.0	ML	AZ	6A
			15 m from Balboa			24
1974		BCI	8.0 N	NB	AZ	
			North of Wheeler			3
1978		BCI	15.5	ML	AZ	
1978		BCI	Zetek8-9	ML	AZ	12
1982	<i>Dipteryx panamensis</i>	Gigante	Site 4,D7	AS	AZ	15
1982	<i>Xanthoxylum</i> sp.	Gigante	Site 4,C6	AS	AZ	16
1983	<i>Miconia argenta</i>	Gigante	Site 6,C14	AS	AZ	19
1983	<i>Pterocarpus rohrii</i>	Gigante	Site 6, no. 9	AS	AZ	17
1984	<i>Tachigalia versicolor</i>	BCI	Plot(16,07); Armour	ML	AZ	5A
1984		BCI	Plot(12,09)	ML	AZ	10BC
1987	<i>Dipteryx panamensis</i>	BCI	Plot(12,11)	SW	AZ	9
1987	<i>Ficus</i> sp.	BCI	Drayton (Plot)	SW	AZ	7
1988	<i>Ochroma pyramidale</i>	BCI	Construction site	JW	AZ	21
1988	<i>Protium tenuifolium</i>	BCI	Construction site	JW	AZ	20
			Behind kitchen, 7/			25
1989	indet.	BCI	29/89	CH	Beta	

layer was stored separately for layer-specific isotopic analysis. We analysed radiocarbon in several layers for two of the samples, one from a tree that died in 1989 and one from a tree that died in 1970. For all the other samples, we analysed radiocarbon in the outer layer (0.0–0.7 cm in most, 0.0–1.0 cm in a few) only, since all the samples were from trees that fell within this range of dates (1970–1989). All of these trees fell after the bomb spike.

Radiocarbon analysis

Radiocarbon analyses were performed at the University of Arizona (Department of Geosciences) and at Beta Analytic, Inc. (Miami, FL). Wood samples were pretreated by first examining for rootlets. The samples were then given a hot acid wash to eliminate carbonates. They were repeatedly rinsed to neutrality and subsequently given a hot alkali soaking to remove humic acids. After rinsing to neutrality, another acid wash followed; subsequently another rinsing to neutrality was performed. Samples were pyrolyzed; the resulting CO_2 was converted to benzene and ^{14}C abundance was determined by scintillation counters. Results are reported as a mean and one standard deviation (based on the random nature of the radioactive disintegration process) in terms of percentage of modern (% modern) (M. Tamers, *pers. comm.*). All ^{14}C activities were corrected to ^{13}C abundance and expressed relative to the United States National Bureau of Standards (NBS) 1950 oxalic acid standard (Worbes & Junk 1989, p. 504).

Digitizing data from another study

To obtain additional data on the relationship between radiocarbon in wood and year of carbon fixation, we digitized the post-bomb spike data on tree rings from Figures 2 and 3 of Worbes & Junk (1989). These figures, respectively, show radiocarbon level in rings of trees from Germany and from the Amazon, including wood dating from the 1950s through the early 1980s; they include the bomb peak. We included data from both hemispheres, as the bomb-peak was known to vary with latitude, with higher levels in the northern hemisphere than in the southern hemisphere (Worbes & Junk 1989). The peak was also temporally displaced between the hemispheres, occurring in 1964 in the north and in 1965 in the south (Worbes & Junk 1989). In as much as our interest in these data was to compare the pattern of decline in ^{14}C in wood after the spike with ^{14}C data from the outer layer of our samples, we only digitized data starting from 1965. We were not interested in the increase in ^{14}C previous to the spike.

Data analysis

To determine whether we could find the ^{14}C signature of the bomb peak in the wood of fallen trees from Barro Colorado Island, Panama, we compared the radiocarbon content of four different layers of wood, 0–0.05, 0.6–1.5, 1.6–2.5 and 4–5 cm (measured as distance from the outer edge). We chose one tree that died in 1970 and one tree that died in 1989 to cover the range of dates of our samples.

To determine the predictability of year of tree death from radiocarbon content of wood, we combined our data with other data relating the year of wood formation to its radiocarbon content. We performed a regression analysis for each of the following groups of data, Panamanian tree falls ($n = 19$) (our collections: outer layers only), Amazonian tree rings ($n = 13$) (Worbes & Junk 1989) and German tree rings ($n = 32$) (Worbes & Junk 1989) (GLM procedure, SAS Institute 1988). We restricted our use of the data from Worbes & Junk to data from years 1970 and above, since this matches dates for which we had tree fall samples, and since the post-bomb peak curve is not strictly linear. The slope before 1970 was steeper, but the slope after 1970 was well-approximated by a line (Worbes & Junk 1989). Next, we performed an analysis of covariance to analyse the homogeneity of slopes and of intercepts and to calculate intercepts for each group based on pooled slope (Sokal & Rohlf 1981: Box 14.10)(GLM procedures for ANCOVA, using a series of models, detailed in the Appendix, for partitioning the sums of squares, SAS Institute 1988). In these analyses, the dependent variable was year and the independent continuous variable was radiocarbon content. The independent grouping variable in the ANCOVA was the data set: Panamanian tree fall, Amazonian tree rings or German tree rings.

RESULTS

The tree that died in 1970 had in its outermost ring a level of ^{14}C that was $153.5 \pm 0.9\%$ modern (Figure 1a). The outer layer was apparently post-bomb

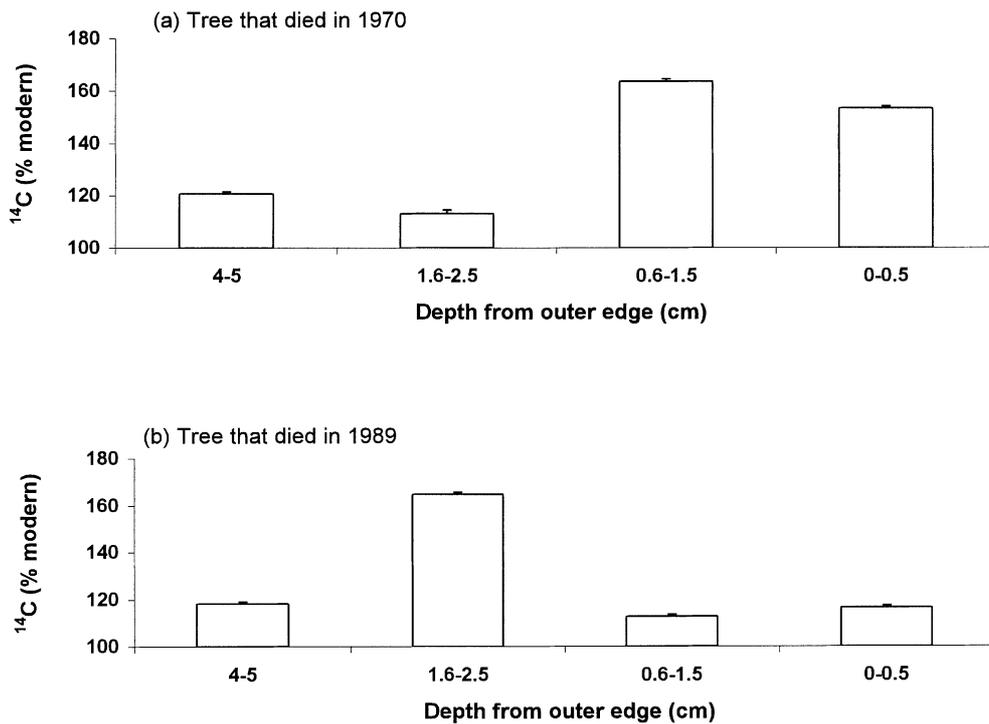


Figure 1. ¹⁴C concentration (% modern) in different layers of wood from two trees that fell on Barro Colorado Island, Panama, (a) a tree that died in 1970 and (b) a tree that died in 1989. The wood layers are arranged along the x-axis chronologically, left to right for year of carbon fixation; the deeper layers were made earlier and the outer layer was made later.

peak; the second layer apparently included the bomb peak, with a relatively higher level of ¹⁴C, $163.7 \pm 1.1\%$ modern (Figure 1a). The tree that died in 1989 apparently included the bomb peak in a deeper layer of wood, with a comparable level of ¹⁴C, $164.9 \pm 0.8\%$ modern, in the third layer (Figure 1b). This tree had an outer layer that was post-bomb peak and considerably lower in ¹⁴C ($116.9 \pm 0.6\%$ modern) (Figure 1b) than the tree that died in 1970 (Figure 1a,b).

In general, the date of tree death or falling was negatively related to the level of ¹⁴C, following a trend similar to the tree rings from German and Amazonian trees (Figure 2). These data suggest that the outer layer of wood mostly contained carbon that was fixed during the year that the tree fell. However, our data were more variable than the tree ring data (Figure 2).

There was a significant predictive effect of radiocarbon on year for all three data sets, including the tree fall samples ($F = 41.2$; $df = 1,17$; $P < 0.001$, $r^2 = 0.71$), the Amazonian tree rings ($F = 490.1$, $df = 1,11$; $P < 0.001$, $r^2 = 0.98$), and the German tree rings ($F = 367.4$, $df = 1,30$; $P < 0.001$, $r^2 = 0.92$). The amount of variance explained was lower for the tree fall samples than for the tree rings. The ANCOVA showed that the slopes of the three groups of data were not significantly different (Table 2); the slope for the pooled data was -0.44

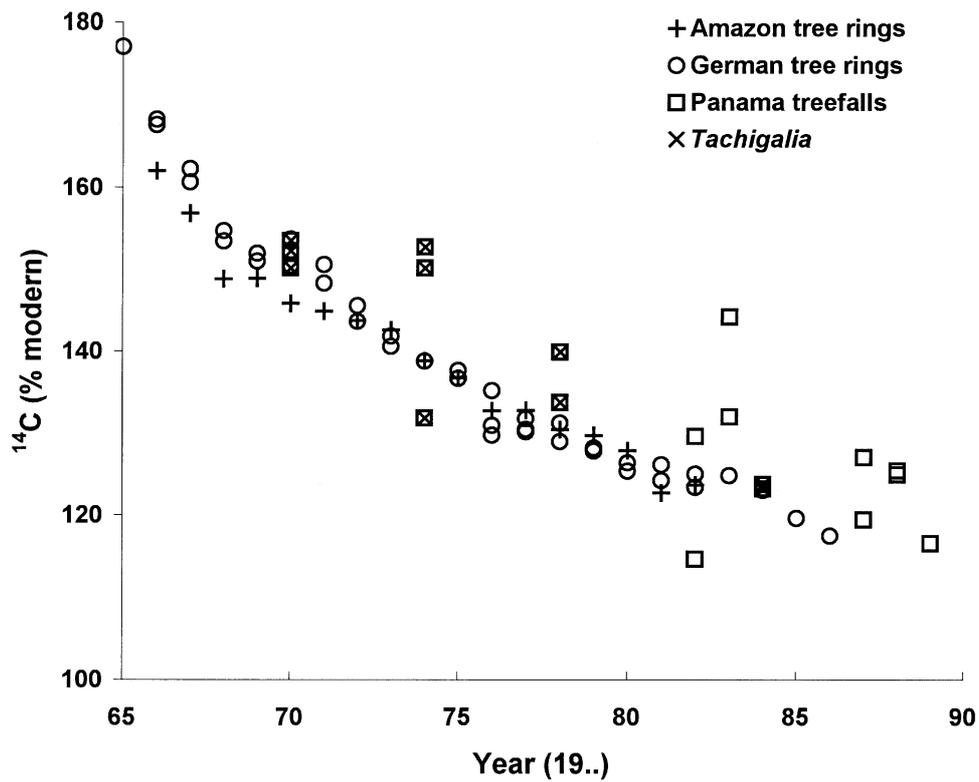


Figure 2. Scattergram of ^{14}C concentration (% modern) vs. year for tree rings that were made after the bomb peak in Germany and in the Amazon (data digitized from Worbes & Junk 1989) and for the outer layer of wood from trees that died or fell in different years on Barro Colorado Island, Panama.

Table 2. ANCOVA of the regression of year on radiocarbon for treefalls from Panama (outer layer of wood), Amazonian tree rings and German tree rings, including partitioning of sums of squares and tests of heterogeneity of slopes, means and y-intercepts among the groups of data (ANCOVA table as in Sokal & Rohlf 1981, p. 528).

Source	df	MS	F	P
Groups	2	86.68		
Within groups	61	25.94		
Common slope within groups	1	1301.43	277.9	***
Deviations from common slope within groups	60	4.68		
Heterogeneity of slopes	2	1.28	0.3	ns
Error	58	4.80		
Groups + within (= total)	63	27.87		
Common slope total study	1	1302.43		
Deviations from common slope total study	62	7.31		
Heterogeneity of means and y-intercepts	2	86.18	18.4	***
Error	60	4.68		

***, $P \leq 0.001$; ns, $P > 0.05$.

Table 3. Slopes and intercepts for the regression analyses of year on radiocarbon for each group of data, treefalls from Panama (outer layer of wood), Amazonian tree rings and German tree rings. The group intercept for the pooled data model is given by the mean year for the group – the slope for the pooled data times the mean radiocarbon for the group (Sokal & Rohlf 1981, p. 524).

Group	Singles data set models		Mean		Pooled data model	
	Slope	Intercept (year*)	Year*	Radiocarbon (% modern)	Slope	Group intercept** (year*)
Treefalls (outer layer)	-0.42	137.0	80.3	133.9	-0.44	139.2
Amazonian tree rings	-0.49	141.5	76.0	134.8	-0.44	135.3
Treefalls (outer layer)	-0.45	136.9	77.1	133.3	-0.44	135.7

* Add 1900 to the tabled quantity to express as calendar year, e.g. 80.3 + 1900 = 1980.3, 137.0 + 1900 = 2037.0.

** $a_i = Y_i - b_{pooled} \cdot X_i$.

(Table 3). However, the ANCOVA revealed that there was significant heterogeneity of the intercepts (Table 2); thus the predictive model for each data group was different (Table 3). The intercept for the tree fall data was higher than for the other two groups of data (Figure 3). Statistical comparison of

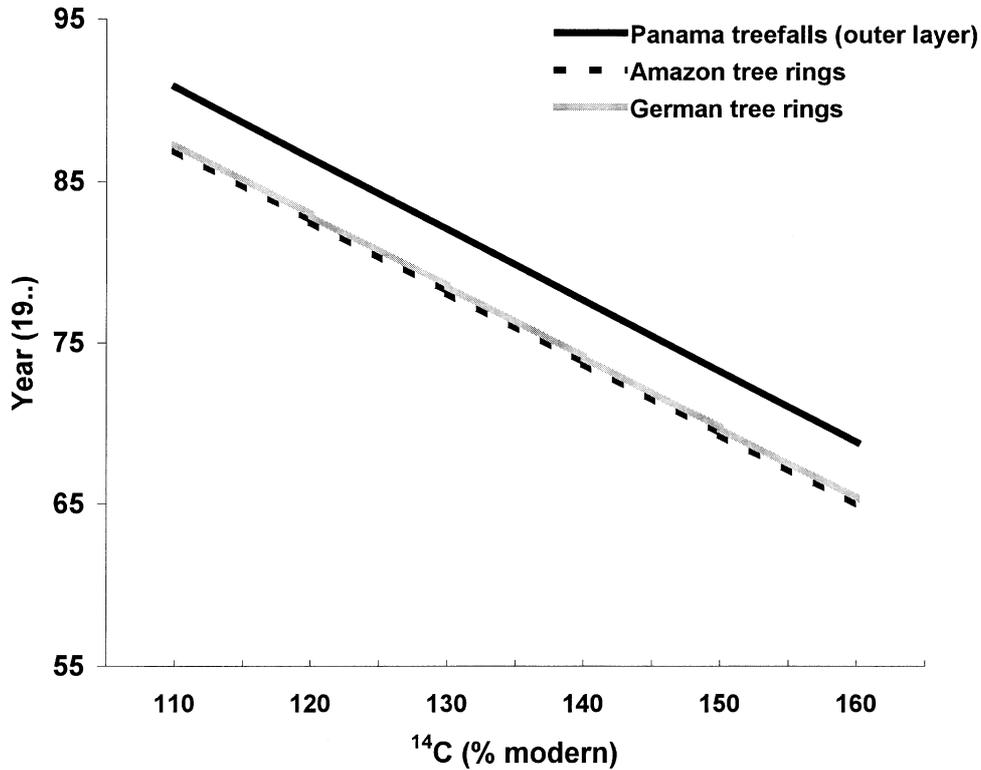


Figure 3. Linear regression model to predict year from ¹⁴C concentration, based on pooled data from three data sets, tree rings from Germany and the Amazon and the outer layer of wood from trees that died or fell in different years on Barro Colorado Island, Panama. This analysis was restricted to data from 1970 or later in all three data sets. Slopes did not differ significantly, but the intercepts did (Table 2); thus separate lines were drawn for each data set group, according to the pooled data model (Table 3).

the least-squares adjusted means of year among the groups indicated that the Panamanian tree fall regression line was significantly different from the two tree ring regression lines ($P < 0.0001$ for each comparison), but that the two tree ring regression lines did not differ from one another ($P = 0.55$). The least-squares adjusted mean years were, respectively, 80.3, 76.9 and 76.5 (add 1900 to read these as dates, 1980.3, 1976.9 and 1976.5) for the Panamanian tree falls, the tree rings from Germany and the tree rings from the Amazon, respectively.

DISCUSSION

The ^{14}C signature of the outer layers of wood for trees that died between 1970 and 1989 showed a clear negative trend with date of death. The highly significant regression of year on ^{14}C concentration for wood produced from 1970–1989 indicated that the gradual decline in atmospheric ^{14}C since the bomb peak (Nydal & Lövsseth 1970, 1983) is reflected in the wood formed in different years. Thus the radiocarbon content of wood was useful as a dating tool for wood made during these years. In predicting the year from ^{14}C , we note that the Panamanian tree-fall data had a larger intercept than the tree ring data. This means that for a given level of ^{14}C , the Panamanian tree-fall regression line predicts a somewhat later year than the tree ring regression lines, *c.* 3.5 y later than the tree ring data. The reason for this difference will be discussed in the next paragraph; this result indicates that calibration with some site-specific wood of known ages is indicated.

We can think of three possible reasons that our results give a later date for a particular ^{14}C concentration when compared to the tree ring data. Firstly, trees may have decreased wood production or even died for a few years prior to falling over, *i.e.*, assumption one (see the Introduction) did not hold. Secondly, the width of the 'outer layer' (0.7 cm) may have been such that more than one year's growth was included, specifically wood from several earlier years may have been included rather than wood from only 1 y. Worbes & Junk (1989) noted that annual rings of tropical trees may be very thin. The layer of wood in most tropical trees that represent a single season's growth is not obviously marked by annual growth rings and it may be much thinner than our outer layer sample width. Thinner samples should be taken in future studies. Thirdly, some of the outer wood may have decayed (despite our best efforts at choosing trunks with intact outer layers), leaving older wood. These factors may have operated singly or together, as any of them would have a similar effect.

Each of these potential problems is resolvable. With respect to the first problem, more on-site experience might help researchers to determine whether sampled logs died standing and then fell or whether they were tip-ups from previously live trees. In addition, some samples of cores from living trees of the dominant species might aid in the calibration of these data. With respect

to the second issue, current technological advances in ¹⁴C dating do not require as much sample to count the radiocarbon activity (Southon *et al.* 1992) per date, and would therefore lend itself to analysis of thinner samples. With the reduced quantity of wood needed, it may also be easier to find clearly intact areas on dead trunks. Choice of only those tree species known to decay more slowly would also address the problem of outer layer decay.

A linear approximation to the pattern of decline in ¹⁴C since the bomb spike is probably only valid over subsets or segments of time; for example, the decline appears much sharper from 1965 to 1970 than thereafter (Figure 2). We suggest that further examination of the slope during the decline covering the last decade would be indicated to estimate dates for wood made, or for trees that have died or fallen during the last decade (1989–present).

The use of ¹⁴C concentration to date tree-fall gaps looks promising as a method to estimate the age structure of gaps in a forest by a single-point-in-time census. We recognize that exact dating of each fallen tree was not shown by our data, but a very significant regression model was obtained. The greatest utility of this technique would be to estimate the age structure of gaps much more quickly than is logistically feasible than by monitoring individual tree-fall events in study plots over long time periods. We also propose that it would be promising to combine this technology with SPOT satellite image technology (10-m × 10-m resolution, Welch 1985) or with higher resolution aerial photographs. If gaps of known ages (whose positions could be identified on the image) could be identified with particular signatures on the satellite image, the gap age structure of a very large area might be estimable. Taking two satellite images over a time sequence would allow an estimate of the ‘birth rate’ of gaps as well as the transitions among gap-phases within one time interval. Such data when combined with gap ‘age structure’ data would tell us about the forest dynamics of a given area in a relatively short time.

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LITERATURE CITED

- ALVAREZ-BUYLLA, E. R. & GARCÍA-BARRIOS, R. 1993. Models of patch dynamics in tropical forests. *Trends in Ecology and Evolution* 8:201–204.
- ALVAREZ-BUYLLA, E. R., GARCÍA-BARRIOS, R., LARA-MORENO, C. & MARTÍNEZ-RAMOS, M. 1996. Demographic and genetic models in conservation biology: applications and perspectives for tropical rain forest trees. *Annual Review of Ecology and Systematics* 27:387–421.
- BROKAW, N. V. L. 1985. Tree falls, regrowth and community structure in tropical forests. Pp. 53–69 in Pickett, S. A. & White, P. S. (eds). *The ecology of natural disturbance and patch dynamics*. Academic Press, San Diego, California.
- BROKAW, N. V. L. & SCHEINER, S. 1989. Species composition in gaps and structure of a tropical forest. *Ecology* 70:538–541.
- CIPOLLINI, M. L., WALLACE-SENFIT, D. A. & WIGHAM, D. F. 1994. A model of patch dynamics, seed dispersal and sex-ratio in the dioecious shrub *Lindera benzoin* (Lauraceae). *Journal of Ecology* 82:621–634.
- CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* 65:419–439.
- CONDIT, R., HUBBELL, S. P., FRANKIE, J. V., SUKUMAR, R., MANOKARAN, N., FOSTER, R. B. & ASHTON, P. S. 1996. Species-area and species-individual relationships for tropical trees: a comparison of three 50-ha plots. *Journal of Ecology* 84:549–562.
- DENSLÖW, J. S. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18:431–451.
- DIRZO, R., HORVITZ, C. C., LOPEZ, A. M. & QUEVEDO, H. 1992. Effects of gap ages and sizes on understorey herb communities of a Mexican tropical forest. *Journal of Ecology* 80:809–822.
- FOSTER, R. B. 1977. *Tachigalia versicolor* is a suicidal neotropical tree. *Nature* 268:624–626.
- HORVITZ, C. C. & SCHEMSKE, D. W. 1986. Seed dispersal and environmental heterogeneity in a neotropical herb: A model of population and patch dynamics. Pp. 169–186 in Estrada, A. & Fleming, T. F. (eds). *Symposium on frugivores and seed dispersal*. Dr. W. Junk Publishers, Dordrecht, Netherlands.
- HORVITZ, C. C. & SCHEMSKE, D. W. 1994. Effects of dispersers, gaps, and predators on dormancy and seedling emergence in a tropical herb. *Ecology* 75:1949–1958.
- HUBBELL, S. P. & FOSTER, R. B. 1986. Biology, chance and history and the structure of tropical rainforest tree communities. Pp. 314–326 in Diamond, J. & Case, T. J. (eds). *Community ecology*. Harper & Row, New York.
- LOVELESS, M. D., HAMRICK, J. L. & FOSTER, R. B. 1999. Population structure and mating system in *Tachigali versicolor*, a monocarpic neotropical tree. *Heredity* (in press).
- MARTÍNEZ-RAMOS, M. 1985. Claros, ciclos vitales de los árboles tropicales y regeneración natural de las selvas altas perennifolias. Pp. 191–239 in Gomez-Pompa, A. & Del Amo, S. (eds). *Investigaciones sobre la regeneración de selvas altas en Veracruz, Mexico*. Editorial Alhambra, Mexico.
- MARTÍNEZ-RAMOS, M. & ALVAREZ-BUYLLA, E. R. 1986. Seed dispersal, gap dynamics and tree recruitment: the case of *Cecropia obtusifolia* at Los Tuxtlas, Mexico. Pp. 333–346 in Estrada, A. & Fleming, T. F. (eds). *Symposium on frugivores and seed dispersal*. Dr. W. Junk Publishers, Dordrecht, Netherlands.
- NYDAL, R. & LÖVSETH, K. 1970. Prospective decrease in atmospheric radiocarbon. *Journal of Geophysical Research* 75:2271–2278.
- NYDAL, R. & LÖVSETH, K. 1983. Tracing bomb ^{14}C in the atmosphere 1962–1980. *Journal of Geophysical Research* 88:3621–3642.
- PASCARELLA, J. B. & HORVITZ, C. C. 1998. Hurricane disturbance and the population dynamics of a tropical understorey shrub: megamatrix elasticity analysis. *Ecology* 79:547–563.
- SANFORD, R. L., BRAKER, H. E. & HARTSHORN, G. S. 1986. Canopy openings in a primary neotropical lowland forest. *Journal of Tropical Ecology* 2:277–282.
- SAS Institute Inc. 1988. *SAS/STAT™ User's Guide*. Release 6.03 Edition. SAS Institute, Inc. Cary, North Carolina. 1028 pp.
- SOKAL, R. R. & ROHLF, F. J. 1981. *Biometry*. W. H. Freeman & Co. New York. 859 pp.
- SOUTHON, J. R., VOGEL, J. S., TRUMBORE, S. E., DAVIS, J. C., ROBERTS, M. L., CAFFEE, M. W., FINKEL, R. C., PROCTOR, I. D., HEIKKINEN, D. W., BERNO, A. J. & HORNADY, R. S. 1992. Progress in AMS measurements at the LLNL Spectrometer. *Radiocarbon* 34:473–477.
- STERNBERG, L. DA SILVEIRA LOBO, DE NIRO, M. J., MCJUNKIN, D., BERGER, R. & KEELEY, J. E. 1985. Carbon, oxygen and hydrogen isotope abundances in *Stylites* reflect its unique physiology. *Oecologia* 67:598–600.
- TAMERS, M. A. 1969. Radiocarbon dating of recent events. *Atompraxis* 15 Heft 4:1–6.
- TRUMBORE, S. E., DAVIDSON, E. A., DE CAMARGO, P. B., NEPSTAD, D. C. & MARTINELLI, L. A. 1995. Below ground cycling of carbon in forests and pastures of Eastern Amazonia. *Global Biogeochemical Cycles* 9:515–528.

- WEBB, E. L. 1998. Gap-phase regeneration in selectively logged lowland swamp forest, northeastern Costa Rica. *Journal of Tropical Ecology* 14:247–260.
- WELCH R. 1985. Cartographic potential of SPOT image data. *Photogrammetric Engineering and Remote Sensing* 51:1085–1091.
- WORBES, M. & JUNK, W. J. 1989. Dating tropical trees by means of ¹⁴C from bomb test. *Ecology* 70:503–507.

APPENDIX

Since the quantities needed for the complete ANCOVA table (Sokal & Rohlf 1981) can be obtained from SAS (GLM procedures, SAS Institute 1988), but only by combining several SAS procedures and analyses, we provide the details here for the interested reader. Here, we refer to our Table 2 by line number, where only lines containing text, not lines for spacing, are counted, resulting in 11 lines. The sums of squares used to calculate the mean squares in lines 1, 2 and 7 were obtained from an analysis of the effect of data-set group on year (PROC GLM DATA = ALL; CLASS GROUP; MODEL YEAR = GROUP). Line 1 was from the model sum of squares in this model; line 2 was from the error sum of squares in this model; and line 7 was from the corrected total sum of squares. The sums of squares used to calculate the mean squares in lines 3, 4 and 10 were obtained from a regression/covariance model including the group variable as a class variable but without an interaction term (PROC GLM DATA = ALL; CLASS GROUP; MODEL YEAR = CARBON GROUP/SOLUTION; LSMEANS GROUP/STDERR PDIFF). Line 3 was from the sum of squares for the effect of CARBON; line 4 was from the error sum of squares from this model; and line 10 was from the sum of squares for the effect of data-set group. The statistical comparison of the least-squares adjusted means year among the groups of data were given by the last statement in the SAS program. The sum of squares used to calculate the mean squares in lines 5 and 6 were obtained from a regression/covariance model including both the group variable as a class variable and the interaction term (PROC GLM DATA = ALL; CLASS GROUP; MODEL YEAR = CARBON GROUP CARBON * GROUP). Line 5 was the interaction sum of squares in this model and line 6 was the error term in this model. The remaining mean squares were calculated from sums of squares calculated as follows: Line 11's sum of squares was obtained from the sum of line 5's and line 6's sums of squares. Line 9's sum of squares was obtained from the sums of the sums of squares of line 10 and line 11. Line 8's sum of squares was obtained as the difference between the sums of squares of line 7 and line 9.