

Abundance, growth and mortality of very large trees in neotropical lowland rain forest

David B. Clark^{*}, Deborah A. Clark

Department of Biology, University of Missouri-St. Louis, St. Louis, MO 63121-4499, USA

Accepted 15 June 1995

Abstract

Very large trees, arbitrarily defined as those over 70 cm diameter above buttresses, account for a major portion of the above-ground biomass in neotropical rain forests. Owing to the scarcity of individuals of a given species and the difficulty of accurate measurement, there are few species-level data on the growth, mortality, and abundance of species that regularly reach emergent status. We report such data for very large individuals from old-growth tropical wet forest at the La Selva Biological Station in the Atlantic lowlands of the Republic of Costa Rica. The landscape-scale abundance of all species reaching over 70 cm diameter was assessed using 515 0.01-ha quadrats located at grid points in a 500 ha area of old-growth forest. In the total sample of 2301 stems 10 cm or more in diameter, very large individuals accounted for 2% of the stems, 23% of the basal area, and 27% of the estimated above-ground biomass. Growth and survival for five species that regularly attain emergent status were measured in a 150 ha area within the 500 ha plot. Survival of 282 very large individuals of the five species was measured over 6 years. The mean annual mortality rate of the total sample was only 0.6% year⁻¹. Mean annual diameter growth increments varied from 1.9 to 5.2 mm year⁻¹ among species, and were negatively correlated with diameter in four of the five species. For a sample of 193 individuals measured over 7 years, growth almost exactly equalled losses in basal area and biomass due to mortality. Because all of these species are regularly recruiting new trees into the over 70 cm diameter class, the amount of biomass in the large-individual size class is increasing over the 150 ha old-growth study area. Historic disturbance and/or current climatic change are hypothesized to account for the increase. We identify lack of standard diameter measurement criteria, and small and potentially unrepresentative plot locations as two problems in assessing the role of very large trees in other neotropical forests. Future studies should sample larger areas; this will increase the generality of the conclusions and will make possible a species-level comparison of the ecology of very large tropical trees.

Keywords: Emergent; Carbon storage; Tropical tree demography

1. Introduction

The largest organisms in any forest are the big trees. This is particularly true in forests where occa-

sional emergents tower over the surrounding canopy-level trees. These massive individuals are much more important ecologically than their density suggests. For example, in tropical wet forest the biomass of one tree 150 cm in diameter equals that of approximately 607 trees 10 cm in diameter (calculated from Brown and Iverson, 1992). If very large trees are still growing at only modest diameter

^{*} Corresponding author at: La Selva Biological Station, INTERLINK-341, P.O. Box 02-5635, Miami, FL 33152, USA.

increments, volume and biomass increments can be substantial. In addition to the carbon stored in living trees, the enormous trunks of fallen emergents can act as important sinks for carbon for decades to centuries after a tree falls (Harmon and Hua, 1991).

Very large trees can also play a key role in forest disturbance regimes. Treefall gap size is generally correlated with the size of the gap-making tree (cf. Tyrrell and Crow, 1994). In forests where the disturbance regime is driven primarily by tree-falls, deaths of emergents may cause the largest disturbances. The longevity of large individuals also increases their potential to generate small-scale heterogeneity in microclimate or soil (cf. Rhoades et al., 1994). If very large trees live substantially longer than their canopy level neighbors, they may create special microenvironments around them due not only to their massive size, but also to greater persistence through time. Growth and death rates of very large trees therefore can affect major ecosystem attributes such as net rate of carbon storage (Lugo and Brown, 1992; Brown, 1995) and the frequency of large endogenous disturbances.

Very large trees are also ecophysiologically unique. Lacking the shelter of neighboring canopy-level crowns, emergents are exposed to the hottest and most evaporative canopy environments. In this exposed and potentially stressed position, very large trees are likely to be more tightly coupled to weather and climate conditions than smaller individuals. For these reasons, one might expect the first effects of changing global climate on canopy tree crowns to be expressed in emergent individuals.

In spite of the inherent interest in very large trees, there are few species-level data on their ecology. This is particularly true for tropical rain forests, where the absolute density of very large trees is low and the total diversity of canopy tree species is extremely high. The number of tree species per hectare in these forests commonly exceeds 100 and can pass 300 (Gentry, 1990; Gentry and Ortiz, 1993), and for individuals 10 cm or more in diameter, most species are represented by less than one individual ha^{-1} . Even plots of substantial area will seldom contain enough very large individuals of a given species to produce a statistically useful sample.

A further reason for the lack of good data on very large tropical trees is the difficulty of obtaining good

measurements. Buttresses reaching 10 m or higher are common, necessitating the use of multiple sections of ladder to measure diameter above buttresses. The upward growth of buttresses frequently renders old points of measurement unusable in studies with long remeasurement intervals. The frequent occurrence of large lianas and hemiepiphytes further hinders accurate measurements.

In this paper we report data on the growth, mortality and landscape-scale abundance of very large trees in a neotropical lowland rain forest. We also contrast the growth and mortality of very large trees to that of smaller trees in the same forest. Finally, we compare our results with data from other tropical sites, and discuss what we consider to be the major outstanding questions in the ecology of very large tropical trees.

To study very large trees one must first make a subjective decision as to 'How large is very large?'. The size of the largest 1–2% of the trees in any forest varies with many factors, including soil, slope, altitude, latitude, disturbance history, and biogeography. For purely practical reasons based on ease of measurement (see Methods) we used a cutoff of 70 cm diameter. Subsequently we discovered that other researchers had also used the same limits (Lugo and Brown, 1992; White, 1994; Brown, 1995) or stratified their data by tree size such that the over 70 cm size class could be analyzed (Gentry and Terborgh, 1990; Rankin-de-Marona et al., 1990). For the species described here most of the individuals over 70 cm in diameter have emergent crowns (Clark and Clark, 1992). We realize that any division point is at least partially arbitrary. However, based on practicality of measurement, facility of data comparison, relative abundance and crown position we believe that 70 cm diameter criterion is a useful division point for neotropical wet or moist forest data.

2. Study site

The study was carried out at the La Selva Biological Station in the Atlantic lowlands of the Republic of Costa Rica. A detailed description of the site is given in McDade et al. (1994). The old-growth forest is classified as Tropical Wet Forest in the Holdridge system (Hartshorn and Peralta, 1988). Rainfall aver-

ages about 4000 mm annually, and no month averages less than 100 mm (Sanford et al., 1994).

3. Methods

The trees measured for growth and survival are part of a long-term ongoing study of tree demography in a 150 ha area of non-swamp old-growth tropical rain forest. Here we report data on the five species (Table 1) in the long-term study which regularly reach emergent status. A full description of the protocols for sampling and annual measurement is given in Clark and Clark (1992). The first individuals in the long-term study were measured in 1983, and new individuals have been added annually according to a standard set of protocols (described in Clark and Clark, 1992). We used all individuals over 70 cm diameter above buttresses at first census to calculate annual mortality (m , Sheil et al., 1995) over a 6 year period for trees that entered the study in 1983, as well as for the subsequent cohorts added each year through 1988. Hence, mortality for the 1983 individuals was assessed over the period 1983–1989, and the 6 year measurement period was shifted one year for the cohorts added in successive years up through 1988. Data from all six 6-year periods were combined for each species. To compare death rates between large and small size classes of the same species, we also calculated 6-year mortality rates using the same methods for all trees 10–70 cm in diameter at first encounter.

In this study almost all trees 70 cm or less in diameter above buttresses were measured annually for diameter growth; only individuals with strongly appressed large lianas, or with major trunk damage

or irregularities to over 7 m height are excluded. Trees over 70 cm in diameter are measured annually only if a cylindrical site of measurement is present within about 7 m of the ground (i.e. reachable from two joined 3-m sections of tree climbing ladders). In 1986 we used up to four sections of ladder to reach a cylindrical measurement site on all trees over 70 cm diameter above buttresses that were not being measured annually. A synthetic fabric wire-reinforced diameter tape (Forestry Suppliers Model 283D) was used to measure diameter to an accuracy of ± 1 mm at a measured 10 cm below a permanent aluminum marker nail. In order to safely work at these heights, the field technicians wore climbing harnesses connected to the ladders with carabiners; the ladders themselves were secured to the trees using chains and carabiners. In 1993 the 106 surviving individuals from this sample were remeasured using the same techniques. Growth data presented here combine these once-remeasured individuals as well as all annually-measured trees over 70 cm in diameter above buttresses ($N = 79$). These very large individuals (both the annually remeasured and once-remeasured) are distributed over the entire 150 ha area of the long-term demographic study. To estimate measurement accuracy, in 1993 we remeasured 20 individuals of the once-remeasured sample a few days after first measurement; the mean absolute difference between measurements was 1.85 mm, and 90% were within ± 2 mm.

To evaluate the landscape-scale abundance of very large trees, we used data from an on-going project in which we are mapping the distributions and measuring the basal area of all species of trees 10 cm or over in diameter in a 500 ha area of old-growth tropical wet forest at La Selva (D.B. Clark and D.A.

Table 1

Above-buttress bole diameter of individuals over 70 cm in diameter whose growth was measured from 1986 to 1993 at the La Selva Biological Station, Costa Rica

Species (Family)	Diameter (cm)		Sample size
	Median	Range	
<i>Dipteryx panamensis</i> (Pittier) Record and Mell (Papilionaceae)	98.8	70.8–175.4	60
<i>Hymenolobium mesoamericanum</i> Lima (Papilionaceae)	100.9	70.2–130.7	12
<i>Hyeronima alchorneoides</i> Allemão (Euphorbiaceae)	91.3	71.2–153.0	36
<i>Lecythis ampla</i> Miers (Lecythidaceae)	91.1	72.4–123.4	27
<i>Pithecellobium elegans</i> Ducke (Mimosaceae)	85.9	70.3–130.2	50
Total sample	91.1	70.2–175.4	185

Clark, unpublished data, 1993/1994). The 500 ha area includes the entire 150 ha area of the long-term demographic work. Circular 0.01 ha plots were measured at grid posts of La Selva's permanent 50 m × 100 m grid. The basal area data reported here come from 515 0.01-ha plots (all those completed by January 1995). These plots span the range of topography and soils gradients in this forest (Sollins et al., 1994), including inceptisols of relatively fertile old alluvial terraces, seasonally flooded swamps, and ridge and valley topography with relatively infertile ultisols. Above-ground biomass (AGBM) was calculated following Brown and Iverson (1992) as

$$\text{AGBM} = 21.297 - 6.953(\text{Diameter}) \\ + 0.740(\text{Diameter}^2)$$

where AGBM is measured in kilograms per individual and diameter in centimeters.

4. Results

4.1. Landscape—abundance of very large trees

The 515 0.01-ha quadrats included a total of 2301 trees over 10 cm in diameter. Of the total sample, individuals of any species over 70 cm in diameter ($N = 46$) accounted for only 2% of the stems and occurred at an average density of 8.9 individuals ha^{-1} . Even at this density, very large trees accounted for 22.7% of the total basal area and 27.2% of the above-ground biomass of this forest landscape.

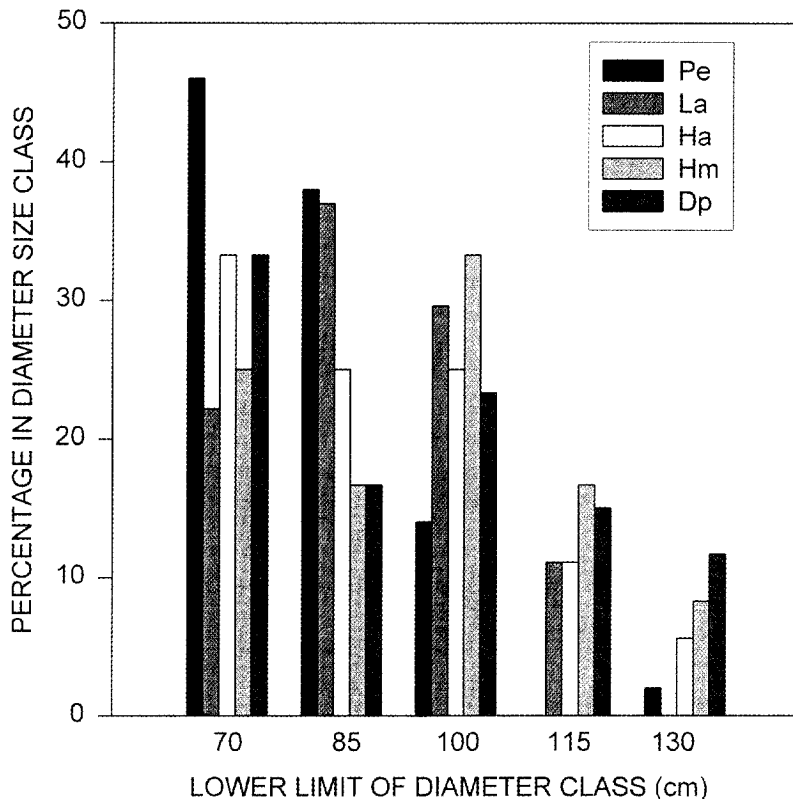


Fig. 1. Diameter distribution of very large trees (over 70 cm in diameter above buttresses) measured for diameter growth from 1986 to 1993. Pe, *Pithecellobium elegans*; La, *Lecythis ampla*; Ha, *Hyeronima alchorneoides*; Hm, *Hymenolobium mesoamericanum*; Dp, *Dipteryx panamensis*. Sample sizes are given in Table 1.

Table 2

Average annual growth (1986–1993) in diameter and basal area for individuals over 70 cm in diameter of five species of very large trees at La Selva, Costa Rica. Species names and sample sizes are given in Table 1. Values followed by the same letters are not statistically different in a Kruskal–Wallis a posteriori comparison of mean ranks (experiment-wise rejection rate 0.05)

	Annual diameter growth (mm)			Annual basal area growth (cm ²)		
	Mean	CV	Range	Mean	CV	Range
<i>Dipteryx</i>	1.9a	105	–3.0–6.6	27a	113	–81–116
<i>Lecythis</i>	2.6a	97	–0.9–11.2	39a	92	–16–134
<i>Hyeronima</i>	3.6a	104	–1.0–16.8	49a,b	89	–12–203
<i>Hymenolobium</i>	5.2a,b	106	–0.4–15.9	73a,b	91	–73–193
<i>Pithecellobium</i>	5.2b	58	0.0–11.6	74b	61	0–182

4.2. Size and growth

All of the five emergent species under long-term demographic study regularly attain diameters exceeding 1 m (Fig. 1). The frequency distributions of stem diameters indicate ongoing recruitment to the over

70 cm diameter class for all five species. In addition, the diameter distributions of very large *Pithecellobium*, *Lecythis*, and *Hyeronima* were unimodal, suggesting that the landscape-scale recruitment of these species has been fairly continuous over a long time period. The size distributions of *Dipteryx* and *Hymenolobium* were bimodal, suggesting that in addition to recent recruitment these species may have experienced higher recruitment at some period in the past.

All species had substantial diameter and basal area growth rates as very large individuals (Table 2). Both diameter growth and basal area growth as large individuals differed among species by a factor of approximately 3 (Kruskal–Wallis test, $P < 0.0001$ in both cases). Rates of diameter growth and basal area addition tended to decrease with increasing diameter (Table 3) except in *Pithecellobium*, which had the overall largest and least variable growth rates (Table 2).

Table 3

Spearman's correlations between diameter of very large trees (over 70 cm in diameter) in 1986 and annual diameter growth or basal area growth from 1986 to 1993. Sample sizes as in Table 1

	Correlation between initial diameter and	
	Annual diameter growth	Annual basal area gain
<i>Dipteryx</i>	–0.40 **	–0.23
<i>Hyeronima</i>	–0.59 **	–0.38 *
<i>Hymenolobium</i>	–0.69 *	–0.68 *
<i>Lecythis</i>	–0.22	–0.12
<i>Pithecellobium</i>	–0.06	0.15

* $P < 0.05$; ** $P < 0.01$.

Table 4

Mortality over 6 years for five species of emergent trees at La Selva Biological Station, Costa Rica. Data cover the 6 years after individuals were first measured (first measurement periods beginning from 1983 to 1988, see Methods). Annual mortality (m) was calculated as $m = 1 - (N_1/N_0)^{1/6}$ (Sheil et al., 1995)

Species	Initial diameter > 70 cm			Initial diameter 10–70 cm		
	N^0	N^{d6yr}	%MORT	N^0	N^{d6yr}	%MORT
<i>Dipteryx</i>	91	2	0.4	59	0	0.0
<i>Hyeronima</i>	53	1	0.3	63	2	0.5
<i>Hymenolobium</i>	16	2	2.2	42	0	0.0
<i>Lecythis</i>	43	1	0.4	54	0	0.0
<i>Pithecellobium</i>	79	4	0.9	140	5	0.6
Total	282	10	0.6	358	7	0.3

N^0 , number at time 0; N^{d6yr} , number that died in the 6 year interval; %MORT, annual mortality rate (%year).

4.3. Mortality and biomass turnover

Annual death rates of very large individuals in the five study species were very low, averaging only 0.6% year⁻¹ (Table 4). Because only ten of 282 individuals of all species died over their first 6 year of measurement, it was not possible to test for interspecific differences in mortality. At the mean mortality rate for the combined sample, the half-life of individuals in the over 70 cm diameter class is 115 years. Of the ten dead trees, six died standing, three were uprooted, and one was snapped off. In these five species, death rates for individuals 10–70 cm in diameter were also very low. The annual death rate for the combined sample of trees 10–70 cm was 0.3% year⁻¹, and was not different from the 0.6% rate of individuals over 70 cm in diameter ($\chi^2 =$

Table 5

Changes over 7 years in basal area and biomass in a sample of five species (Table 1) of trees over 70 cm in diameter in 1986

	Basal area (m ²)	Biomass ^a (kg)
Total in 1986 (<i>N</i> = 193)	145.9	1249398
Added by growth	+ 6.2	+ 55167
Lost by death	- 7.1	- 60884
Total in 1993 (<i>N</i> = 185)	145.0	1243681
λ^b (% year ⁻¹)	- 0.09	- 0.07

^a Calculated from basal area following Brown and Iverson (1992).

^b Exponential rate of change over the 7 year interval.

1.54, 1 d.f., $P > 0.20$). Table 5 shows the rate of change of basal area and biomass for the sample of very large individuals measured for growth. Although eight of 193 individuals in the sample died in

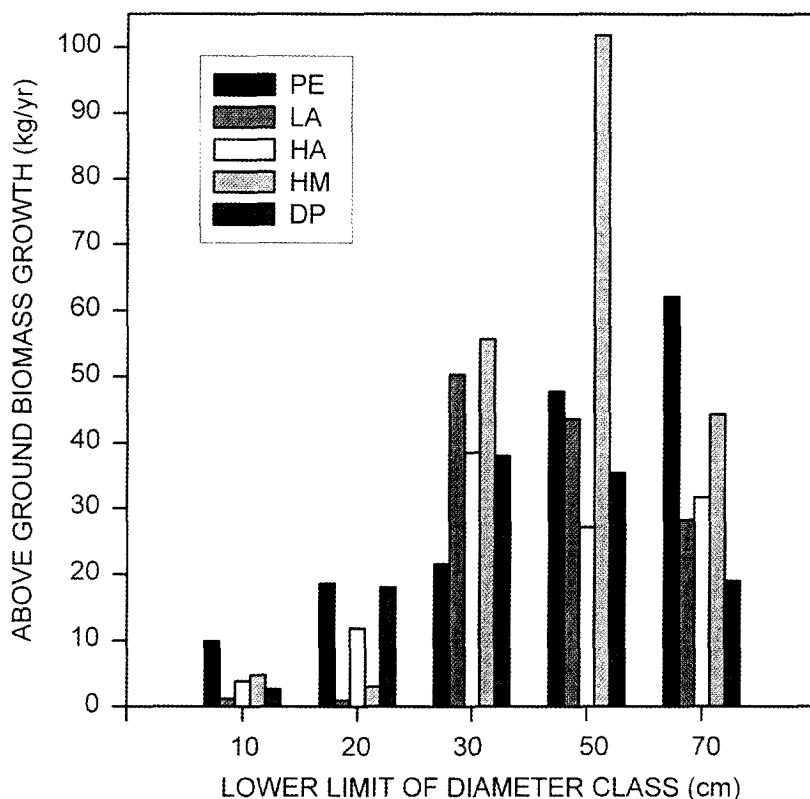


Fig. 2. Rates of biomass addition at different sizes for five species of very large trees at La Selva, Costa Rica. Biomass was calculated from diameter from allometric equations for trees of tropical wet forest given in Brown and Iverson (1992). Median diameter growth rates for trees less than 70 cm in diameter are from Clark and Clark (1992, table 8), rates for the over 70 cm diameter classes are from this study. Growth was calculated for an individual at the size class midpoint, except for the over 70 cm diameter class, where a 90 cm diameter criterion was used. Abbreviations are as in Fig. 1.

the 7 year period, basal area and biomass growth almost offset the losses due to mortality. Four individuals that were measured in 1986 and survived until 1993 could not be remeasured at the same spot due to buttress growth. Because these four trees undoubtedly had measurable growth, the actual rate of change in area and mass is even less than that shown in Table 5, and might even have been slightly positive.

5. Discussion

5.1. Ecology of very large trees at La Selva

Emergent trees live substantially longer than most individuals reaching canopy and subcanopy status at La Selva. The whole forest tree mortality rate for stems 10 cm or over in diameter at La Selva is 2.34% year⁻¹ (Lieberman et al., 1990), while the comparable rate for the five species studied here is only 0.5% year⁻¹ (calculated from Table 4). This low mortality is coupled with continued substantial growth (Table 2). Except for *Pithecellobium*, absolute rates of biomass addition at the over 70 cm diameter stage are somewhat lower than at the 30–70 cm diameter stages (Fig. 2). Nevertheless, the long residency time in the over 70 cm diameter class (median half-life 115 years), as well as the very large size attainable (Table 1) means that much or even most of the carbon accumulated by these species is fixed at the over 70 cm diameter size stage. For example, for individuals that reach 100 cm diameter, about half of the above-ground biomass is added after they reach 70 cm diameter (calculated from Brown and Iverson, 1992). In summary, very large trees at La Selva are a minor fraction (2%) of the stems, but contain a significant fraction of the above-ground biomass (27%). Owing to their longevity and continued growth, the substantial amounts of fixed carbon in very large trees must cycle at a considerably slower rate than the carbon in smaller trees (Lugo and Brown, 1992).

The upland old-growth in La Selva is considered to be largely uninfluenced by historic human intervention. Some artisanal extraction of Spanish Cedar (*Cedrela mexicana*) is reported to have occurred (Rafael Chaverría, personal communication, 1980),

and there is evidence of harvesting of at least one palm species for heart of palm in one small section of the reserve (Clark et al., 1995). Although the five emergent species studied here are all commercial timber species of moderate to high value, there is no anecdotal, historical, or field evidence that they were ever extracted from the old-growth areas of La Selva studied here. La Selva old growth is not known to have been affected by landscape-scale disturbances such as fire, landslides, or hurricane damage (Clark, 1990). Between 1969 and 1985 the number of stems 10 cm or over in diameter in 12.4 ha of old-growth forest changed only -0.8%, indicating a stable, non-successional forest (Lieberman et al., 1990). For these reasons, we assumed prior to this study that the biomass stored in the large individuals of the five study species would be more or less constant at the scale of the 150 ha study area.

Two lines of evidence suggest that this assumption was incorrect. Table 5 shows that the sample of very large trees followed in this study is currently maintaining its present biomass, with growth offsetting losses due to mortality. From the diameter distributions of this sample (Fig. 1) as well as previous demographic work (Clark and Clark, 1987, 1992) it is also clear that all five species are continuously recruiting individuals into the over 70 cm diameter class. With this sample of large individuals currently maintaining its biomass, and with continual recruitment into this size class occurring, the total biomass of these species in the over 70 cm diameter size class must be increasing in this area of old-growth forest.

There are several possible explanations for these data. These species may be increasing in biomass owing to a period of more favorable recruitment in the past. For example, even a moderately strong El Niño–Southern Oscillation event is sufficient to greatly increase canopy tree mortality rates in tropical moist forest in Panama (Condit et al., 1995). Meggers (1994) has suggested, based on archaeological evidence, that drastic changes in Amazonian forests may have occurred at the times of rare mega-ENSO events in the last two millennia. Such events, killing many canopy trees, could have differentially favored the recruitment of emergent species in the past. Another possibility is that the 7 year period sampled in this study was exceptional in either death or growth rates. We currently cannot test

this directly. Short-term climate variation does not appear to be a likely explanation, given that the average annual rainfall during this period (3972 mm) was not unusual compared with the 29 year mean of 3962 mm (Sanford et al., 1994). One possibility that cannot be ruled out from these data is that climate or atmospheric conditions are currently changing to favor increased tree growth, for example due to increasing concentrations of atmospheric CO₂. Continued monitoring will be necessary to determine if the observed landscape-scale increase in the biomass of large individuals of these tree species is due to historical disturbance, climatic change, or some additional unknown factor.

5.2. Comparison of mortality rates with other tropical forests

The death rates of emergents at La Selva are significantly lower than almost all published whole-forest tree death rates for tropical moist and wet forest. Phillips and Gentry (1994, Table 2) reviewed data from 22 tropical forests with long-term inventory histories. The mean annual mortality in the most recent periods analyzed was 2.00% year⁻¹ (range 0.51–3.63%), and only one site had a death rate as low as that found here (0.6% year⁻¹). Other than the data presented here, we are not aware of species-level data on death rates of very large trees from tropical rain forests. Numerous studies, however, have found that whole-forest tree death rates are independent of tree size class for individuals over 10 cm in diameter (Lieberman and Lieberman, 1987; Manokaran and Kochummen, 1987; Swaine et al., 1987; Carey et al., 1994). Although whole-stand death rates correctly describe the aggregate behavior of whole forests, our results show that whole-stand rates have little applicability at the species level. This is to be expected. Whole stand rates mix species of vastly differing stature and longevity. Averaging the high death rate of a pioneer species with the very low death rate of emergents provides useful information about the forest, but none about the individual species. At La Selva, emergent tree species as a class have lower death rates than forest-wide averages. We believe that when species-level data are available from other sites, this will emerge as a common pattern.

5.3. The abundance of very large trees in tropical forests

Two factors need to be considered in cross-site comparisons of abundances of very large trees. The first is methodological. We and many other researchers (Manokaran and Kochummen, 1987; Swaine et al., 1987; Hubbell and Foster, 1990; Lieberman and Lieberman, 1994) measure bole diameter at a point above any buttresses. Diameters always measured at breast height (dbh) will not be directly comparable to diameters measured above buttresses. For example, Kahn (1986) reports 5–6 stems ha⁻¹ of at least 1.3 m dbh in Tocantins, Brazil. This could indicate a high abundance of large trees, but could equally well reflect a high incidence of buttressing, which is extremely common in many tropical forests.

A second factor, more difficult to assess, is how representative of a given forest is a particular plot. Our data on abundance of very large trees, for example, come from a regular, highly replicated ($N = 515$ quadrats) sampling design applied over a 500 ha area. The area sampled includes all the known soil and topographic variation present in old-growth at La Selva, and covers an area sufficiently large to encompass all phases of forest regeneration (gap, building, and mature-phase sites). As the area sampled by a study decreases, the importance of knowing the criteria for site selection increases, at least if one wishes to generalize the results to the surrounding landscape. Scaling up data from non-representative plots can produce extremely biased estimates of landscape-scale patterns (Botkin and Simpson, 1990).

In a 50 ha plot in tropical moist forest in Panama (Barro Colorado Island, Hubbell and Foster, 1990), the number of trees over 70 cm in diameter in 1982, 1985, and 1990 were 803, 499, and 532 (R. Condit, personal communication, 1995). The 1990 density (10.6 individuals ha⁻¹ over 70 cm in diameter measured above buttresses) is similar to the data reported here (8.9 ha⁻¹), but clearly the Panama forest is extremely dynamic at the landscape scale.

In central Amazonia, Rankin-de-Merona et al. (1990) analyzed five 1-ha plots of upland old-growth forests. They found an average density of 5.8 trees ha⁻¹ 70 cm or over in diameter measured at breast

height. Annual exponential death rates over a 5 year period for these large individuals was 1.4% (calculated from their table 29.3). These Central Amazonian forests therefore have fewer very large trees than Costa Rican or Panamanian forests, and the whole-plot death rates for individuals 70 cm or over are substantially higher than those of the five species studied at La Selva.

Gentry and Terborgh (1990) summarized data from one 1-ha and nine 0.1-ha plots from the upper Amazon. The 1 ha Peruvian Cocha Cashu site had 17 trees 70 cm or over in diameter measured at breast height in a single hectare, while the other plots ranged from 4 to 11 individuals ha^{-1} . It is difficult to compare these data to the Panamanian and Costa Rican data owing to the very restricted spatial scale of these samples and the different heights of diameter measured. Nonetheless, the densities from the small plots fall within the range of the Costa Rican, Panamanian, and central Amazonian numbers. The high density of large trees at Cocha Cashu is interesting and should be verified by larger-scale sampling.

6. Conclusion and recommendations

To our knowledge the data presented here are the first species-level data on the growth and mortality of a statistically useful sample of tropical tree species that regularly exceed 70 cm diameter. We therefore cannot determine if these five species are 'normal' tropical emergents. At La Selva, it is clear that the emergents store a major fraction of the above-ground biomass and have very different life histories than 'average' canopy species. Given their demonstrated biomass importance and unusual life histories, very large species merit specific study at other tropical sites. To make these studies comparable across sites, and so that the individual trees can be studied for many years, diameters should be measured above buttresses. Details of diameter measurement (including statistics of accuracy) should be included in methods descriptions.

Obtaining statistically useful information on the landscape-scale distribution of very large trees, or studying the demography of a given emergent species, will require sampling large areas. Long transects (Korning and Balslev, 1994) or small quadrats replicated on a regular, strictly random, or stratified

random design at large spatial scales (Botkin and Simpson, 1990; Brown, 1995; Clark et al., 1995) are cost-effective ways to sample large areas. In addition, these methods minimize subjective judgments for placing sample points, and therefore have the potential to provide unbiased estimates of landscape-scale parameters.

Future studies should be designed to address the following issues. (1) Are very large trees accumulating biomass in other old-growth tropical forests? (2) What is the range of normal population densities for very large tropical trees? Are there sites at which this density is increasing due to historical perturbation, either natural or anthropogenic? (3) More data on growth and mortality of very large trees in tropical wet and moist forests are needed. With these data it will be possible to begin a comparative analysis of life histories of very large trees. There are thousands of canopy level tree species in tropical rain forests, but relatively speaking, only a handful of these regularly reach emergent status. Why is this? A comparative analysis of the life history characteristics of very large tree species is a logical first step towards understanding this pattern.

Acknowledgments

We gratefully acknowledge the dedicated field and laboratory work of paraforesters Leo Campos, William Brenes, and Gerardo Vega. Without their willingness to scale any tree, regardless of the field conditions, this project would have never taken place. We thank Richard Condit and Suzanne Lao for providing data from the Barro Colorado Island 50 ha plot. Sandra Brown guided us to references on basal area to biomass conversions and big trees. Field work and analysis were supported by several grants from the National Science Foundation (most recently DEB94-07581), and a grant from the Andrew Mellon Foundation. We thank the staff of the La Selva Biological Station for their continued dedication to making La Selva a friendly and exciting research facility.

References

- Botkin, D.B. and Simpson, L.G., 1990. Biomass of the North American boreal forest. *Biogeochemistry*, 9: 161–174.

- Brown, S. 1995. Tropical forests and the global carbon cycle: estimating state and change in biomass density. In: M. Apps and D. Price (Editors), *The Role of Forest Ecosystems and Forest Management in the Global Carbon Cycle*. NATO Series, Springer. In press.
- Brown, S. and Iverson, L.R., 1992. Biomass estimates for tropical forests. *World Resour. Rev.*, 4: 366–384.
- Carey, E.V., Brown, S., Gillespie, A.J.R. and Lugo, A.E., 1994. Tree mortality in mature lowland tropical moist and tropical lower montane moist forests of Venezuela. *Biotropica*, 26: 255–265.
- Clark, D.A. and Clark, D.B., 1992. Life history diversity of canopy and emergent trees in a neotropical rainforest. *Ecol. Monogr.*, 62: 315–344.
- Clark, D.A., Clark, D.B., Sandoval, M.R. and Castro, C., M.V., 1995. Landscape scale variation in community structure of neotropical rain forest palms: edaphic and human effects. *Ecology*, in press.
- Clark, D.B., 1990. The role of disturbance in the regeneration of neotropical moist forests. In: K.S. Bawa and M. Hadley (Editors), *Reproductive Ecology of Tropical Forest Plants*. UNESCO/Parthenon Publishing Group, Paris, pp. 291–315.
- Clark, D.B. and Clark, D.A., 1987. Population ecology and microhabitat distribution of *Dipteryx panamensis*, a neotropical rain forest emergent tree. *Biotropica*, 19: 236–244.
- Condit, R., Hubbell, S.P. and Foster, R.B., 1995. Changes in tree species abundance in a neotropical forest over eight years: impact of climate change. *J. Trop. Ecol.*, in press.
- Gentry, A.H., 1990. Floristic similarities and differences between southern Central America and upper and central Amazonia. In: A.H. Gentry (Editor), *Four Neotropical Rainforests*. Yale University Press, New Haven, CT, pp. 141–157.
- Gentry, A.H. and Ortiz, S.R., 1993. Patrones de composición florística en la Amazonia Peruana. In: R. Kalliola, M. Puhakka and W. Danjoy (Editors), *Amazonia Peruana*. PAUT and ONERN, Jyväskylä, Finland, pp. 155–166.
- Gentry, A.H. and Terborgh, J., 1990. Composition and dynamics of the Cocha Cashu 'mature' floodplain forest. In: A.H. Gentry (Editor), *Four Neotropical Rainforests*. Yale University Press, New Haven, CT, pp. 542–564.
- Harmon, M.E. and Hua, C., 1991. Coarse woody debris dynamics in two old-growth ecosystems. *BioScience*, 41: 604–610.
- Hartshorn, G.S. and Peralta, R., 1988. Preliminary description of primary forests along the La Selva–Volcan Barba altitudinal transect, Costa Rica. In: F. Almeda and C. Pringle (Editors), *Tropical Rainforests: Diversity and Conservation*. California Academy of Science, San Francisco, pp. 281–295.
- Hubbell, S.P. and Foster, R.B., 1990. Structure, dynamics, and equilibrium status of old-growth forest on Barro Colorado Island. In: A.H. Gentry (Editor), *Four Neotropical Rainforests*. Yale University Press, New Haven, CT, pp. 522–541.
- Kahn, F., 1986. Life forms of Amazonian palms in relation to forest structure and dynamics. *Biotropica*, 18: 214–218.
- Korning, J. and Balslev, H., 1994. Growth and mortality of trees in Amazonian tropical rain forest in Ecuador. *J. Veg. Sci.*, 4: 77–86.
- Lieberman, D. and Lieberman, M., 1987. Forest tree growth and dynamics at La Selva, Costa Rica (1969–1982). *J. Trop. Ecol.*, 3: 347–358.
- Lieberman, D., Hartshorn, G.S., Lieberman, M. and Peralta, R., 1990. Forest dynamics at La Selva Biological Station, 1969–1985. In: A.H. Gentry (Editor), *Four Neotropical Rainforests*. Yale University Press, New Haven, CT, pp. 509–521.
- Lieberman, M. and Lieberman, D., 1994. Patterns of density and dispersion of forest trees. In: L.A. McDade, K.S. Bawa, H.A. Hespentheide and G.S. Hartshorn (Editors), *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. University of Chicago Press, Chicago, pp. 106–119.
- Lugo, A.E. and Brown, S., 1992. Tropical forests as sinks of atmospheric carbon. *For. Ecol. Manage.*, 54: 239–255.
- Manokaran, N. and Kochummen, K.M., 1987. Recruitment, growth and mortality of tree species in a lowland dipterocarp forest in Peninsular Malaysia. *J. Trop. Ecol.*, 3: 315–330.
- McDade, L.A., Bawa, K.S., Hespentheide, H.A. and Hartshorn, G.S., 1994. *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. University of Chicago Press, Chicago.
- Meggers, B.J., 1994. Pre-Columbian Amazonia. *Natl. Geogr. Res. Explor.*, 10: 398–421.
- Phillips, O.L. and Gentry, A.H., 1994. Increasing turnover through time in tropical forests. *Science*, 263: 954–958.
- Rankin-de-Merona, J.M., Hutchings, R.W. and Lovejoy, T.E., 1990. Tree mortality and recruitment over a five-year period in undisturbed upland rainforest of the Central Amazon. In: A. Gentry (Editor), *Four neotropical rainforests*. Yale University Press, New Haven, CT, pp. 573–584.
- Rhoades, C.C., Sanford, R.L. and Clark, D.B., 1994. Gender dependent influences on soil phosphorus by the dioecious lowland tropical tree *Simarouba amara*. *Biotropica*, 26: 362–368.
- Sanford, R.L., Jr., Paaby, P., Luvall, J.C. and Phillips, E., 1994. Climate, geomorphology, and aquatic systems. In: L.A. McDade, K.S. Bawa, H.A. Hespentheide and G.S. Hartshorn (Editors), *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. University of Chicago Press, Chicago, pp. 19–33.
- Sheil, D., Burslem, D.F.R.P. and Alder, D., 1995. The interpretation and misinterpretation of mortality rate measures. *J. Ecol.*, 83: 331–333.
- Sollins, P., Sancho, M.F., Mata Ch., R. and Sanford, R.L., Jr., 1994. Soils and soil process research. In: L.A. McDade, K.S. Bawa, H. Hespentheide and G.S. Hartshorn (Editors), *La Selva: Ecology and Natural History of a Neotropical Rainforest*. University of Chicago Press, Chicago, pp. 34–53.
- Swaine, M.D., Hall, J.B. and Alexander, I.J., 1987. Tree population dynamics at Kade, Ghana (1968–1982). *J. Trop. Ecol.*, 3: 331–345.
- Tyrrell, L.E. and Crow, T.R., 1994. Structural characteristics of old-growth hemlock–hardwood forests in relation to age. *Ecology*, 75: 370–386.
- White, L.J.T., 1994. The effects of commercial mechanised selective logging on a transect in lowland rainforest in the Lope Reserve, Gabon. *J. Trop. Ecol.*, 10: 313–322.