

How old are tropical rain forest trees?

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Recent reports indicate that trees can survive to be 1000 years old in the Amazonian rain forest. This appears to contradict the idea that tropical rain forests are highly dynamic systems. However, there is very little information on how common these ancient trees are. Tropical rain forest turn-over rates have been estimated to be less than 400 years, which would suggest that millenary trees would be non-existent or very rare. Recent radiocarbon-based dating techniques suggest that centuries-old trees are common among big canopy trees, but it is not clear how accurate the technique is compared with other methods: age determinations on this long timescale are necessarily based on estimates, and some methods may be more reliable than others. To examine the apparent contradiction between tree age and forest dynamics tree-ageing methods should be discussed in the context of the ecological significance of longevity in tropical forests. These issues are important for understanding the structure, dynamics and conservation of this highly diverse ecosystem.



Two general types of methods have been used to age tropical rain forest trees. Direct methods assign ages by following the fate of individuals from seedling emergence until tree death, using morphological, anatomical or architectural features that record the passage of time, or using natural atmospheric radiocarbon traces. Indirect methods can use size indicators and the relationship between tree growth and time, tree demographic and community processes, or by dating on the basis of nuclear bomb radioisotopes in tree growth zones.

Direct age estimates

Cohort monitoring

The possibility of following individuals in real time is restricted to very short-lived tree species. In tropical rain forests, species that are extremely light-demanding can complete their entire life cycle in less than ten years. For example, at Los Tuxtlas, Mexico, emerging seedlings of papaya (*Carica papaya*) in a tree-fall canopy gap were tagged and monitored¹. Only eight months later, several individuals had begun to flower, and after eight years all the trees had died. Such ephemeral trees are, however, very rare and most trees survive for much longer. As a consequence, 'horizontal' surveys are not a suitable means of estimating tree longevity. Age estimates that are based on monitoring the fate of cohorts (i.e. groups of individuals born about the same time) have only been obtained for early life cycle stages of tropical rain forest trees. These studies have highlighted the existence of among-species variability in survival and seedling growth rates under the light-limited conditions of the forest understorey^{1,2}.

Temporal regular growth rings

In seasonal temperate regions, trees generally form regular growth rings that can be used to establish age scales. This approach is generally unreliable for tropical rain forest in relatively non-seasonal climatic conditions where trees tend not to form growth rings. In the few cases where they do, these may not be chronologically regular³, but some tropical trees living

in climates with a long drought season can produce annual rings, as was found for *Tectona grandis* in Northern Thailand⁴. Also, under specific seasonally flooded environments, some tropical rain forest tree species may produce datable growth rings⁵. Such is the case of the camu-camu tree (*Myrciaria dubia*) found along the Amazon river margins in Peru⁶. During the rainy season the trees

Box 1. Age estimates based on ¹⁴C techniques

These methods take advantage of the presence of natural and human-induced radiocarbon in the atmosphere. However, they are seldom used because they are very expensive and technically elaborate^{16,17}.

Natural radiocarbon dating

This technique can be used to date ages up to 40 000 years before present. When the center-most wood of a tree dies a radioactive 'timer' starts because that dead wood is no longer in equilibrium with atmospheric carbon. By comparing how much carbon remains with the known atmospheric content, the age can be directly determined. The amount of time elapsed since the radiocarbon was incorporated into the wood is estimated as $t = HI \ln (A_o/A_s)$, where HI is the half-life of ¹⁴C (5568 ± 30 years), A_o is the ¹⁴C present in the atmosphere in the year 1950, and A_s is the estimated ¹⁴C in the wood sample. Tree samples should be obtained from the core of the trunk. For time estimates between 1000 and 2000 years this technique has 25–50% precision¹⁷.

Human-induced radiocarbon dating

After the nuclear detonations carried out in the 1950s and 1960s, the atmospheric ¹⁴C:¹²C ratio increased from near zero to a maximum in 1961–62, and has since been declining^{7,16,17}. This trend is reflected in the wood that has accumulated since 1955. An annual average growth rate can be estimated by dividing tree radius for the section that includes the ¹⁴C:¹²C trend cited above by the number of years since 1955. Tree age can then be estimated by calculating the number of years that are needed to reach a given total trunk diameter if the estimated growth rate is assumed to be constant. One limitation of this technique is the assumption of a constant diameter growth rate during the tree life-cycle. Trees generally have sigmoid-like growth curves in which very young and old trees tend to grow more slowly than intermediate-age trees. Therefore, this radioisotope technique tends to overestimate ages in large slow-growing trees, because ¹⁴C traces are recorded in the outer trunk sections that have accumulated during the period of slowest growth.

Box 2. Deterministic methods to estimate tree ages based on size growth rates

Basic information is obtained from a sample of trees representing the whole range of individual sizes found in the population. For each tree, trunk diameter at breast height (DBH = 1.3 m above the ground) is usually measured at different times during a period in excess of five years.

Periodic annual increment (PAI)

DBH classes are defined for the whole size range and the average annual DBH growth rate for each class is obtained. The number of years (Y_i) required for a tree to grow from the lower limit to the upper limit within a DBH class is estimated by dividing the DBH class interval by the corresponding DBH annual growth rate. To construct average age-size curves, Y_i values are sequentially accumulated, from smaller to larger DBH classes. As an example of a PAI method, consider the case of the mid-canopy tree *Pseudolmedia oxyphyllaria* at Los Tuxtlas rain forest. This species reaches a maximum DBH of 58 cm. Annual DBH growth rates (in parenthesis) were obtained for the following DBH classes (M. Martínez-Ramos and E.R. Alvarez-Buylla, unpublished): 1–5 cm (0.15 cm year⁻¹), 5.1–10.0 cm (0.28), 10.1–20.0 cm (0.43), 20.1–40.0 cm (0.57), 40.1–58 cm (0.19). For instance, the Y_i value for the first DBH class is (1–5 cm)/0.15 cm year⁻¹ = 27 years. Thus, starting with 1 cm DBH, the resulted cumulative age (in parentheses) since this minimum size is: 5 cm (27 years), 10 cm (45 years), 20 cm (68 years), 40 cm (103 years), 58 cm (197 years).

Passage of time (PT)

This method uses the time that an average tree takes to go from one class to the next size class. PT is calculated as the reciprocal of the annual proportion of trees in a size class that reach the next class. The age of trees is then obtained by accumulating sequentially, from smaller to larger size classes, the estimated number of years that a tree spends in each size class. As an example, consider again the case of *Pseudolmedia oxyphyllaria*. For the same DBH classes established above, proportions of individuals moving to the next class (in parenthesis) are as follows: 1–5 (0.05), 5.1–10.0 (0.22), 10.1–20.0 (0.11), 20.1–40.0 (0.09). Starting with a DBH of 1 cm, after obtaining reciprocal values, the estimated cumulative age (in parentheses) with increasing DBH is: 5 cm (19 years), 10 cm (24 years), 20 cm (33 years) and 40 cm (44 years). We do not have information to estimate ages after 40 cm DBH. It can be noted that the age estimate obtained with PT is much shorter than that obtained with PAI.

remain under water and grow at slower rates than in the short dry season. This seasonal growth variation is reflected in clear annual growth rings. The existence of such rings has been detected in other species growing in flooded forests along the Rio Negro and the Amazon in Brazil⁷.

Natural atmospheric radiocarbon dating

Historical radiocarbon (¹⁴C) stored in the dead core of trees (Box 1) was used to estimate the age of a *Bertholletia excelsa* tree in Amazonia, and revealed it to be 500 years old⁸. Using the same technique, Chambers *et al.*⁸ provide age estimates for twenty emergent trees of different species in Central Amazonia. Seven trees (40%) were found to be 200–400 years old, ten (50%) were 400–1000 years old, and two (10%) were between 1200 and 1400 years old.

Indirect estimates**Estimates based on growth of the trunk diameter**

Most tropical rain forest tree-age estimates have been obtained from size–growth-rate relationships^{5,9}. Periodic annual increment (PAI) and passage time (PT) are two methods frequently employed to generate growth curves and size–age estimates¹⁰ (Box 2). Both approaches are deterministic and do not incorporate size-related, between-individual variation. A probabilistic technique that overcame this limitation was developed by incorporating individual growth rates in the calculations of size–age relationships¹⁰ (Box 3). This approach yielded average longevity (defined as the time needed to grow from 10 cm to maximum trunk diameter at breast height [DBH] or 1.3 m above ground), from 52 to 442

years, at La Selva, Costa Rica¹¹. The shortest and longest longevity estimates decreased to 16 and 309 years, respectively, when maximum growth curves were used. A similar type of reduction is observed when longevity estimates are based on the faster growing trees within each size category. Longevity estimates based on fast growers, were between 1.7 and 3.8 times shorter than those based on average growth rates (Fig. 1). It has been estimated that the time needed to grow from 10 to 100 cm DBH varied between 90 and 600 years among five canopy and emergent tree species when median and maximum growth rates were used¹².

However, the probabilistic approach assumes that an individual's growth rates are distributed as a time-independent random variable within each size class. These assumptions may bias age estimates for trees that have spurts of fast growth rates during growth in a tree fall forest gap, and yield overestimated minimum life-spans. This may lead to serious errors in determining the age of trees that track high intensity light environments (such as pioneer trees), but may be a minor problem for trees that are adapted to live in shade conditions.

Estimates based on vertical growth

Age estimates based on vertical growth are restricted to palms, as these tend to grow along a single vertical axis and accumulate leaf scars produced by the single apical meristem. When such scars form rings it is possible to age the tree by relating the size-specific rate of scar production with stem length gained per unit time. This method yielded an estimate of 130 years for the tallest understorey palms of *Astro-*

*caryum mexicanum*¹³. The shade-tolerant palm *Chamaedorea elegans* has been shown to be able to live up to 100 years, growing at a constant stem elongation rate of 1.2 cm year⁻¹ at Veracruz, Mexico (M. Martínez-Ramos *et al.*, unpublished). The light-demanding palm, *Chamaedorea tepejilote*, was estimated to live for 33 years using the same technique¹⁴.

Estimates based on mortality rates

Age estimates based on mortality rates can only be used to obtain maximum age (longevity) estimates for trees of a certain size. Using an exponential model (Box 4), longevity estimates of between 35 and almost 2000 years have been estimated for several shrub and tree species at Barro Colorado Island, Panama¹⁵. Using a hyperbolic model (Box 4) it has been estimated that longevity varies by between 11 and 623 years among 23 tree species (Fig. 1) in the Los Tuxtlas forest (M. Martínez-Ramos and E.R. Alvarez-Buylla, unpublished). However, all these estimates have constraints imposed upon them by the assumptions of the model used in each case (Box 4).

Estimates using radioactive indicators

Radioisotopes produced by nuclear tests are fixed by trees and can be used as tracers to obtain an indirect age estimate (Box 1). Radioisotope age estimates of between 360 and 1060 years were obtained for six different tree species in different tropical rain forest regions⁵.

Estimates based on historical community disturbance events

Environmental disturbances can be recorded in anatomical and morphological structures of

Box 3. Probabilistic approach to estimate age of trees based on size growth rates

Liebermans' approach¹⁰ simulates growth trajectories for individual trees by incorporating the between-individual growth variation to PAI and PT principles. Besides providing average size-specific age estimates, this approach also gives maximum, minimum, and median age estimates.

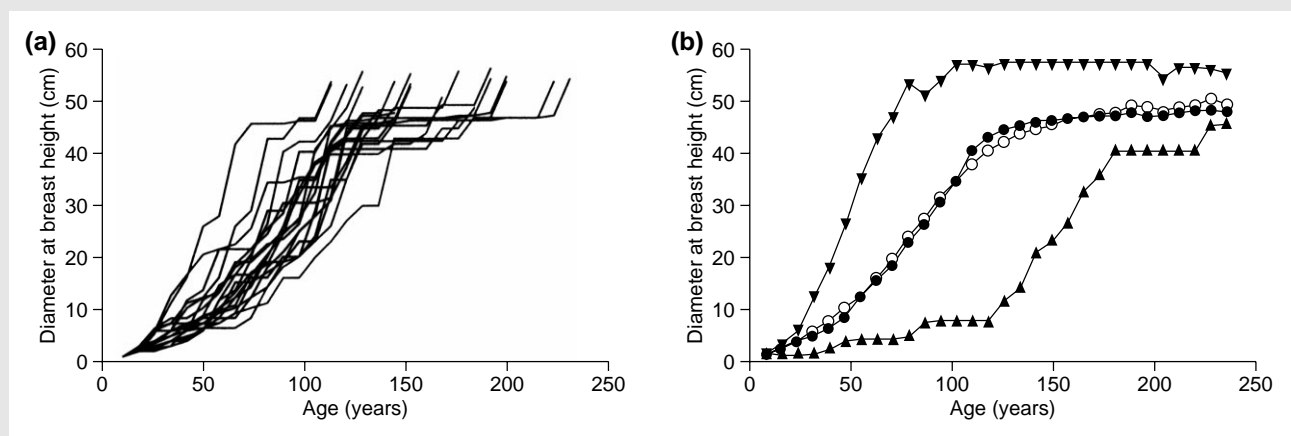
These statistics are obtained after simulating several (in the order of hundreds) growth trajectories. The data base is organized in a matrix of n rows (trees) and two columns: initial tree size and growth rate. The matrix is ordered by ascending initial tree size. Maximum and minimum age estimates are obtained from the trajectories constructed with the slowest and fastest growth rates, respectively, that are available in the matrix. The existence of trees with null or negative growth make maximum estimates unreliable.

Simulation based on PAI

First, ranges of trees (l) from which an individual tree will be randomly selected are defined ($5 > l < 100$ individuals¹⁰). Growth simulation starts by randomly selecting one tree from the l group with smallest trees. Size of the chosen tree defines tree size (S_1) at time 1. Size of model tree at time 2 (S_2) is obtained by adding the growth rate of selected tree to the size at time 1 (S_1). Tree size for subsequent times (3, 4, 5, ..., i) is determined following a standard protocol:

- (i) from the data matrix, a new tree with the closest size to S_i is selected
- (ii) this tree marks the midpoint of a new l group of trees from which a tree is randomly chosen
- (iii) the growth rate of the chosen tree is added to S_i to obtain the model tree size at time $i + 1$.

This protocol is repeated until the observed maximum tree size is reached. Simulation of several growth trajectories enable statistical analysis of the age–size relationship. As an example, we show (a) the 20 simulated growth trajectories for the Los Tuxtlas tree *Pseudolmedia oxyphyllaria* and (b) the average (open circles), median (closed circles), maximum and minimum (triangles) growth trajectories calculated using 500 simulated trajectories (M. Martínez-Ramos and E.R. Alvarez-Buylla, unpublished).



Simulation based on PT

In this case, columns of the $n \times 2$ data matrix contain the original size (S_i) of trees and their size one unit time after (S_{i+1}). The matrix is divided in s equal size categories. From the smallest size category a tree is randomly selected and its size at time $i + 1$ is determined. If the new size is within the limits of the first category the model tree remains in the same category for one unit time. In such cases, a new tree is randomly selected from the first category and its size at time $i + 1$ is determined. Units of time are added until S_{i+1} of the selected tree falls in the next size category. When this happens, a new tree is randomly selected from the new size class, and the protocol is repeated until the simulated tree reaches or exceeds the maximum size class. Simulation of several growth trajectories enable statistical analysis of the age–size relationship.

trees. At Los Tuxtlas, tree fall disturbance can be dated using stems of the monopodial understory palm *Astrocaryum mexicanum*¹⁸. These palms endure tree falls, which open gaps in the canopy, by bending under the weight of fallen trees and limbs. After one year, the palms recover vertical growth and a clear kink on the stem is formed. Vertical stem growth gives a good time estimate, and thus it has been possible to estimate gap age by mapping and measuring bent palms in a forest plot. This dating tool is particularly useful for measuring the age of trees that begin their life-cycle when a canopy gap opens. Using this approach, age estimates of between 8 and 35 years have been made for several pioneer tree species¹⁹.

A comparison of ageing methods

How do age estimates obtained using these different methods compare? Longevity estimates based on four different methods, are shown in Fig. 1. Average longevity values obtained using the periodic annual increment method ranged from 22 years for a small pioneer tree (*Hampea nutricia*) to 1030 years for an upper canopy tree (*Brosimum alicastrum*). The large variation around mean estimates is mainly caused by among-individual variation in growth rates. These estimates are, on average, 168% greater than the longevity values calculated using periodic annual increment of individuals with maximum growth rates; 187% greater than estimates provided by mortality rates (hyperbolic

function); and 169% greater than longevity values based on patch age estimates using *Astrocaryum mexicanum* bent stems. The latter three methods yield more similar longevity estimates: age estimates based on maximum growth rates were different by only 3% from those based on patch age, and by 38% from those estimated using mortality rates. Considering that patch age provides an independent index of tree age, at least for pioneer species, it seems that periodic annual increment estimates, based on individuals with maximum growth rates, yield good estimates for this group of tree species. This is reasonable because pioneer trees that reach maturity are those growing at fast rates in favourable environmental patches^{20,21}.

In conclusion, PAI based estimates of mean growth rates tends to provide higher tree age determinations, while PAI based on maximum growth and mortality rates tends to give lower tree age estimations. The methods that rely on growth rates can be improved by incorporating between-individual growth variability and temporal within-individual autocorrelation in growth rate¹⁰. Models based on mortality rates need to incorporate size-dependent and long-term mortality variation, in order to yield better longevity estimates.

Trees of the same size may have different ages. Mortality rates may be higher in the oldest individuals if they lose vigour and become more liable to predation by natural enemies and physical damage. However, the fact that most tropical rain forest species show little evidence of a drop in fecundity with age, suggests that tropical trees do not lose vigour with age, except in short-lived species^{1,25}. Finally, most age methods fail to include seedling and sapling stages which may survive for years growing at very slow rates.

All radiocarbon age estimates obtained to date fall within the longevity ranges based on growth and mortality estimates. However, techniques based on ¹⁴C are expensive and tend to be inaccessible to most tropical rain forest research facilities. Therefore, they cannot be considered as standard tools.

How useful are age estimates for understanding tropical rain forest tree ecology?

Age estimates of tropical rain forest tree species provide a fascinating overview of the among-species variation in tree longevity. The range of such variation is from 8 to 2000 years, and reflects the diverse life histories of tropical rain forest tree species²². This diversity may have evolved from the complex selective pressures promoted by tree fall disturbance^{23,24}, and the spatial and temporal environmental heterogeneity (such as in soil variation and canopy light regimes)^{15,21}.

Although age may be useful for describing demography^{1,25}, its usefulness for studies on tree population dynamics is weak. In trees, as in most plants, age is usually a poor indicator of individual vigour. Survival, growth and fecundity rates are size-dependent rather than age-dependent²⁶. Tree size depends on the immediate environment they experience, and individuals of the same age may dramatically differ in size and darwinian fitness²⁷.

Light is an important resource for tree growth during immature stages and for reproduction at maturity. Light availability changes across spatio-temporal scales²⁸ and individuals of the same age may perform very differently depending on the light regime they experience. For example, the size (DBH) of individuals from the same cohort of the gap

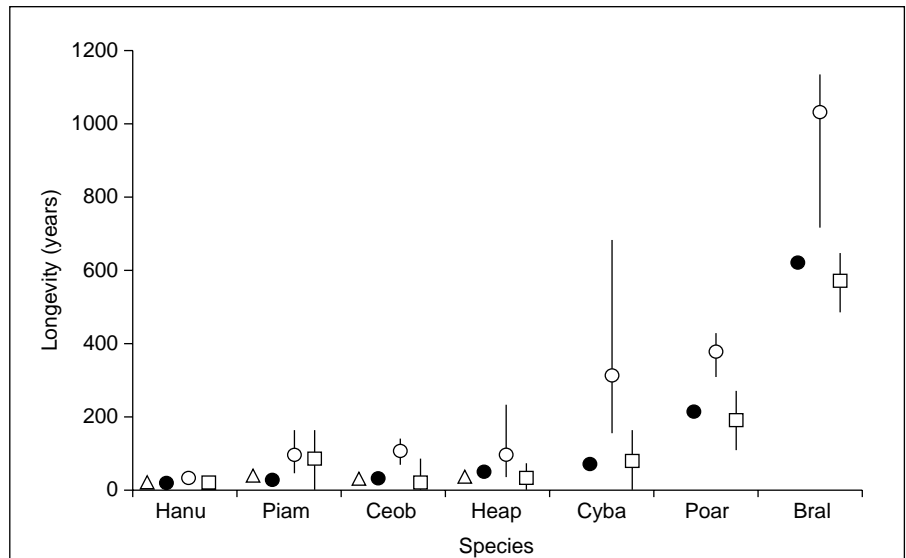


Fig. 1. Maximum age (longevity) estimates for tree species at Los Tuxtlas rain forest, Mexico (M. Martínez-Ramos and E.R. Alvarez-Buylla, unpublished). Data were obtained for trees ≥ 1 cm DBH in a 5-ha permanent plot for the period 1982–1990. Only species (14 in total) with an initial population size of >32 individuals were analyzed. Mean longevity estimates, using average DBH growth rates (PAI; open circles), and mortality rate (MR; squares) methods, are displayed with one standard error (vertical lines). Estimates based on maximum growth rates (MG; closed circles) and patch age (PA; triangles) are displayed as single points. PA estimates are provided only for the four pioneer species. Following species abbreviation showed on X-axis, name of species, tree type, and maximum DBH (cm) are as follows: Hanu = *Hampea nutricia* (pioneer, 11), Piam = *Piper amalago* (pioneer, 40), Ceob = *Cecropia obtusifolia* (pioneer, 60), Heap = *Heliocarpus appendiculatus* (pioneer, 70), Cyba = *Cymbopetalum baillonii* (canopy, 70), Dear = *Poulsenia armata* (canopy, diameter above buttresses 85), Bral = *Brosimum alicastrum* (upper-canopy, diameter above buttresses 134).

Box 4. Tree aging methods based on mortality rates

A sample of individuals representing the size range of a population is used. Each tree is permanently tagged and revisited every year for five or more years. Tree longevity estimates are based on the proportion of dead individuals per unit time using two main models.

Negative exponential model

This approach estimates the time needed for a population of size N_0 , that suffers a constant annual mortality rate (m), to be reduced to one individual (N_1); longevity (L) is estimated as $L = (\ln N_0)/m$. This method does not provide absolute longevity estimates because L depends on N_0 . For example, if a constant $m = 0.01$ is considered, longevity is 691 years if $N_0 = 1000$ but only 461 years if $N_0 = 100$. Therefore, this method provides a means of establishing a relative index of longevity among species.

Hyperbolic model

In this approach, the function $L = 1/m$ yields an absolute estimate of longevity, but it has the same limitations as the exponential model, which assumes a constant m . Moreover, this function is very sensitive to changes in m , and large sample sizes (N) must be obtained in order to reduce statistical errors. For example, for a population with an estimated $m = 0.04$, longevity is estimated to be 25 years, with confidence intervals equal to 13–1237 years if $N = 100$ individuals, but if $N = 1000$ then confidence intervals = 19–36 years.

Given the difficulty of finding and managing large population sample sizes, it is difficult to obtain statistically sound longevity estimates based on mortality rates. Also, both the exponential and hyperbolic models are limited because they assume a constant mortality rate, which is rarely the case among tropical trees. Mortality rate can vary with tree size and with time. Condit *et al.*¹⁵ showed, for example, that small trees (1 to 9.99 cm DBH) have higher mortality rates than larger trees (DBH ≥ 10 cm), and that mortality rates vary significantly in years differing in climatic conditions. Thus, dating tree age with mortality rates can give good estimates when size-specific mortality rates are fairly constant, and when they have been obtained for sufficiently long periods of time to allow long-term mortality variation to average out (>10 years).

tree species *Cecropia obtusifolia* varied ten-fold depending on the light microenvironment experienced²⁰. In Barro Colorado Island, individuals of the same cohort of the emergent species *Tachigalia versicolor* grew ten times faster in gaps than in the shade (R. Foster, pers. commun.). At Manaus, Brazil, half-sibling seedlings of the canopy tree *Chrysophyllum pomiferum*, grew ten times faster in a secondary regrowth patch, with high light levels, than in the shaded forest understorey (J. Benitez-Malvido, pers. commun.).

Tropical rain forest tree population dynamics have been successfully studied with matrix models based on size-classified populations²³. Such models are valuable for exploring basic questions, and for conservation and management issues, as they help in evaluating the sensitivity of population growth rate to natural or human-induced disturbance. For example, these models suggest that the population growth rate of fast growing, short-lived trees is sensitive to any disturbance that affects early life-cycle stages, while the population growth rate of slow growing, long-lived trees, is most sensitive to disturbance that affects survival at mature stages^{1,23}. Thus, in order to manage and preserve tree populations, we need different harvesting programmes to exploit short- or long-lived tree populations.

The existence of very old trees⁸ seems to contradict the notion that tropical rain forests are dynamic systems. How can we reconcile the fact that tropical rain forest turnover rates vary between 50 and 400 years²⁹, with the existence of very long-lived trees? To answer this question, we first need to understand the process of tropical rain forest turnover or renewal. This process depends on the opening and closure of canopy gaps that are created mostly by the fall of large trees. After reaching a large enough size to produce a gap (i.e. when a tree reaches the forest canopy), a canopy tree has usually reached about half its total life-span²⁵.

Average values can be misleading. Turnover rates may vary across forest micro-environments because of changes in species composition, community structure and environmental factors that affect tree fall rates³⁰. Forest patches with slow turnover rates are those dominated by a few slow-growing, long-lived trees, while forest patches with higher turnover rates are dominated by short-lived trees^{29,30}. This spatial variation in turnover rates can explain the existence of very long-lived trees in tropical rain forests with fast average turnover rates. Also, some trees may only reach very old age because of chance. Despite being very old, the majority of trees attain a maximum age of less than 400 years. This modal or mean estimate is much more compatible with mean turnover rate estimates.

Concluding remarks

Chambers *et al.* have discussed the importance of tree age estimates for understanding ecosystem-level processes such as the forest carbon cycle⁸. Above-ground standing biomass partitions differently among trees. About 50% of this biomass is contained in canopy and emergent trees that represent a minor proportion of the total number of forest trees⁸. Thus, the existence of very old individuals among big trees implies that a fraction of the forest carbon bank is very old. Carbon allocated to leaves, flowers, fruits, twigs, and small branches return to the atmosphere within months or some years, while that fixed in trunks and roots returns over much longer periods. In tropical forests, it has been documented that about 25% to 40% of the net primary productivity is allocated to woody structures^{31,32}. The speed at which such carbon is released depends on mortality rates of trees and on the rate of wood decomposition. Decomposition rate is negatively related to wood density, which in turn decreases with growth rate. In this context, tree demography is an important tool for understanding forest carbon cycling. Because tree demographic behavior is poorly related to age, it may be relevant to obtain good estimates of size-dependent, rather than age-dependent, demographic rates. Furthermore, the mean rate of carbon cycling stored in woody structures will depend more on the modal and mean tree longevities than on the largest values. The modal tree longevity value is more likely to be between 200 and 400 years¹¹.

Thus, in order to analyse carbon fluxes in tropical rain forests, we require studies of community structure and dynamics that incorporate models similar to those used to study the dynamics of size-categorized populations^{23,24}. Although knowledge of the age of trees is useful, tree size can be obtained more readily and is an important parameter for understanding tropical rain forest ecology and dynamics.

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Plant disease reality

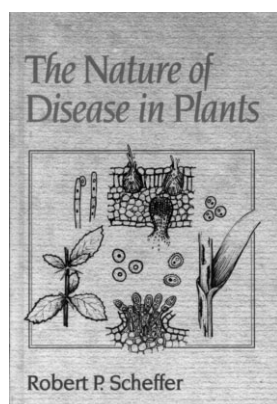
The Nature of Disease in Plants

by R.P. Scheffer

Cambridge University Press, 1997.

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In the real world, plant diseases rarely boil down to a single gene or protein or signal transduction pathway. These can be crucial, but other factors also play an important part, such as the weather, the changing practices of farmers, the shifting genotypes of pathogens, and the deliberate or inadvertent movement of plants and pathogens to new locations. It is in this changing environment that plant diseases rise and fall, and this is the reality that we learn about in this book.

Robert Scheffer was a highly respected plant pathologist and biochemist. The book, published posthumously after his submission of the typescript to the publisher, is the work of a true scholar. The discussion ranges widely and admirably between modern molecular plant pathology, historical plant pathology, and the factual realities of farming in the face of disease epidemics. The text is not meant to be encyclopedic, but instead aims to give a broad general understanding. We are clearly reminded of the very serious role of plant pathology, like medicine, in solving problems of humanity.

The primary thesis of the book, stated at the outset, is that agricultural systems create conditions that favor disease. Plants are in widespread coexistence with their pathogens, but diseases become highly destructive in the context of human activities. Our challenge lies in identifying why these epidemics arise and in identifying what can be done to prevent them. Scheffer takes on this challenge using a series of case studies of specific diseases, grouped into chapters based on the primary factors that cause disease. This case-study approach is marvelously holistic, detailed and informative. In the case of *Fusarium* wilt of banana, for example, we learn about banana farming, their history from ancient to modern times, the triploid genetics of banana, and the United Fruit Company's monopolistic influence on the rural sociology, politics and economy of many Caribbean, South and Central American nations. We read about the early appearance of 'Panama disease' and how this grows into a threat to all plantation farming in the western hemisphere as a consequence of the

cultivation of a single genotype for export markets. We also learn, among many other things, of molecular markers to identify vegetative incompatibility groups and pathogenic races of the causal agent *Fusarium oxysporum* f. sp. *cubense*. Host resistance is manifested as xylem occlusions that block pathogen spread, and disease occurs in genotypes where the pathogen persistently outgrows a slow resistance response, leading to extensive xylem blockages. Scheffer's bottom line, however, is that this disease must be attributed not only to genotype-specific xylem blockage, but also to human movement of contaminated rhizome stocks and to the development of large monoculture plantations. He concludes the section with a plea for aggressive breeding programmes to diversify the genetic base of cultivated bananas.

The case-study approach is an excellent vehicle through which readers will gain an integrative 'feel' for diseases of cultivated plants and for the evolution of the science of plant pathology. Scheffer's writing is firmly grounded in specifics. More than 700 references are provided, primarily of recent vintage but often reaching back over the last 140 years. Unfortunately, with 200 pages of similarly structured case studies, the reading becomes laborious. Many readers will enjoy sections of the book, but few will read it cover-to-cover in the absence of external incentives. In addition, because of space considerations and generalist coverage, some of the topics are represented by small slices of information that are not entirely representative. The first 70 pages of the book contain an introduction to the basic biology of plant diseases. This