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Inferred longevity of Amazonian rainforest trees based on a long-term demographic study

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Abstract

We used data from a long-term (14–18 years) demographic study to infer the maximum longevity for populations of 93 relatively abundant tree species in central Amazonia. We also assessed the influence of several life-history features (wood density, growth form, mortality rate, recruitment rate, stem diameter, growth increment, population density) on tree longevity. Data on 3159 individual trees were collected in 24 permanent, 1 ha plots in undisturbed forest arrayed across a large (ca. 1000 km^2) study area. For each species, three estimates of longevity were generated (by dividing the stem diameter of the largest tree by the median, upper quartile, and upper decile of observed diameter-growth rates), and the mean of these three values was used as a longevity estimate. Longevity values ranged from 48 years in the pioneer *Pourouma bicolor* (Cecropiaceae) to 981 years for the canopy tree *Pouteria manaosensis* (Sapotaceae), with an overall mean of 336 ± 196 years. These growth-based estimates of maximum tree age were concordant with those derived from analyses of mean mortality rates. Tree longevity was positively correlated with wood density, maximum stem diameter, and population density, and negatively correlated with annual mortality, recruitment, and growth rates. On average, pioneer species had much lower longevity than did non-pioneers, whereas among old-growth trees, emergent species had greater longevity than did canopy species. Our results are consistent with radiocarbon-based studies that suggest that Amazonian trees can occasionally exceed 1000 years of age.

Keywords: Amazon Basin; Demography; Growth rate; Mortality rate; Tree age; Tree longevity; Tropical forest

1. Introduction

How old are tropical trees? Does the longevity of species vary in predictable ways with their ecological and life-history features? These questions have key implications for understanding the population dynamics and genetic structure of tree populations, for evaluating long-term patterns of forest disturbance, for quantifying rates of carbon cycling, and for developing sustainable forestry practices (Ashton, 1981; Bormann and Berlyn, 1981; Chambers et al., 1998, 2001; Martinez-Ramos and Alvarez-Buylla, 1998).

Unfortunately, accurately estimating the ages of tropical trees is very challenging because, unlike temperate species, growth rings in tropical trees are frequently absent, poorly developed, or highly variable among species, individuals, and sites (Daubenmire,

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1972; Whitmore, 1975; Ashton, 1981). For this reason, investigators have resorted to alternative strategies for estimating tree ages. The most common approaches involve using demographic studies to infer tree age based on growth rates of trunk diameters (e.g. Lieberman and Lieberman, 1987; Lieberman et al., 1985; Korning and Balslev, 1994) or mean rates of tree mortality (e.g. Condit et al., 1995). Radiocarbon dating has also been used to quantify tree ages (e.g. Chambers et al., 1998, 2001) but is expensive, technically difficult, and of limited reliability for younger (<350 years old) trees, and thus is difficult to apply except in small-scale studies (cf. Martinez-Ramos and Alvarez-Buylla, 1998).

Here we use data from a large-scale demographic study spanning an 18-year period in central Amazonia to infer maximum longevity of 93 tree species, based on measured rates of trunk-growth and tree mortality. We also test for associations between longevity and various life-history features (wood density, growth form, mortality rate, recruitment rate, stem diameter, growth increment, population density) of each species. Our analysis provides new data on tree longevity and life history for a large number of relatively abundant tree species in the central Amazon.

2. Methods

2.1. Study area

This study was conducted within the experimentally fragmented landscape of the Biological Dynamics of Forest Fragments Project (BDFFP), which is located about 80 km north of Manaus, Brazil (2°30′S, 60°W). Rainforests in the area are evergreen and *terra-firme* (not seasonally flooded), ranging from 50 to 100 m elevation (Lovejoy et al., 1986). Rainfall varies from 1900 to 3500 mm annually with a pronounced dry season from June to October (Laurance, 2001). The forest canopy is typically 30–37 m tall, with emergents to 55 m. Species richness of trees is very high and can exceed 280 species (≥10 cm dbh) per hectare (de Oliveira and Mori, 1999). About 88% of the tree species in the study area can be classified as rare (<1 stem of ≥10 cm dbh ha^{-1}) and most have patchy distribution patterns (Laurance, 2001).

The dominant soils in the study area are xanthic ferralsols, which are heavily weathered, acidic, and very poor in nutrients such as P, Ca, and K (Chauvel et al., 1987). Similar nutrient-poor soils are prevalent throughout much of the Amazon Basin (Richter and Babbar, 1991). Cation concentrations tend to be higher in more clayey soils, which are prevalent in flatter areas and ridgetops; these areas generally support greater tree biomass than do gullies and slopes, which have higher sand contents and lower cation concentrations (Laurance et al., 1999).

2.2. Plot description and species analyzed

Since 1980, a long-term study of tree-community dynamics, biomass, and composition has been conducted in fragmented and continuous forests in the BDFFP study area (Rankin-de Merona et al., 1990). For this study, data were pooled from twenty four 1 ha plots in undisturbed (unfragmented and unlogged) forest arrayed across an area spanning about 1000 km^2. All plots were located >300 m from the nearest forest-pasture edge to minimize the influence of edge effects on tree communities (cf. Laurance et al., 1997, 1998a,b).

Following an initial, exhaustive census of all trees in the early-mid 1980s, each plot was recensused two to three times at regular (typically 4–7 years) intervals to assess tree mortality, recruitment, and growth, with the final census conducted in mid-1999 (Laurance et al., 1998a,b). The 24 plots were censused for up to 18.2 years, with a mean duration of 14.6 ± 2.4 years. During each census, the diameter at breast height (dbh) of each tree was measured with dbh tapes at 1.3 m height or above any buttresses (to minimize measurement errors, a horizontal line was painted on each trunk at the point of diameter measurement). Species identifications (often by recognized taxonomic experts) were based on sterile or fertile material collected for each tree, with material lodged in the BDFFP reference collection, Manaus, Brazil. About 1260 tree species (≥10 cm dbh) have been identified in the study area to date (Laurance, 2001).

We included in the study all tree species for which both a minimum sample size of 10 individuals (mean sample size = 34.0 ± 40.2 stems) and data on wood density were available. The 93 tree species and 3159 individual trees examined in this study account for

22% of all stems, 27% of the basal area, and 9.5% of all species encountered in the twenty four 1 ha plots. Selected species encompassed a wide range of variation in growth form, stature, and successional status.

2.3. Estimating tree age

For each species, maximum longevity was estimated as follows. First, the mean annual growth rate for each individual tree was estimated by subtracting its initial dbh (from the first census) from its final dbh (from the last census), and dividing this value by the total number of years between the two censuses. Second, three estimates of annual growth rate were generated for each species, based respectively on the median, upper quartile, and upper decile of long-term average values observed in the population. Non-parametric descriptive statistics, rather than parametric values, were used to reduce possible bias from outliers. Third, three separate estimates of tree longevity were generated by dividing the dbh of the largest tree encountered by the median, upper quartile, and upper decile of observed growth rates. Finally, these three values were averaged to derive a single estimate of tree longevity for each species.

Our use of median, upper quartile, and upper decile growth values for estimating the longevity of each species reflects a general concensus that the largest trees in a population likely achieved above-average growth rates during their lifetimes, by encountering better growing conditions and/or by being inherently more vigorous than their conspecifics (e.g. Ashton, 1981; Martinez-Ramos and Alvarez-Buylla, 1998; Chambers et al., 2001). Minimum to median growth rates almost certainly overestimate tree longevity and do not accord closely with independent estimates of tree age (Martinez-Ramos and Alvarez-Buylla, 1998). Our approach does not incorporate age- or size-related changes in tree growth rates, which are averaged out when determining the median, upper quartile, and upper decile growth rates for a number of individuals of each species.

2.4. Life-history features of tree species

We assessed the influence of wood density, stem diameter, growth rate, growth form, mortality rate, recruitment rate, and population density on estimates of tree longevity. Wood-density (wood specific gravity) data were gleaned from a review of wood-density values in Amazonian trees (Fearnside, 1997) and from a survey of >130 publications and graduate theses (W.F. Laurance and S. D'Angelo, unpublished database). When multiple wood-density estimates were available for a particular tree species, the mean of the estimates was used. The growth forms of adult trees (pioneer, subcanopy, canopy, and emergent species) were inferred from our long-term study and from published sources (e.g. Ribeiro et al., 1999). Annualized estimates of tree mortality and recruitment for each species were generated using maximum likelihood methods to find parameters that best fit the observed data from our 24 plots (Nascimento et al., in press). Mean population densities (no. of ≥ 10 cm dbh stems ha^{-1}) and maximum stem diameters (dbh) for each species were also generated using data from the 24 plots.

3. Results

3.1. Tree growth and age

Of the 93 species in the study, 6 were classified as pioneers, 14 as understory trees, 55 as canopy trees, and 18 as emergents. Growth rates varied greatly among species (Table 1), with median values ranging from 0.25 to 6.39 mm per year ($X \pm \text{S.D.} = 1.40 \pm 1.12$ mm per year). As expected, median growth rates varied significantly among trees in different guilds ($F_{3,89} = 9.93$, $P < 0.0001$; one-way ANOVA with log-transformed growth-rate data). On average, subcanopy species had significantly ($P < 0.001$) slower growth than did pioneer, canopy, and emergent species, whereas pioneers had significantly higher growth than canopy species ($P < 0.05$; Tukey's HSD tests). There was no significant difference in absolute growth rates of pioneer and emergent species, although, in relative terms, pioneers (which were much smaller than emergents) grew considerably faster.

For all species, mean estimated longevity was 330 ± 192 years, with a median of 296 years (Table 1). Longevity values were non-normally distributed (Fig. 1). About a quarter of all species were relatively short-lived (<200 years), nearly six-tenths had intermediate longevities (200–500 years), and the remaining 15% were long lived (500–1000 years). The

Table 1
Family, guild, maximum diameter (maximum dbh), diameter growth rates, and maximum longevity data for 93 species of Amazonian trees[a]

Species	Family	Growth form	Maximum dbh (cm)	Growth rates (mm per year)			Estimated age (years)			
				Median	Upper quartile	Upper decile	Median	Upper quartile	Upper decile	Mean age
Anacardium spruceanum	Anacardiaceae	Canopy	69.1	2.61	3.74	9.12	265	185	76	175
Aniba canelilla	Lauraceae	Canopy	37.8	1.31	1.72	2.24	289	220	168	226
Aspidosperma marcgravianum	Apocynaceae	Emergent	99.1	1.08	2.29	3.48	914	432	285	544
Aspidosperma oblongum	Apocynaceae	Emergent	90.4	2.08	3	3.52	435	301	257	331
Astronium le-cointei	Anacardiaceae	Canopy	50.7	1.19	1.42	2.28	426	357	223	335
Bocageopsis multiflora	Annonaceae	Canopy	33.1	1.72	2.34	2.67	192	141	124	152
Brosimum acutifolium	Moraceae	Canopy	58.3	1.25	3.08	4.26	465	189	137	264
Brosimum guianense	Moraceae	Canopy	58.8	0.77	1.42	2.27	759	413	259	477
Brosimum parinarioides	Moraceae	Canopy	60	0.86	1.37	1.9	695	438	315	483
Brosimum rubescens	Moraceae	Canopy	65.2	0.94	1.55	2.73	692	421	239	450
Cariniana micrantha	Lecythidaceae	Emergent	86.2	2.67	4.47	5.62	323	193	153	223
Caryocar glabrum	Caryocariaceae	Canopy	114.8	1.22	2.42	7.01	943	474	164	527
Casearia arborea	Flaccourtiaceae	Canopy	20.1	1.26	3.2	4.09	160	63	49	91
Casearia sylvestris	Flaccourtiaceae	Canopy	25.5	0.78	1.56	2.25	325	164	114	201
Clarisia racemosa	Moraceae	Canopy	83.7	1.56	3.69	4.07	536	227	205	323
Cordia sagotii	Boraginaceae	Subcanopy	26.3	0.48	2.09	2.54	550	126	104	260
Corythophora rimosa	Lecythidaceae	Canopy	50.6	1.65	2.31	2.82	307	219	179	235
Couepia longipendula	Chrysobalanaceae	Canopy	46.6	1.29	1.71	3.13	360	272	149	260
Couma macrocarpa	Apocynaceae	Canopy	51.8	1.95	2.2	2.62	265	236	197	233
Couratari stellata	Lecythidaceae	Emergent	53.5	0.46	1.31	2.54	1158	409	210	592
Dipteryx odorata	Leguminosae	Emergent	78.4	1.66	2.97	3.35	472	264	234	323
Drypetes variabilis	Euphorbiaceae	Subcanopy	31	0.79	1.49	1.99	390	208	156	252
D. cestroides	Duckeodendraceae	Emergent	153.2	0.95	2.64	6	1618	580	255	818
Ecclinusa guianensis	Sapotaceae	Canopy	69.7	0.99	1.82	2.69	701	383	259	448
Endopleura uchi	Humiriaceae	Canopy	57.6	1.81	3.09	3.48	318	186	166	223
Eriotheca globosa	Bombacaceae	Canopy	20.1	0.91	2.02	2.32	220	100	87	135
Eschweilera amazoniciformis	Lecythidaceae	Emergent	56.1	1.05	1.82	2.13	534	309	264	369
Eschweilera coriacea	Lecythidaceae	Canopy	118.8	1.01	1.79	2.62	1182	665	453	767
Eugenia pseudopsidium	Myrtaceae	Subcanopy	19.1	0.53	0.57	1.45	364	335	132	277
Fusaea longifolia	Annonaceae	Subcanopy	26.5	0.38	0.79	1.27	696	335	209	413
Glycydendron amazonicum	Euphorbiaceae	Canopy	44	0.81	1.23	1.74	547	357	253	386
Goupia glabra	Celastraceae	Emergent	106	1.57	3.36	5.21	675	315	203	398
Guatteria olivacea	Annonaceae	Canopy	33.1	4.24	6.94	9.17	78	48	36	54
Gustavia elliptica	Lecythidaceae	Subcanopy	24.7	0.55	0.87	1.41	447	283	175	301
Helicostylis tomentosa	Moraceae	Canopy	44.7	0.82	1.77	3.22	542	253	139	311
Hevea guianensis	Euphorbiaceae	Canopy	45.7	1	1.85	2.85	457	247	161	288
Inga capitata	Leguminosae	Pioneer	26.4	0.91	1.97	4.1	289	134	64	162
Inga paraensis	Leguminosae	Pioneer	40.2	3.23	6.31	8.59	124	64	47	78
I. splendens	Leguminosae	Pioneer	38.2	5.33	7.01	13.46	72	55	28	52
Iryanthera juruensis	Myristicaceae	Subcanopy	26.9	0.29	0.59	0.81	918	458	332	569
Iryanthera laevis	Myristicaceae	Subcanopy	27.2	0.51	0.88	1.9	539	310	143	331
Jacaranda copaia	Bignoniaceae	Pioneer	30.8	0.7	2.13	3.52	442	144	88	225
Lecythis barnebyi	Lecythidaceae	Subcanopy	28.7	0.66	0.73	1.63	437	394	176	336
Lecythis poiteaui	Lecythidaceae	Canopy	34.4	0.26	0.51	1.35	1313	674	255	747
Lecythis zabucajo	Lecythidaceae	Emergent	135.7	1.21	2.66	5.31	1118	510	255	628
Licania apetala	Chrysobalanaceae	Canopy	38.4	1.28	2.01	3.63	299	191	106	199
Licania oblongifolia	Chrysobalanaceae	Canopy	54.2	2.26	2.74	3.6	240	198	151	196
Licania octandra	Chrysobalanaceae	Subcanopy	35	0.73	1.17	1.46	478	299	239	339
Licaria cannella	Lauraceae	Canopy	56.5	1	1.79	2.85	565	315	198	359

Table 1 (*Continued*)

Species	Family	Growth form	Maximum dbh (cm)	Growth rates (mm per year)			Estimated age (years)			
				Median	Upper quartile	Upper decile	Median	Upper quartile	Upper decile	Mean age
Macrolobium angustifolium	Leguminosae	Canopy	40.5	0.94	1.26	1.62	433	321	251	335
M. bidentata	Sapotaceae	Emergent	90.3	0.72	1.32	2.37	1252	686	381	773
Manilkara huberi	Sapotaceae	Emergent	100.6	1.96	3.29	4.39	513	305	229	349
Maquira sclerophylla	Moraceae	Emergent	65	0.83	2.32	3.36	787	280	193	420
Mezilaurus itauba	Lauraceae	Canopy	44	0.44	0.67	1.12	1002	657	393	684
Micropholis guyanensis	Sapotaceae	Canopy	55.5	1.58	2.34	3.57	351	237	155	248
Micropholis venulosa	Sapotaceae	Canopy	61.4	0.79	1.64	1.9	775	375	323	491
Minquartia guianensis	Olacaceae	Emergent	79.9	1.06	1.98	2.59	757	404	309	490
Myrciaria floribunda	Myrtaceae	Subcanopy	29.1	0.39	0.65	1.02	741	445	285	490
Onychopetalum amazonicum	Annonaceae	Canopy	29.9	1.1	1.74	2.13	273	172	140	195
Parkia decussata	Leguminosae	Canopy	66.1	3.54	3.8	4.85	187	174	136	166
Parkia multijuga	Leguminosae	Emergent	119	4	7.11	7.76	298	167	153	206
Peltogyne paniculata	Leguminosae	Canopy	40.8	0.95	2.13	3.08	428	191	132	251
P. bicolor	Cecropiaceae	Pioneer	29.8	4.15	7.17	9.54	72	42	31	48
Pourouma guianensis	Cecropiaceae	Pioneer	31.3	3.77	6.17	8	83	51	39	58
Pouteria ambelaniifolia	Sapotaceae	Canopy	38	0.71	1.79	2.8	538	213	136	296
Pouteria anomala	Sapotaceae	Emergent	77.9	1.1	2	3.03	709	390	257	452
Pouteria caimito	Sapotaceae	Canopy	43.2	1.24	1.9	3	347	228	144	240
Pouteria eugeniifolia	Sapotaceae	Canopy	44.1	0.88	1.42	2.54	502	310	174	329
Pouteria guianensis	Sapotaceae	Canopy	81.8	0.61	1.67	2.54	1350	489	322	720
Pouteria macrophylla	Sapotaceae	Canopy	29.6	0.44	0.92	1.77	674	321	167	387
P. manaosensis	Sapotaceae	Canopy	54.7	0.29	0.95	1.09	1867	575	501	981
Pouteria multiflora	Sapotaceae	Canopy	35.5	0.32	0.95	2.46	1123	373	144	547
Pouteria opposita	Sapotaceae	Canopy	35.8	0.73	1.45	3.93	493	247	91	277
Pouteria venosa	Sapotaceae	Canopy	45.8	0.34	1.1	1.4	1363	416	327	702
Protium altsonii	Burseraceae	Emergent	74.1	1.96	3.64	5.6	378	204	132	238
Protium decandrum	Burseraceae	Canopy	32.8	1.35	2.38	3.54	244	138	93	158
Protium heptaphyllum	Burseraceae	Canopy	26.2	1.98	2.21	7.17	133	118	37	96
Protium tenuifolium	Burseraceae	Canopy	38.2	1.66	2.49	3	230	153	127	170
Ptychopetalum olacoides	Olacaceae	Subcanopy	24.1	1.21	2.61	4.02	200	93	60	117
Qualea paraensis	Vochysiaceae	Emergent	75.7	1.11	2.49	5.08	685	304	149	379
Scleronema micranthum	Bombacaceae	Emergent	93.9	1.76	2.96	4.57	535	317	205	353
Sloanea guianensis	Elaeocarpaceae	Subcanopy	28.5	0.89	2.23	3.17	319	128	90	179
Swartzia corrugata	Leguminosae	Subcanopy	21.1	0.25	0.86	1.5	837	244	140	407
Swartzia recurva	Leguminosae	Canopy	38.4	1.54	2.49	3.03	250	154	127	177
Swartzia ulei	Leguminosae	Canopy	50.9	1.34	1.96	2.13	381	259	239	293
Tachigali paniculata	Leguminosae	Canopy	27.7	1.99	3.81	4.52	139	73	61	91
Tapirira guianensis	Anacardiaceae	Canopy	41.6	6.39	7.81	9.42	65	53	44	54
Tetragastris panamensis	Burseraceae	Canopy	38.4	0.85	1.28	1.84	451	300	208	320
Vantanea parviflora	Humiriaceae	Canopy	69.6	2.26	3.87	5.46	308	180	128	205
Virola calophylla	Myristicaceae	Subcanopy	30.8	0.62	1.33	2.03	494	232	152	293
Virola multinervia	Myristicaceae	Canopy	32	0.47	1.18	1.83	675	270	175	373
Virola sebifera	Myristicaceae	Canopy	30.2	1.48	2.12	2.23	204	142	135	161
Vochysia obidensis	Vochysiaceae	Canopy	47.4	3.73	5.92	7.01	127	80	68	92

[a] Data are based on sample sizes of 10–279 individuals per species.

species with the oldest individual was *Pouteria manaosensis* (Sapotaceae), at 981 years, followed by *Duckeodendron cestroides* (Duckeodendraceae) at 818 years and *Manilkara bidentata* (Sapotaceae) at 773 years. The species with the shortest longevities were the pioneers *Pourouma bicolor* (Cecropiaceae) at

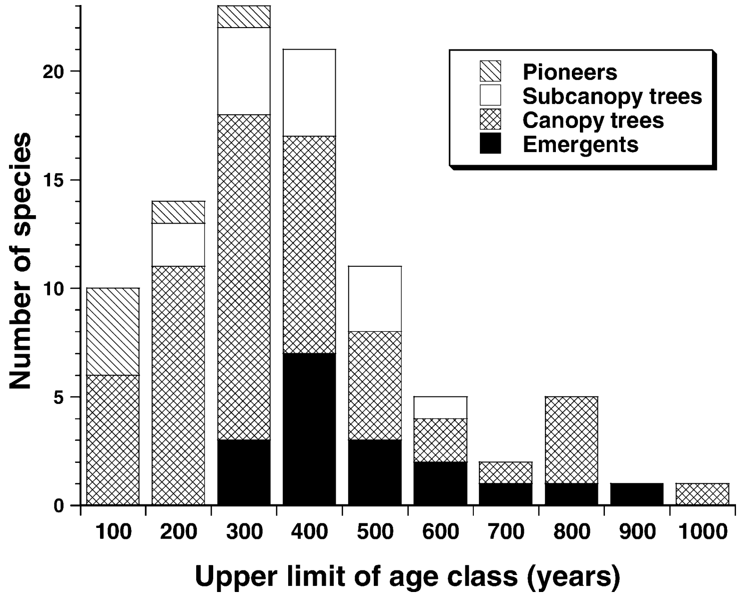

Fig. 1. Histogram of estimated maximum longevities for 93 species of central Amazonian trees.

48 years, and *Inga splendens* (Leguminosae) at 51 years (Table 1).

3.2. Life-history correlates of tree age

Tree longevity varied significantly among tree guilds ($F_{3,89} = 11.32, P < 0.0001$; one-way ANOVA with log-transformed longevity data). As expected, pioneer trees had significantly ($P < 0.001$) lower longevity (104 ± 73 years) than did subcanopy (326 ± 118 years), canopy (320 ± 200 years), and emergent (438 ± 175 years) species. In addition, emergent trees had significantly ($P < 0.05$) greater longevity than did canopy species (Tukey's HSD tests).

Tree size (maximum dbh) was positively correlated with tree age (Fig. 2), as expected, but size accounted for only a fifth of the total variation in tree age ($F_{1,91} = 22.23, P < 0.0001, R^2 = 19.6\%$; linear regression analysis with log-transformed dbh data). The relationship between tree age and the composite growth rate (the combined average of the median, upper quartile, and upper decile rates) was somewhat stronger (Fig. 3), explaining a third of the total variation among species ($F_{1,91} = 44.34, P < 0.0001, R^2 = 32.8\%$; linear regression with log-transformed growth data). Thus, the largest trees in the forest were not necessarily the oldest, and the growth rate of each species was a better correlate of tree longevity.

Wood density was positively correlated with tree age (Fig. 4), as expected ($F_{1,91} = 13.47, P = 0.0004, R^2 = 12.9\%$; linear regression), but explained only an eighth of the total variation in longevity. As anticipated, mortality and recruitment rates were both negatively correlated with tree longevity, with mortality accounting for a somewhat greater amount of variation ($F_{1,91} = 19.01, P < 0.0001, R^2 = 17.3\%$) than did recruitment ($F_{1,91} = 13.31, P = 0.0004, R^2 = 12.8\%$; linear regressions with log-transformed mortality or recruitment data).

Tree population density was weakly and positively correlated with longevity ($F_{1,91} = 8.45, P = 0.0046, R^2 = 8.5\%$; linear regression with log-transformed density data), suggesting that more-abundant species tended to have greater longevities than did rarer species. However, this pattern was probably a statistical artifact. Other factors being equal, very large (and therefore generally older) trees are more likely to be present in large than in small populations, as demonstrated by a positive relationship between tree density and maximum tree size ($F_{1,91} = 10.99, P = 0.0013, R^2 = 10.8\%$; linear regression with log-transformed data for both axes) for our 93 species. When effects of

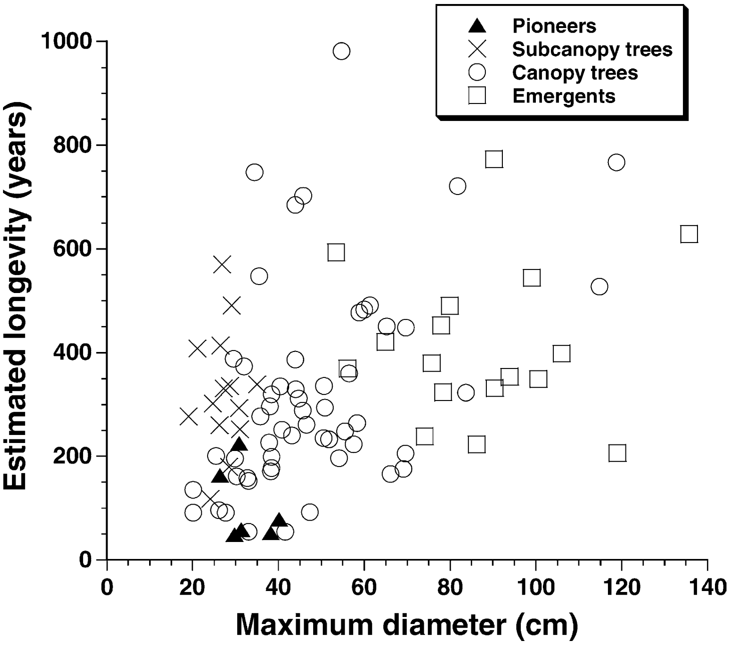

Fig. 2. Relationship between tree size (maximum diameter at breast height) and estimated longevity in 93 Amazonian tree species.

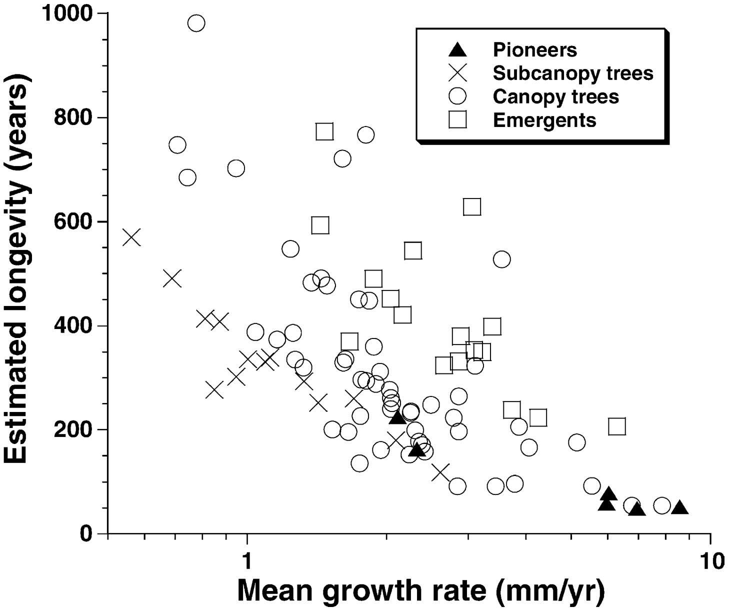

Fig. 3. Relationship between growth rate (the average of the median, upper quartile, and upper decile of observed growth rates in the population) and estimated longevity in 93 Amazonian tree species.

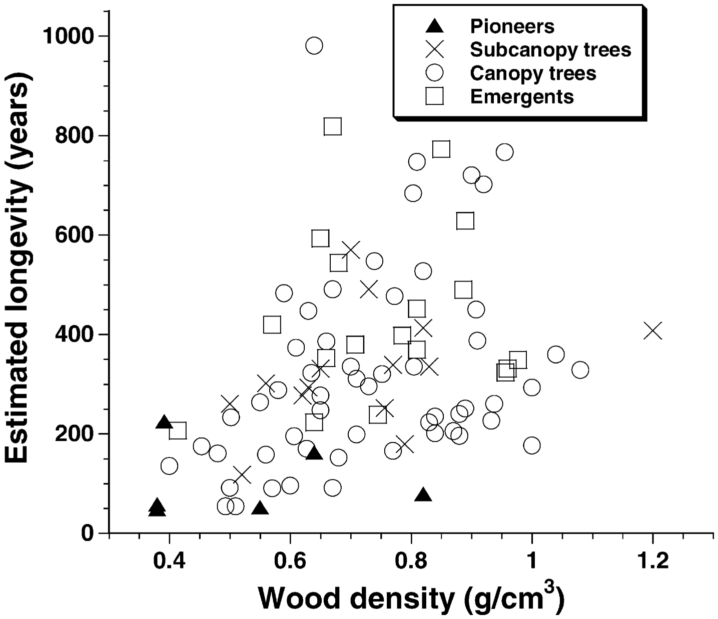

Fig. 4. Relationship between wood density and estimated longevity in 93 Amazonian tree species.

variation in tree diameter were removed with a partial correlation analysis, there was no significant relationship between tree population density and longevity ($r = 0.173$, d.f. $= 91$, $P = 0.10$). However, when effects of population density were removed statistically, the relationship between tree diameter and age was still highly significant ($r = 0.385$, d.f. $= 91$, $P = 0.0002$; partial correlations with log-transformed dbh and density data).

3.3. Estimating longevity using mortality rates

Our longevity estimates based on long-term growth rates suggest that the oldest individual in our sample of 3159 trees was approximately 981 years old. We can provide an independent test of tree longevity by using long-term data on tree mortality. Over the course of our 18-year study, the mean annualized rate of mortality (the net average of mortality rates for all species, weighted by the abundance of each species) for the 93 species in our 24 plots was 0.86% per year. Beginning with a cohort of 3159 trees and applying a negative exponential model that assumes constant mortality over time (where maximum longevity = ln (cohort size)/mortality rate; Martinez-Ramos and Alvarez-Buylla, 1998), we would expect the oldest tree in the sample to persist for 937 years. This analysis is generally concordant with our inferences based on growth rates, in that both predict that the oldest tree in our sample should range from 900 to 1000 years old.

Mortality data can also be used to predict the density of very old trees in our forests. When all tree species are included, the long-term average rate of tree mortality in our study plots is $1.23 \pm 0.45\%$ per year (W.F. Laurance, unpublished data). Assuming a constant mortality rate over time and a mean density of 610 trees per hectare ($\geq$10 cm dbh), the negative exponential model predicts that 1000-year-old trees should occur at a mean density of one per 358 ha (0.0005% of all trees) and 1200-year-old trees at a mean density of one per 4184 ha (0.00004% of all trees). However, 500-year-old trees should be relatively common, with a mean density of 1.3 trees per hectare (0.2% of all trees).

4. Discussion

4.1. Assumptions of the analysis

Our use of growth-rate data for inferring tree age relies on two important assumptions. The first is that growth conditions during our 18-year study were typical of those experienced by trees over much longer time intervals. Clearly, rates of tree growth can vary markedly among years (Clark and Clark, 1992, 1994) and during the lifetime of a tree (Clark and Clark, 1999; da Silva et al., 2002), but the expectation is that, at least during a relatively long-term study like ours, mean growth rates reasonably approximate those over the long term.

It is important to ask, however, whether weather conditions during our study were typical. In fact, El Niño-Southern Oscillation (ENSO) events have evidently increased in frequency this century (Trenberth and Hoar, 1996; Dunbar, 2000) and such events promote droughts or rainfall deficits in the central Amazon (Marengo and Hastenrath, 1993; Williamson et al., 2000). Strong droughts occurred in 1982/1983 and 1997/1998, with a weaker drought in 1992/1993 (Laurance et al., 2001). If these droughts reduced tree growth, then our estimates of mean growth rates might be somewhat too low, thereby inflating our estimates of tree age. At most, however, growth rates are likely to have been depressed for only 2–3 years of our 18-year study, and ENSO events have been a feature of Amazonian forests for millennia (Meggers, 1994). Moreover, the relationship between rainfall and tree growth is complex; in very wet forests in Costa Rica, for example, dry years tend to produce above-average growth of canopy trees, possibly because available photosynthetically active radiation increases during years with less cloud cover (Clark and Clark, 1994).

The second assumption is that our composite estimate of tree growth (the average of the median, upper quartile, and upper decile of observed measurements for each species) reasonably reflects the long-term growth trajectories of the oldest individuals of each species. We believe our method is reasonable because it is based on a relatively large sample (10–279 trees) for each species and assumes that the largest individuals of each species achieved above-average growth during their lifetimes, a conservative but probably realistic assumption (Martinez-Ramos and Alvarez-Buylla, 1998).

For six tree species, we can compare our composite estimates of annual growth with those derived from an independent study. Chambers et al. (1998, 2001) used radiocarbon dating to estimate the age of the largest (and therefore among the oldest) trees from a 4000 ha logging operation located about 250 km southeast of our study area, in an area with similar elevation, topography, soils, rainfall, and forest type. They dated 44 trees of 15 species, of which six were among the species that we studied. Radiocarbon dating can have large errors (roughly ±100–150 years) for trees less than 350 years old (Chambers et al., 2001), but five of the six species had mean ages of 350–900 years. Estimates of mean growth rate were determined for each tree by dividing its diameter by its inferred age (Chambers et al., 2001). Each species was represented by one to six individuals, and we averaged the growth-rate data for each species.

A comparison of our growth-rate data with those from Chambers et al. (2001) demonstrates reasonable concordance in the two estimates (Fig. 5). The two sets of values were positively correlated ($r = 0.54$) and the overall mean value for all six species was very close in the two studies (2.74 mm per year from Chambers et al. versus 2.63 mm per year in our study). Thus, at least for six tree species, our growth-rate estimates were in relatively good agreement with those from an independent study based on radiocarbon dating.

Finally, among the 93 species we studied, there was close agreement between the estimated age of the oldest tree based on mortality and growth data (937 versus 981 years). The mortality-based estimate required an assumption that mortality rates during our study were typical of much longer intervals. The validity of this assumption is uncertain given that ENSO droughts appear to have increased in frequency. However, because such droughts increase tree mortality (Williamson et al., 2000), more frequent droughts would reduce our estimates of tree age and are therefore a conservative bias.

4.2. *Tree longevity and environmental conditions*

Our findings appear to be consistent with the notion that central Amazonia supports ancient (>1000 years old) trees (cf. Chambers et al., 1998, 2001), although such individuals probably comprise only a tiny fraction of all trees in the forest. At least for the populations of trees within our study plots, many species appear to have moderate longevities (200–500 years), with about 15% of all species attaining maximum ages of 500–1000 years. Analyses of mortality data suggest that even older trees are likely present but at low

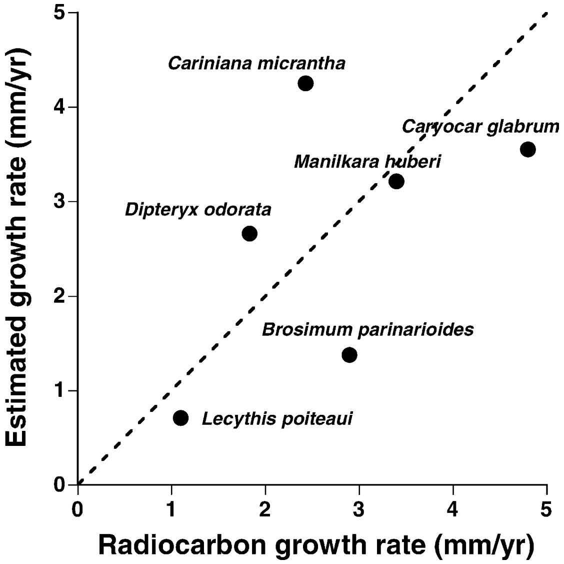

Fig. 5. Comparison of estimated growth rates for six Amazonian tree species based on radiocarbon dating (from Chambers et al. (1998, 2001)) and this study. Composite growth rates used in this study were the average of estimates based on the median, upper quartile, and upper decile of observed, long-term growth rates for each species. The dashed line shows $y = x$.

densities; for example, our findings suggest that 1000-year-old trees should occur at a density of about one per 360 ha, which is somewhat lower than that predicted by a simulation of mortality and growth data (one per 40 ha) in a subset of our study plots (Chambers, 1998) and from a simple analysis of stem diameters (one per 90 ha) at a nearby logging site (Williamson et al., 1999). However, because our longevity estimates were based on studies of a limited expanse (twenty four 1 ha plots) of forest, they should be regarded as typical values for local populations, not the absolute maximum longevity for any species as a whole. Clearly, had we sampled an area 10 times as large, we would have encountered larger individuals of most species, which would have increased their estimated longevities.

Central Amazonian forests have environmental features that may promote tree longevity. Natural forests in our study area exhibit rather low dynamism, with turnover rates of trees (the average of annualized mortality and recruitment rates for $\geq$10 cm dbh stems) averaging just $1.20 \pm 0.37\%$ per year (Laurance, 2001), compared to $1.66 \pm 0.46\%$ per year for other non-flooded neotropical forests (Phillips and Gentry, 1994). One factor that may promote low dynamism is the acidic, heavily weathered soils of the region (Chauvel et al., 1987; Richter and Babbar, 1991). Under such nutrient-poor conditions, the growth rates of trees, and hence the intensity of competition for light among individuals, are likely to be reduced (Leigh, 1999), and this may reduce tree mortality. Large-scale disturbances are also rare. Downbursts from convectional thunderstorms can cause intense local disturbances, but these events are uncommon, affecting only a tiny fraction of the basin (<0.05%) each year (Nelson, 1994; Nelson et al., 1994). Charcoal fragments are common in soils of the study area, indicating past fires (Bassini and Becker, 1990), but there is no evidence of agriculture, and the vicinity of our study area appears to have been continuously forested for at least 4500 years (Piperno and Becker, 1996). Finally, lightning strikes (Magnusson et al., 1996) and pools created by wet-season rains (Mori and Becker, 1991) kill some trees, but these affect only a small area of the forest each year.

4.3. Tree longevity and its life-history correlates

Our results suggest that maximum longevities vary greatly among different Amazonian tree species, ranging from roughly 50 to 1000 years in the 93 species we examined. These patterns were partly based on life-history differences among tree guilds. On average, for example, pioneer species exhibited rapid growth and short longevity, subcanopy species had slow growth and high longevity, and canopy and emergent species had moderate to high growth and generally high longevity. These among-guild differences accord well with patterns observed in western Amazonian (Korning and Balslev, 1994), Central American (Lieberman and Lieberman, 1987; Condit et al., 1996), and Southeast Asian forests (Thomas, 1996). For example, subcanopy trees evidently grow much more slowly than pioneer, canopy, and emergent species because they have less available sunlight beneath the forest canopy; slow growth is also associated with high wood density, which may help subcanopy trees to withstand recurring physical damage from litterfall and pathogen attack in the humid understory (Thomas, 1996). Despite such clear differences among guilds, considerable variation in growth and longevity was evident among species within the same guild (cf. Clark and Clark, 1992) and also among individuals of the same species (cf. da Silva et al., 2002).

Among our 93 species, tree size was a relatively weak correlate of tree age, explaining less than a fifth of the total variation in age (Fig. 2). Similarly, Chambers et al. (1998, 2001) found that tree size explained only a quarter of the total variation in tree age. Growth rates were generally a better correlate of tree age, explaining about a third of the total variation (Fig. 3) in our analysis. Thus, the largest trees in a forest are not necessarily the oldest, and some slow-growing, moderate-sized trees can attain very impressive ages.

As expected, wood density was positively associated with tree longevity (Fig. 4). Wood density is strongly correlated with most measures of wood strength (Panshin and DeZeeuw, 1970; Williamson, 1975) and is inversely related to tree growth rate, mortality rate, trunk snapping (Putz et al., 1983), seral status (Richards, 1952; Budowski, 1965; Lawton, 1984), elevation (Williamson, 1975), and windiness of the environment (Lawton, 1984). In general, high wood density may characterize long-lived species as a consequence of their instrinsically slow growth (as occurs in most subcanopy trees), although some long-lived canopy and emergent trees may attain high growth rates when they reach the full sunlight of the forest canopy, where they begin to produce lower-density wood (Thomas, 1996). Such complexities in the life histories of tropical trees may help to explain why wood density accounted for only a sixth of the total variation in tree longevity.

4.4. Summary

Based on relatively conservative assumptions, results from our large-scale, long-term demographic study support the notion that central Amazonia harbors ancient trees. Most (85%) tree species in our study area appear to attain maximum longevities of less than 500 years, with the remainder occasionally living to 500–1000 years or even longer. Our estimated longevities for trees are generally higher than those from comparable studies in Central America (Lieberman and Lieberman, 1987; but see the mortality-based extrapolations of Condit et al. (1995)) and western Amazonia (Korning and Balslev, 1994), and may reflect the poor soils, low dynamism, and infrequent large-scale disturbances in central Amazonian forests. Estimates of tree longevity from long-term demographic studies are relatively sensitive to growth-rate values, and improvement of these data (by increasing the duration, number, and quality of demographic studies, and by comparing plot-based and radiocarbon studies) will help to improve assessments of tree longevity.

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