

LEAF DEMOGRAPHY AND PHENOLOGY IN AMAZONIAN RAIN FOREST: A CENSUS OF 40 000 LEAVES OF 23 TREE SPECIES

PETER B. REICH,^{1,6} CHRISTOPHER UHL,² MICHAEL B. WALTERS,³ LAURA PRUGH,⁴ AND DAVID S. ELLSWORTH⁵

¹*Department of Forest Resources, University of Minnesota, St. Paul, Minnesota 55108 USA*

²*Department of Biology, Pennsylvania State University, University Park, Pennsylvania 16802 USA*

³*Department of Forestry, Michigan State University, East Lansing, Michigan 48824 USA*

⁴*Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4*

⁵*School of Natural Resources and Environment, University of Michigan, Ann Arbor, Michigan 48109 USA*

Abstract. The periodicity, synchrony, and causes of variability in the demography of tree leaves in ecosystems with relatively aseasonal climates, such as tropical rain forests, is still poorly understood. To address this issue, we surveyed the timing of birth and death of >40 000 leaves of 1445 individuals of 23 evergreen rain forest species in several late primary and early secondary successional plant communities at San Carlos de Rio Negro, Venezuela, in the northern Amazon basin. In all species, the mortality rate generally increased with leaf age. However, in many species, deceleration of death rates with extreme leaf age was noted. In general, for each species, the age structure of leaf populations and the frequency distribution of leaf life span were broad. Species differed substantially in their leaf demography. Measured in their native habitats, seven species common to disturbed open sites had shorter median life spans (0.7 yr) than five species common to open but infertile Bana primary communities (1.9 yr average) or six species common to two tall primary forest communities (Tierra Firme and Caatinga), when measured in high-light conditions in the canopy (2.0 yr average).

Variation in light availability had consistent effects on leaf life span in all species. Species native to Tierra Firme forest had average leaf life spans of 3.2, 1.9, and 1.6 yr, respectively, in deeply shaded understory microsites, in small gaps, and in sunlit mature tree canopies. Species native to Caatinga forest had average leaf life spans of 4.2, 3.4, and 2.5 yr, respectively, in these same microsite types. Two species common in gaps and in disturbed sites had much longer leaf life span in shaded understory than in open, disturbed microsites. For all species, responses were similar when trees were planted in sites differing in light availability, as when trees naturally established across light gradients.

The rate of leaf production, the risk of leaf mortality, and the leaf life span were not periodic or related consistently to seasonality of climate. Negligible relationships existed between the mild annual dry season and either leaf production or leaf mortality in all species. Thus, leaf phenology and demography were essentially aseasonal in this tropical forest environment.

Key words: Amazonian rain forest; leaf life span; leaf longevity; light; nutrients.

INTRODUCTION

Leaf longevity and phenology are important characteristics of species that reflect the influence of evolution and the environment on plant traits and that, in turn, have substantial implications for plant functioning at leaf, whole-plant, and ecosystem scales (Chabot and Hicks 1982, Coley 1988, Reich et al. 1992, 1997). This is true in tropical forests as elsewhere (Frankie et al. 1974, Borchert 1980, Reich and Borchert 1984, Coley 1988, Reich et al. 1991, Mulkey et al. 1995), although much uncertainty remains for such systems. In the markedly seasonal temperate and boreal forest biomes, trees of most species have leaf phenologies, life spans (if deciduous), and demographies that are usually syn-

chronized with seasonal patterns. A similar linkage of tree species phenology with seasonality occurs in many, but not all, species in markedly seasonal tropical forests and woodlands (Frankie et al. 1974, Reich and Borchert 1984, Shukla and Ramakrishnan 1984, Reich 1995, Williams et al. 1997). In contrast, in relatively aseasonal environments, phenology, longevity, and demography may be relatively asynchronous within and among different species (Borchert 1980), but the degree of asynchrony and details about leaf survivorship and mortality patterns are not well known.

Data regarding the leaf life span of tropical rain forest plants have only become available during the past quarter century. A pioneering study by Bentley (1979) reported two-year survivorship of 135 leaves (five leaves from each of 27 woody species). Since that time, only a relatively small number (~15–25) of detailed leaf demography studies have been made that are relevant to the ecology of tropical evergreen moist forests.

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⁶ E-mail: preich@umn.edu

Many of the published studies (e.g., Bentley 1979, Williams et al. 1989, Hegarty 1990, Miyaji et al. 1997, Nitta and Ohsawa 1997) were carried out for a relatively short time (1–2 years) and/or used indirect methods of assessing leaf life span (Williams et al. 1989, Sterck 1999), so in these cases little information is available on seasonal, intercohort and interannual variation. Several studies made over periods of 4–10 years (Clark et al. 1992, Lowman 1992*a, b*, Sharpe 1997) have addressed issues of intercohort and interannual variability. Beyond these studies, few data are available on long-term patterns for multiple species and individuals within a forest.

The collective body of work referenced above found a wide variation in leaf longevity and demography among species, but significant relationships of leaf production, mortality, and life span to seasonality (either precipitation or temperature). For instance, rates of leaf production varied with seasons in subtropical Australia (Hegarty 1990, Lowman 1992*a*), in evergreen subtropical forest in Japan (Nitta and Ohsawa 1997), in montane tropical cloud forest in Mexico (Williams-Linera 2000), and in wet tropical forest in Panama (Coley 1983, Aide 1993). Rates of leaf mortality (when measured) also were seasonal in each of those studies. In most of the few studies where patterns were reported, leaf life spans varied for cohorts produced at different times of year or for leaves that died at different times of year (Shukla and Ramakrishnan 1984, Lowman 1992*a*, Nitta and Ohsawa 1997). The observed variation in leaf life span was apparently related to the influence of modest to marked seasonality (cool seasons in subtropical forests and dry seasons in moist tropical forests) on leaf mortality rates.

Hence, where even moderate seasonality (in temperature or moisture) occurs, data suggest that climate exerts marked control on the temporal patterns of leaf dynamics. The evidence is not definitive in areas with mildly seasonal climates (Cuevas and Medina 1986, Miyaji et al. 1997, Sharpe 1997). Therefore, the degree to which tropical rain forest tree species exhibit seasonality and synchrony of leaf demography is still unclear, and many important questions remain unanswered. How similar is leaf life span among individuals within species, or within individuals among years? What is the probability of mortality for a leaf as it ages or in relation to modest seasonal variation in climate? Do species differing in shade tolerance vary in leaf demography within and across varying light environments?

Light availability affects leaf life span directly via plastic responses (i.e., acclimation) (Ackerly and Bazzaz 1995, Miyaji et al. 1997) and indirectly via adaptation in leaf life span (Coley 1988). As a result, shade-tolerant tropical rain forest species have longer leaf life span than intolerant species when both are measured in their most common native habitat (Williams et al. 1989, Reich et al. 1995). Under such con-

ditions, both genotypic and environmental factors are at play. Although it is generally considered that shade-tolerant species tend to have greater leaf longevity than intolerant species in rain forests, even under comparable light conditions (Coley 1988, Williams et al. 1989, Lusk and Contreras 1999; but see Valladares et al. 2000), there are surprisingly few adequate tests of this.

Evidence on acclimation responses to variation in light is also surprisingly scant. Tree leaves growing in deeply shaded canopy positions lived longer than those in high-light environments in a total of 10 temperate evergreen, subtropical, and tropical species (Lowman 1992*a*, Reich et al. 1995, Miyaji et al. 1997). However, in three studies with a total of 17 woody tropical species, only four species had shorter leaf life span when growing in higher light microsites (Williams et al. 1989, Sterck 1999, Rose 2000). Thus, data are inconsistent regarding whether extended leaf longevity in deeper shade is a common acclimation response.

To address the above issues, we made a long-term study of the demographics of leaves of 23 tree species growing in several different communities within an Amazonian rain forest complex. This involved a long-term (9-year) census of the birth and death of ~40 000 leaves of 1445 individuals at San Carlos de Rio Negro, Venezuela (hereafter referred to as San Carlos). We studied naturally established and planted trees in both high- and low-light conditions and assessed changes in leaf production and mortality in relation to climate, year, and environmental position. The relationships between the average life span of a small subset of leaves in selected environments and other physiological and ecological processes have been addressed in previous reports (Uhl 1987, Reich et al. 1991, 1994, 1995). Here we focus in detail on the variation in leaf demography, including leaf production and life span, within and among species and environments, to address the following set of questions and related hypotheses:

1) How do species common to different communities and successional stages, or adapted to different light habitats, differ in the demographics of their leaf populations? *H1*: Species common to low-resource habitats will have longer leaf life span than those common to higher resource habitats, even when measured in a common environment.

2) How does light environment influence variation in leaf demography within species? *H2*: Leaf life span will increase with increased shading.

3) How does the risk of mortality vary with leaf age? Do age-related changes in mortality follow similar or different patterns among species and communities? *H3*: Once beyond the juvenile stage, mortality rates will accelerate with leaf age.

4) How heterogeneous is leaf production, mortality, and longevity among individuals? Given that different individuals grow at different rates, in varying microhabitats, and exhibit different degrees of suppression from competitors, it would not be surprising if different

TABLE 1. Monthly and annual rainfall, and the median rainfall (precipitation) and pan evaporation (evaporation) (all in mm) at San Carlos de Rio Negro, Venezuela, over an 11-year period.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1980	132	89	310	209	306	369	401	285	489	345	365	107	3408
1981	152	248	272	369	328	382	545	276	172	166	168	308	3385
1982	133	224	277	368	492	454	520	377	217	193	231	210	3696
1983	73	201	230	329	401	359	334	247	305	187	137	219	3022
1984	283	256	217	212	425	334	372	424	240	410	249	250	3670
1985	115	64	299	169	428	413	445	419	253	235	289	176	3305
1986	220	253	179	274	296	387	442	251	254	326	347	346	3575
1987	185	156	193	322	394	363	340	340	394	217	191	100	3194
1988	304	163	101	158	331	565	459	265	345	240	311	225	3466
1989	256	150	290	254	434	404	333	216	246	381	281	173	3418
1990	232	117	274	312	456	518	406	370	107	241	202	454	3690
Median precipitation	185	163	272	274	401	387	406	285	253	240	249	219	3408
Median evaporation	154	142	167	140	137	115	131	148	153	152	143	149	1703

Note: Data from Venezuelan Hydrology and Meteorology Network.

individuals showed marked variation in leaf demography in an aseasonal climate (Borchert 1980). *H4*: Phenology will be asynchronous among individuals and species.

5) Does seasonality influence the rates of leaf births, deaths, and overall patterns of leaf longevity or phenology? Is the risk of mortality greater during the (relatively mild) annual dry season at San Carlos, and if so, does this differ among species and/or among leaf age classes (i.e., young, mature, old leaves)? *H5*: Leaf production will be lower and mortality rates will be higher during the annual dry season than during the wet season, and in dry years vs. wet years.

METHODS

Sites and species

The research site was located near San Carlos de Rio Negro, Venezuela (1°56' N, 67°03' W) at 119 m elevation in the north-central Amazon Basin. The climate of the region is humid equatorial, with a mean temperature of 26°C, a mean annual rainfall of 3565 mm, and a mean annual potential evaporative demand of 1700–1900 mm (Ministerio del Ambiente y de Recursos Naturales Renovables). Temperature varies slightly month-to-month or year-to-year; the mean temperature is between 25° and 27°C in every year. During the period of this study (~1982–1990), annual precipitation ranged from a low of 3022 mm in 1983 to a high of 3696 mm in 1982 (Table 1). Although substantial rainfall occurs throughout the year, there is pronounced seasonality, with December through March being the driest period and May through July the wettest time of year. The driest months in the 9-year study period (and the only months with <100 mm rainfall) were February 1985 (64 mm) and January 1983 (73 mm). In both of these months, pan evaporation exceeded precipitation by >100 mm. The driest 2-month period during this study was January–February 1985 when a total of 179 mm rain fell.

Several well-differentiated communities occur in the Rio Negro region, each associated with distinct geo-

morphological positions and soil types that occur with slight elevation differences (Cuevas and Medina 1986, Reich et al. 1991). We studied 15 species from four undisturbed late-successional forest communities within 1 km of each other: species-rich Tierra Firme on oxisol, legume-dominated Tierra Firme on ultisol, Tall Caatinga, and Bana. Tierra Firme forests occur on the highest sites, while the Caatinga and Bana communities are at lower elevation, on periodically flooded fine-sand and coarse-sand sites, respectively (Cuevas and Medina 1986). The Bana community is considered the most nutrient limited of the tree primary communities (Cuevas and Medina 1986, Reich et al. 1994). The Caatinga community is more N limited than the Tierra Firme community, which may be more P or Ca limited (Reich et al. 1995). In addition, we studied eight species growing in cultivated and/or recently abandoned farm plots on Tierra Firme sites. We studied cultivated *Manihot esculenta* in farm plots, and seven early-successional tree species that colonize farm plots during cultivation and after abandonment. Sites were cultivated for 1–2 years following forest cutting and burning. Throughout this paper we will refer to species by genera, unless genus and species names are required for clarity.

The legume-dominated Tierra Firme community was represented by only the dominant tree species, *Eperua purpurea*. Data for this species are lumped hereafter with the other Tierra Firme species. Each of the other three primary communities was represented by four or five common species. Bana trees are relatively short and open grown, and a leaf demography census was carried out for midcanopy branches on such trees. For Tierra Firme and Caatinga (both tall forests), we censused naturally established individuals of all species in deeply shaded forest understory; for a subset of species, we censused leaves of individuals in forest treefall gaps and in canopy branches of tall, dominant trees (Table 2). These three microenvironments represent a gradient from deep shade to high light availability.

For four of the Tierra Firme and three of the Caatinga species, we also censused branches of young pole-sized

TABLE 2. Number of trees (total number of leaves) and median and maximum leaf life span (not available in all cases) for species established naturally and planted in various environments at San Carlos de Rio Negro, Venezuela.

Environment and species	No. trees (no. leaves)	Median leaf life span (d)	Maximum life span (d)
Tierra Firme			
Farm plot open			
Caesalpinaceae, <i>Eperua purpurea</i>	14 (470)	693	1307
Chrysobalanaceae, <i>Licania heteromorpha</i>	15 (388)	845	1490
Lauraceae, <i>Ocotea costulata</i>	9 (243)	456	1125
Burseraceae, <i>Protium</i> spp.	29 (1131)	687	1398
Canopy			
Caesalpinaceae, <i>Eperua purpurea</i>	31 (116)	541	1125
Chrysobalanaceae, <i>Licania heteromorpha</i>	152 (1796)	736	1763
Lauraceae, <i>Ocotea costulata</i>	138 (1594)	462	1490+
Gap			
Lauraceae, <i>Ocotea costulata</i>	6 (106)	708	1125
Understory			
Caesalpinaceae, <i>Eperua purpurea</i>	22 (212)	1037	2341
Chrysobalanaceae, <i>Licania heteromorpha</i>	31 (567)	1161	2675
Lauraceae, <i>Ocotea costulata</i>	30 (378)	1122	2584
Burseraceae, <i>Protium</i> spp.	30 (378)	1006	2219
Fabaceae, "Cabari" sp.	24 (165)	1544	2554
Second-growth understory			
Chrysobalanaceae, <i>Licania heteromorpha</i>	6 (429)	1502	2310
Lauraceae, <i>Ocotea costulata</i>	7 (132)	1110	2037
Burseraceae, <i>Protium</i> spp.	10 (1273)	1420	2219
Caatinga			
Farm plot open			
Clusiaceae, <i>Caraipa heterocarpa</i>	10 (146)	948	1581+
Caesalpinaceae, <i>Eperua purpurea</i>	8 (90)	757	1763+
Euphorbiaceae, <i>Micrandra sprucei</i>	7 (100)	845	1581
Canopy			
Clusiaceae, <i>Caraipa heterocarpa</i>	137 (2533)	885	2371+
Caesalpinaceae, <i>Eperua purpurea</i>	119 (602)	1076	1824
Euphorbiaceae, <i>Micrandra sprucei</i>	90 (708)	766	1490+
Gap			
Clusiaceae, <i>Caraipa heterocarpa</i>	1	1146	
Caesalpinaceae, <i>Eperua purpurea</i>	7 (132)	1228	1702
Euphorbiaceae, <i>Micrandra sprucei</i>	8 (225)	1338	1763
Burseraceae, <i>Protium</i> spp.	5	529	
Understory			
Clusiaceae, <i>Caraipa heterocarpa</i>	24 (530)	1268	2493+
Caesalpinaceae, <i>Eperua purpurea</i>	29 (188)	1389	2797
Euphorbiaceae, <i>Micrandra sprucei</i>	33 (401)	1623	3070+
Sapotaceae, <i>Micropholis maguirei</i>	27 (413)	1620	2888+
Burseraceae, <i>Protium</i> spp.	31 (363)	1693	2797
Bana			
Canopy			
Apocynaceae, <i>Aspidosperma album</i>	28 (890)	888	2523
Nyctaginaceae, <i>Neea obovata</i>	54 (1646)	377	1642
Burseraceae, <i>Protium</i> spp.	32 (585)	945	1946
Rubiaceae, <i>Retiniphyllum truncatum</i>	31 (4751)	474	1672
Bombacaceae, <i>Rhodognaphalopsis humilis</i>	20 (300)	748	1307
Early secondary successional			
Farm plot (open)			
Euphorbiaceae, <i>Manihot esculenta</i>	2 (156)	55	
Early second growth (open)			
Melastomataceae			
<i>Bellucia grossularioides</i>	46 (4734)	173	1003
<i>Clidemia sericea</i>	24 (1084)	258	730
<i>Miconia dispar</i>	2 (49)	334	

TABLE 2. Continued.

Environment and species	No. trees (no. leaves)	Median leaf life span (d)	Maximum life span (d)
Moraceae, <i>Cecropia ficifolia</i>	19 (1188)	76	
Celastraceae, <i>Goupia glabra</i>	23 (617)	365	1003+
Clusiaceae			
<i>Vismia japurensis</i>	27 (4908)	255	790
<i>Vismia lauriformis</i>	31 (2668)	234	730
Tierra firme understory			
Melastomataceae			
<i>Bellucia grossularioides</i>	24 (686)	745	1003
<i>Miconia dispar</i>	1 (47)	553	912

trees planted in high-light environments in recent clearings. Leaf demography was also studied for three of the Tierra Firme species that had been planted in the understory of a young (5–10 year old), naturally regenerated, second-growth forest. Two of the early successional species were studied in both high-light sites (abandoned farm plots) and in the forest understory where they were naturally established. The other early successional and Bana species were studied in a single (open) environment.

Leaf census approach and methods

Leaf demography was surveyed beginning in 1982 on one or two branches of 1445 trees of 23 species in 45 species–site combinations (Table 2). Branches in mid-to-upper canopy positions in large trees were censused by tree climbing. For all species except *Manihot* and *Cecropia* (see next paragraph), the timing of birth and death of individual leaves was tracked over time at repeated census intervals for every tree. Census intervals typically ranged from 1 to 4 months among species, with shorter intervals used for species with faster leaf turnover rates. Newly produced leaves were identified as those that had emerged since the prior census. A leaf (from the prior live-leaf census population) was identified as newly dead if it had either disappeared or was present but visibly dead. A systematic drawing of branch, subbranch, and leaf position was used to make these surveys, with different colored pencils used at every census date to draw every new leaf (or to indicate that no new leaves were observed) and to cross out every newly dead leaf (death). The life span of each leaf was calculated as the time between the census of first appearance and the first census of death or disappearance.

For *Manihot* and *Cecropia* the mean leaf life span per plant was assessed using a technique commonly used for species with relatively continuous and equal leaf birth and death rates (Williams et al. 1989, Ackerly 1999). The total cumulative number of leaves produced and dead are plotted over time, and the mean distance in time between the two theoretically parallel lines is equivalent to the average leaf longevity.

The leaf life spans reported in this paper are in some cases shorter than in our earlier publications (Reich et al. 1991, 1995), for two reasons. First, the data presented in the earlier leaf physiology papers represented a small subset of all leaves, and the average life span reported was pooled across light environments that were skewed toward the understory. Second, in those papers (and done similarly by Lowman 1992a, b), we used mean life span of leaves that did not die during the first one-fifth of the average life span (considering that those that died young were likely due to herbivory, disease, or other noninternally regulated factors, and thus did not reflect the intrinsic life span). Hence those earlier papers used the life span of all leaves that did not die a premature death, given the desire to relate the intrinsic leaf life span with other leaf ecophysiological traits of young, mature leaves. Thus, using the entire population, leaf life spans reported here would be shorter than those reported earlier.

Statistics

We analyzed for environment and species differences in survival with proportional hazards modeling (Fox 1993) using JMP software (SAS 1997). Leaves that were harvested for physiology measurements for other studies (e.g., Reich et al. 1991) were “right censored” in the data set (this amounted to a tiny fraction of the total), as were leaves that lived beyond the final census date. Right censoring indicates that a leaf was alive at the time it was removed from the population pool used for statistical analysis. We chose semiparametric proportional hazards modeling over parametric approaches, since preliminary analyses of Weibull, and log-log transformations of product limit (Kaplan-Meier) survival curves indicated that the risk of mortality varied substantially among environments and species. Under such a situation, Fox (1993) recommended proportional hazard modeling. Based on the results of the proportional hazards analyses, we developed estimates of proportional survival over time or leaf age for species in each environment using the Kaplan-Meier approach. We tested for significant differences in Kaplan-Meier estimates among species, within and across environ-

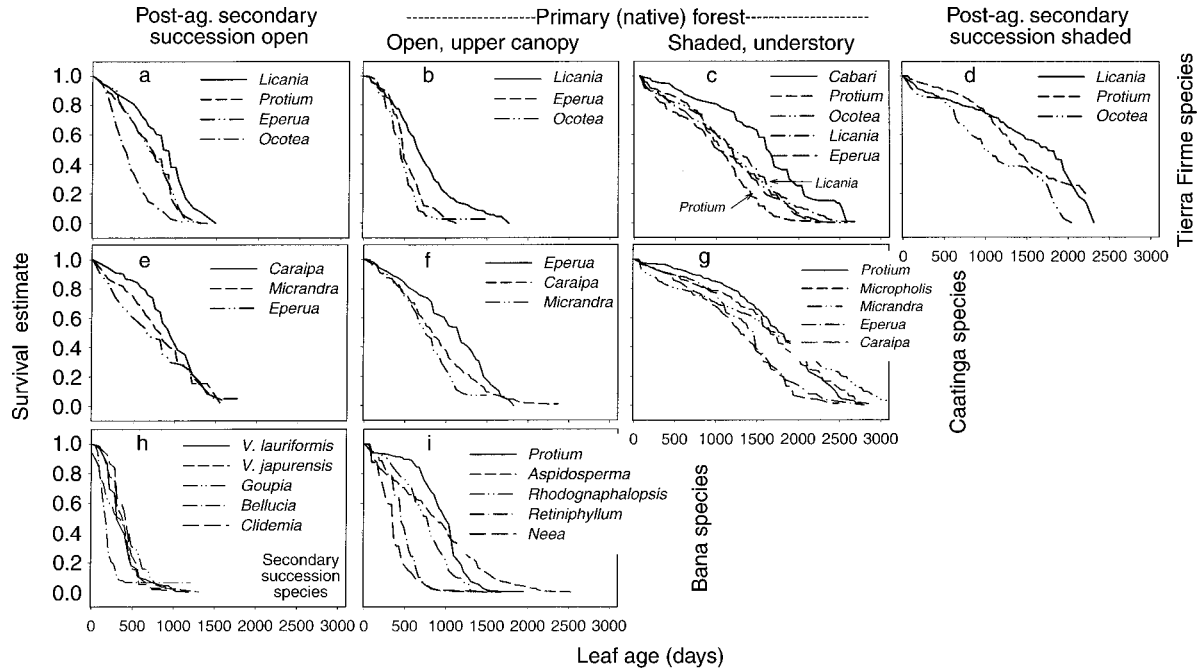


FIG. 1. Mortality curves (i.e., Kaplan-Meier survivorship curve) for species in open and shaded postagricultural secondary successional Terra Firme sites (panels a, d, e, and h) and three different primary forests (panels b, c, f, g, and i), corresponding largely to the nongap sites in Table 2. In addition to species naturally regenerated in these sites, these panels include species common to the Terra Firme and Caatinga forests that were planted in postagricultural Terra Firme sites with differing degrees of canopy closure (a, d, and e). All curves were significantly different. For each curve, data from all individuals and all leaf cohorts were pooled.

ments, and within species among environments; and for different cohorts with log-rank and Wilcoxon tests (Kalbfleish and Prentice 1980). The log-rank test places more weight on larger survival times and is most useful when the ratio of hazard functions (hazard function = instantaneous failure rate at a given time) in the groups being compared is approximately constant. The Wilcoxon test places more weight on early survival times and is the optimum rank test if the error distribution is logistic. Median leaf life span was calculated as the half-life from the Kaplan-Meier estimates. Contrasts among community types and habitats (understory, gap, canopy, farm plot) were made using analysis of variance, with species as replicates.

To assess whether temporal patterns of leaf production or mortality displayed periodicity or synchronicity among leaves of different ages, among trees within a species or among species on a site, we utilized simple correlations of either proportional productivity rates or percentage mortality rates per month (30.4 d) for a number of census dates. For example, to test whether leaf mortality in trees A and B were synchronized or not, we correlated pairs of proportional mortality data for all census intervals in common. In essence, if tree A had high proportional mortality during census intervals where tree B also had high mortality, and low mortality when tree B had low mortality, their mortality rates would tend to be significantly correlated across

all common census intervals. We used this approach to assess correlations of production and mortality among and within species, microenvironments, and sites. To do this, we classified leaves into age classes (e.g., expanding, young fully expanded, mature, old).

RESULTS

Variation among species and environments

Species differed substantially within and among communities in the dynamics of their leaf population demography. For the 23 species (in a total of 47 species-microsite combinations), median leaf life span varied from 0.2 to 4.7 yr and the maximum life span was >8.4 yr. All species common to disturbed early-successional sites tended to have short average and maximum leaf life spans, while those occupying infertile Bana or shaded tall primary forest sites tended to have longer leaf life spans (Figs. 1 and 2, Table 2; differences significant at $P < 0.001$).

Plants that pass a significant part of their life history in shaded understories had longer leaf life spans (under comparable light levels) than species that typically occupy higher light microhabitats. In the shaded Terra Firme understory (Table 2), late-successional shade-tolerant species had greater leaf life spans (average of 3.2 yr) than *Bellucia* and *Miconia* species (1.5–1.75 yr), which are more commonly gap inhabitants. Similar

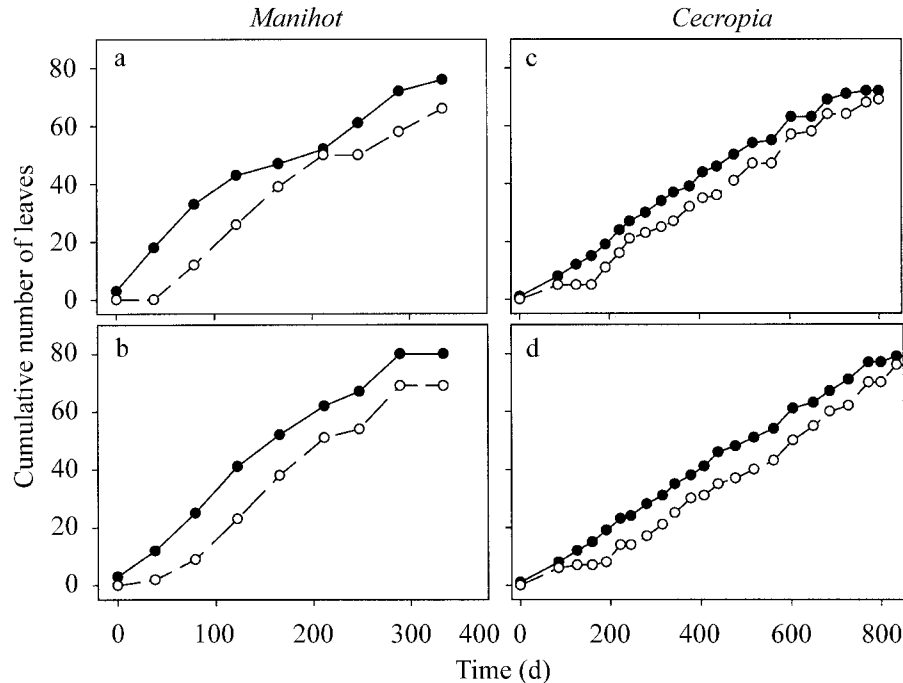


FIG. 2. Measured values for cumulative number of produced (solid circles) and senesced (open circles) leaves over time for two individuals each of *Manihot esculenta* and *Cecropia ficifolia* (total numbers of trees of each were 2 and 19, respectively). These data in total were used in determining the leaf life spans in Table 2.

patterns occurred at high light. Species that typically occur early during succession under high light availability (Reich et al. 1995, Ellsworth and Reich 1996) have a shorter leaf life span (mean of 0.8 yr for seven species) than later successional species, when both groups were contrasted in comparably sunlit, open environments (mean of roughly 1.7 yr for upper canopy forest trees or open-grown saplings) (Table 2).

Among the three primary communities, the average leaf life span in sunlit microhabitats ranged from 2.5 yr in Caatinga, to 1.9 yr in Bana, and 1.6 yr in Tierra Firme, with substantial variation among species in each community (Table 2). Contrasts of the two tall forest types (Caatinga and Tierra Firme) provide evidence to test Hypothesis 1 (regarding differences in leaf life span among forest communities differing in resource availability). Caatinga species had longer leaf life span, on average, than Tierra Firme species in each of four comparably lit habitats (Table 2): 2.3 vs. 1.8 yr when planted in an open farm plot; 2.5 vs. 1.6 yr in well-lit mature forest canopy; 3.4 vs. 1.9 yr in gap; and 4.2 vs. 3.2 yr in natural understory. In analysis of variance, these differences were significant for both community type ($P < 0.0001$) and habitat ($P < 0.0001$), and the differences between communities was not affected by habitat ($P = 0.49$). These contrasts of Caatinga (average leaf $N = 1.02 \pm 0.012\%$; mean ± 1 SE) and Tierra Firme species (average leaf $N = 1.65 \pm 0.12\%$; $P < 0.005$) are consistent with the hypothesis that for communities with similar light environments, and con-

trolling for light environment, species from the more nutrient-poor community would have longer lived leaves. The results also strongly support Hypothesis 2 that leaf longevity decreases with increasing habitat irradiance. For both forest community types, trees in the two well-lit habitats (open farm plot and forest canopy) had shorter leaf life span than trees in the small gaps, with trees in the deeply shaded forest understory having the longest life span of all habitats.

Contrasts among species within sites.—Among species growing in a common environment, those with the shortest median leaf life span tended to show a greater risk of mortality for leaves at every leaf life stage (the survivorship curves continued to diverge over time) (Fig. 1). This was generally true, although there were exceptions.

For instance, in the Bana community 21% of all *Aspidospermum* leaves died by the age of 270 d (Fig. 1), similar to the 20% mortality by 270 d shown by *Retiniphyllum*. Yet average leaf life span in *Aspidospermum* was 2.4 yr (888 d) vs. 1.3 yr (474 d) for *Retiniphyllum* (Table 2), because the mortality rates for older leaves were greater for the latter species. Two other Bana species (*Protium* sp. and *Rhodognaphalopsis*) with median leaf life span similar to *Aspidospermum* had substantially lower cumulative mortality (7% and 6%, respectively) by leaf age of 270 d than *Aspidospermum*. However, the monthly mortality rate remained low in *Aspidospermum* until leaves were 5 yr old (shallow slope, Fig. 1), whereas for *Protium* and

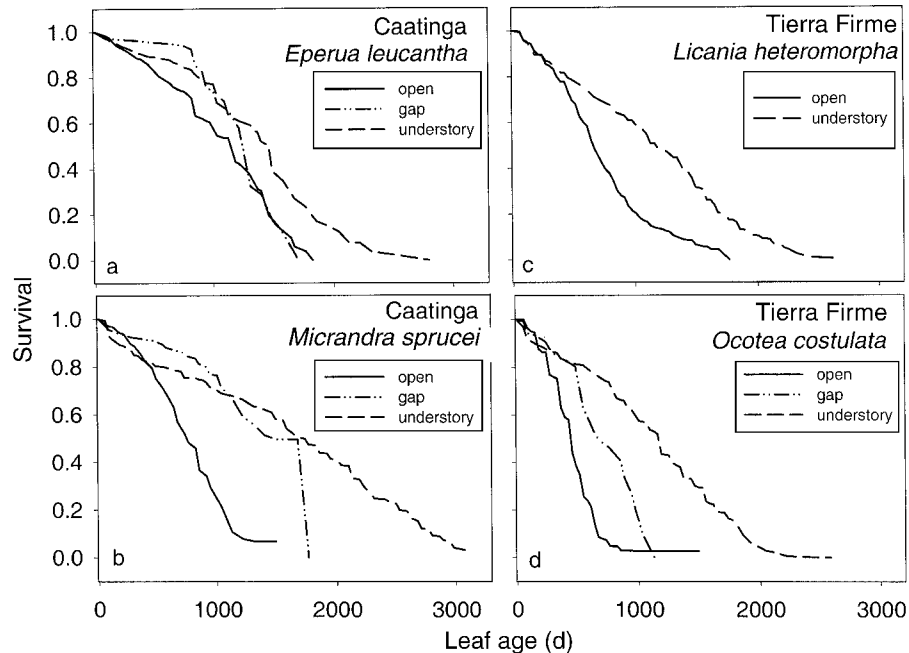


FIG. 3. Mortality curves (Kaplan-Meier survivorship curve) for a subset of species across light environments. Shown are two species each from Tierra Firme and Caatinga forests, each compared in mature tall forest canopy (open), forest gap, and understory environments. All curves were significantly different.

Rhodognaphalopsis, the monthly mortality rate rose more quickly with leaf age (steeper slope). Hence the survivorship curves cross for *Aspidospermum* and these other species (Fig. 1 showing all five Bana species curves). By leaf age of 4 yr old, 15% of all *Aspidospermum* leaves were still alive, contrasted with 2% of *Protium* (Bana) and none of *Rhodognaphalopsis*.

A similar pattern (including a crossover in survivorship curves) occurred in the Caatinga understory for *Micrandra*, *Micropholis*, and *Protium*, all of which had similar average leaf life span (~4.5 yr). *Micrandra* had greater early mortality (compare species at 250–500 d leaf age) than all four other Caatinga species, but its mortality rates remained low for many years. Hence, 11% of all *Micrandra* leaves were alive at age 7.6 yr when only negligible percentages of leaves of other Caatinga species were alive.

Contrasts within species among sites and microsites.—For 10 species, leaf demography was tracked in different light environments (Table 2). In all cases, leaf life span was significantly ($P < 0.001$) longer in shaded than open-grown sites, either for naturally established or planted individuals. For naturally established trees within Tierra Firme and Caatinga, census data were compared for large trees with sunlit crowns vs. smaller trees in gaps and in the understory within the same forest stand. In every such case, there were large significant differences in leaf survival among light environments (Table 2, Fig. 3), with 50–100% greater leaf life span in more shaded environments. Three Tierra Firme species were also planted in open and in shaded

postagricultural sites; in these cases, leaf life span was twice as great in the more shaded individuals (Table 2, $P < 0.001$). Large differences in leaf life span were also observed for the mid-to-intolerant *Bellucia* compared in different light environments. *Bellucia* had median leaf life span of 0.40–0.48 yr in three different recently abandoned farm fields (data otherwise pooled), and leaf life span of 2.0 yr growing in the Tierra Firme understory.

Additionally, in relatively comparable light environments, species had similar leaf life spans (Table 2), regardless of other potential sources of variation. Six species common to tall forests had similar leaf life spans, on average, as young trees planted in the open (2.1 yr, average of the six species) as in natural sunlit upper canopy positions for older trees (2.0 yr).

Variation among trees and with seasons and years

How variable is leaf production and mortality from tree to tree, season to season or year to year? Different individual trees of a species growing in the same environment tended to show different temporal patterns of leaf production or mortality (e.g., Fig. 4). For all species, there was considerable variability in median leaf life span among trees within a site (Fig. 5), especially for trees with low leaf populations. Given that only one or two branches were surveyed per tree, and that there is high variability in light microsites in the understory and even in the upper canopy (e.g., Tjoelker et al. 1995), it is difficult to assess how much of the tree-to-tree variability shown in Fig. 5 is due to dif-

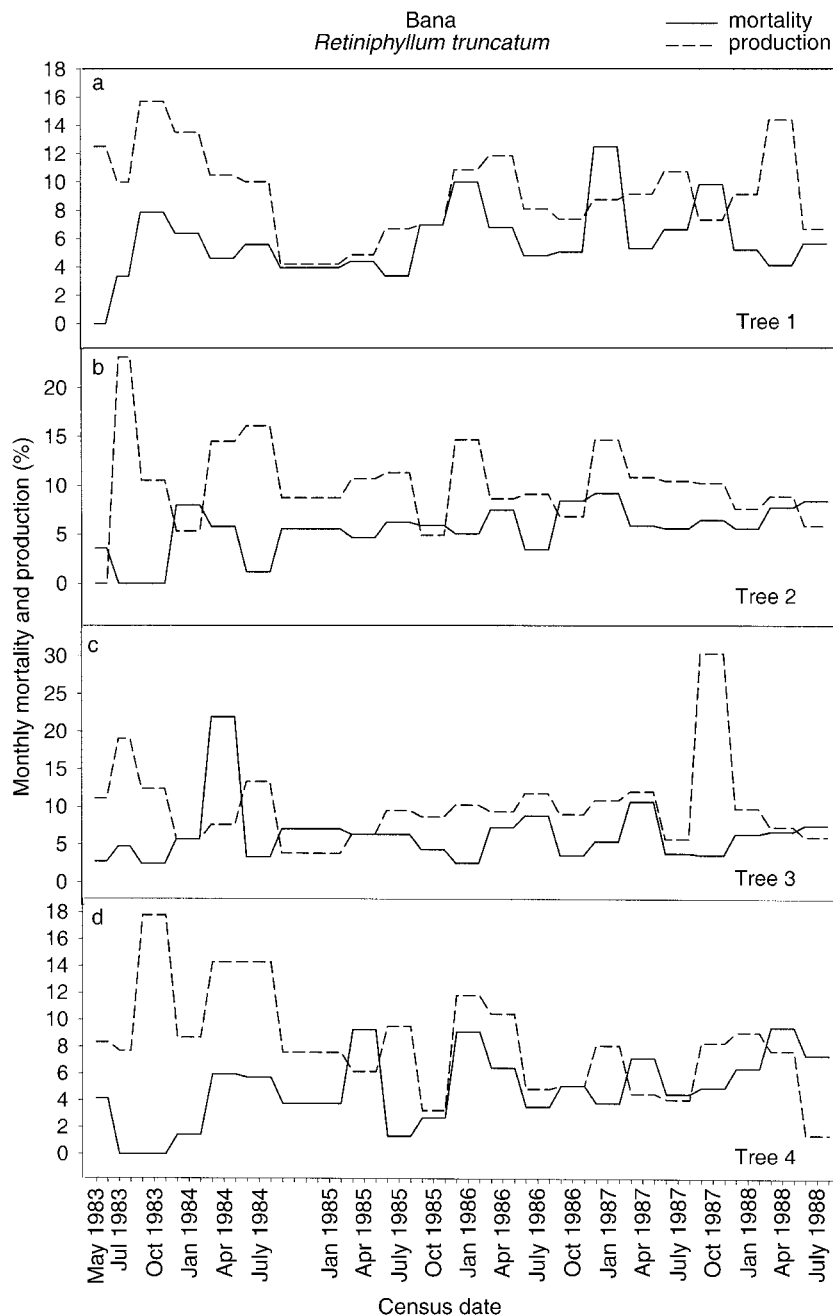


FIG. 4. Monthly leaf mortality and production rates for four *Retiniphyllum* trees over a 5-year time frame. For each census interval, mortality and production rates were calculated for the population of leaves at the end of the interval in relation to the population of leaves at the beginning of the interval.

ferences in branch microenvironment, how much to genotypic variation among trees, and how much due to branches with low leaf sample sizes.

For four randomly selected *Retiniphyllum* trees with relatively large sample sizes, different trees had generally similar overall survivorship curves (e.g., Fig. 6a), and similar median leaf life span and leaf age population structure. For all *Retiniphyllum* leaves ($n = 4571$) pooled across trees ($n = 31$), there were signif-

icant differences ($P < 0.001$) in survivorship for leaves produced in different months and years (Fig. 6b) or in different seasons, pooling across years (Fig. 6c). However, the differences were relatively small. For example, leaves produced in August–October or November–January, before or during the driest time of year (Table 1), respectively, had slightly shorter median life span (1.19 and 1.23 yr, respectively) than those produced before (February–April) or during (May–July) the wet-

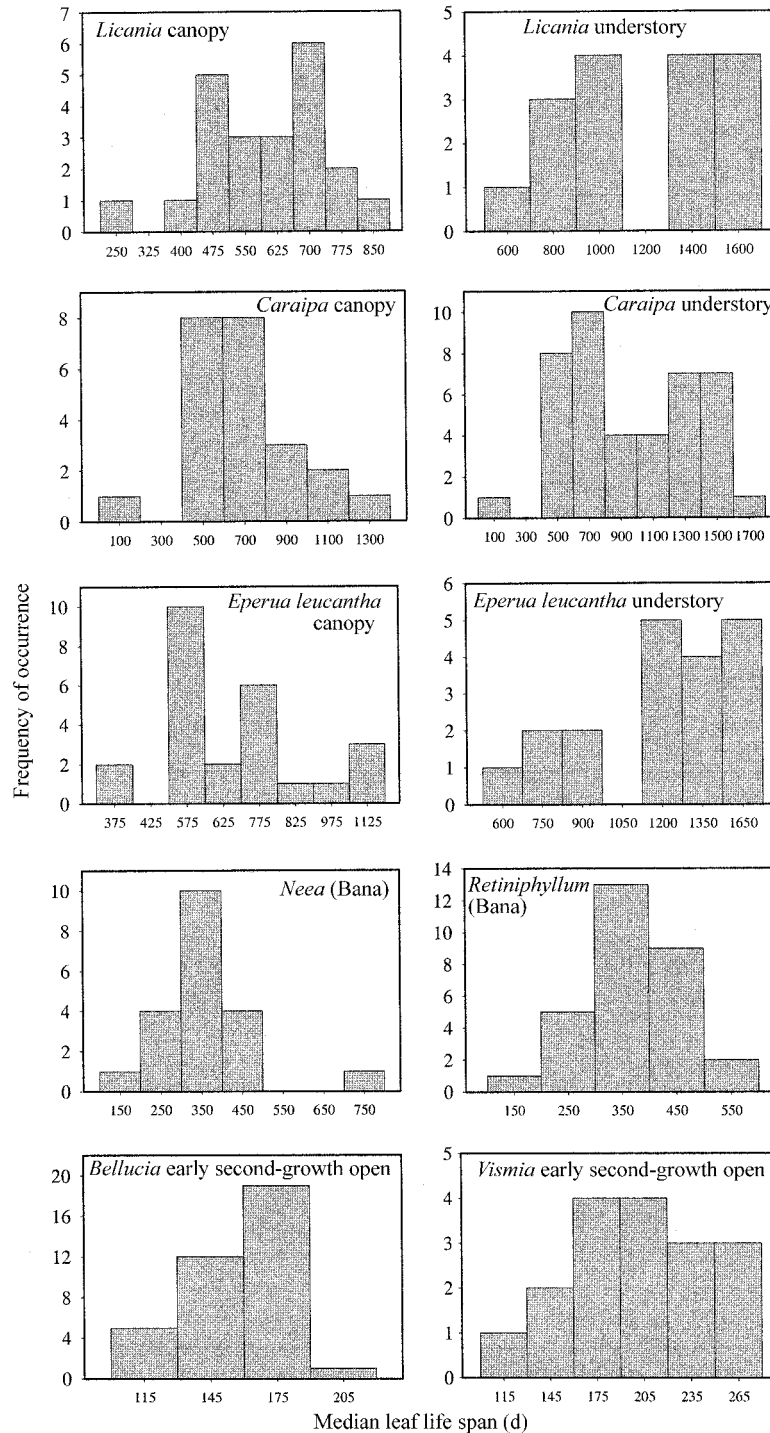


FIG. 5. The frequency distribution among trees of median leaf life span (per tree) for seven species, three of which are shown in contrasting light microenvironments.

test time of year (1.28 to 1.32 yr, respectively). Differences in survival over time among leaf cohorts produced in different times of year were even smaller, and not significant ($P > 0.05$), when the comparison was restricted to a single tree (Fig. 6d). For all *Retiniphyll-*

lum trees, survival for cohorts produced during the same seasonal period, but in different years, varied as much as among seasons within years (Fig. 6b). For individual trees examined over time (e.g., Fig. 4), we see no evidence of climate-related variation in pro-

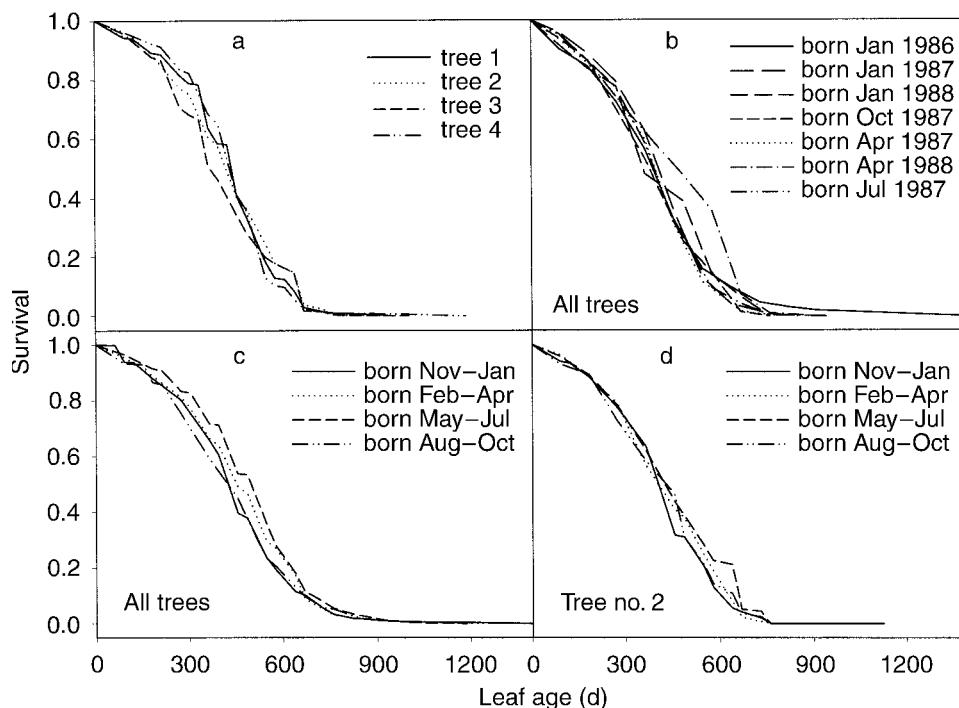


FIG. 6. Survivorship curves for *Retiniphyllum* leaves in several contrasts: (a) comparing four randomly chosen trees growing in the same stand (pooling all leaf cohorts per tree); (b) pooling among all trees in the stand, contrasting the month and year of leaf emergence; (c) pooling all trees in the stand, contrasting the season of leaf emergence (pooling across all years); and (d) for a single tree, contrasting the season of leaf emergence (pooling across all years).

duction or mortality. The driest months during that period of time (January–February 1985 and December 1987) are not noticeably different than other periods. Changes in the cumulative production and mortality of leaves for *Cecropia* and *Manihot* (Fig. 2) also showed no discernible impact of seasonality in climate. Neither leaf production nor mortality rates showed any relation to the wetter vs. drier times of year.

For most species, the median leaf life span (pooled across individuals) tended to be relatively stable over time (both across seasons and years), but not for all (compare *Retiniphyllum* to *Aspidospermum*, both in the Bana) (Fig. 7). Although there was appreciable variation in some species, this was not generally related to any particular year (as there would be if an unusual climate event occurred) nor to any particular season (as would occur if leaf life span was positively or negatively influenced by the time of birth relative to seasonality).

Interannual variation.—Pooling all leaves produced within a calendar year, there was modest variation among years in leaf life span for most species growing in relatively high-light environments (Table 3), and the observed variation was without temporal pattern. In contrast, in shaded natural understory environments, more than half the species showed a general decline in median leaf life span over the course of 5–6 years. This was especially pronounced in *Eperura purpurea*, *Li-*

cania, *Micrandra*, and *Micropholis* in forest understory (Table 3) (see *Discussion*).

In contrast to the shortening of leaf life span with years among the sampled population in natural understory, three of the same species showed increasing leaf life span over a 3-year period in the second-growth understory (Table 3). Plants in this site experienced a variable light environment over time. Given the age of the stand and the rate of canopy infilling for young forests at San Carlos (C. Uhl, *unpublished data*), it is likely that these individuals became increasingly shaded by the closing of the canopy over a period of several years, as observed more generally at San Carlos (Ellsworth and Reich 1996). Thus, these individuals shifted from moderate shade (somewhere between a gap and a tall forest understory) to increasingly deep shade over time. The response of increasing leaf longevity with decreasing light availability is consistent with responses across environments that differ, on average, in light conditions.

Variation with respect to season and climate.—Production and percentage mortality were generally unrelated to season or climate variation (Figs. 4 and 6–8, Table 1). To examine this latter issue directly, we tested for significant correlation of either production rate or mortality rate with one of three climate indices: mean monthly precipitation, evaporative demand, or their difference; each was averaged over the time in-

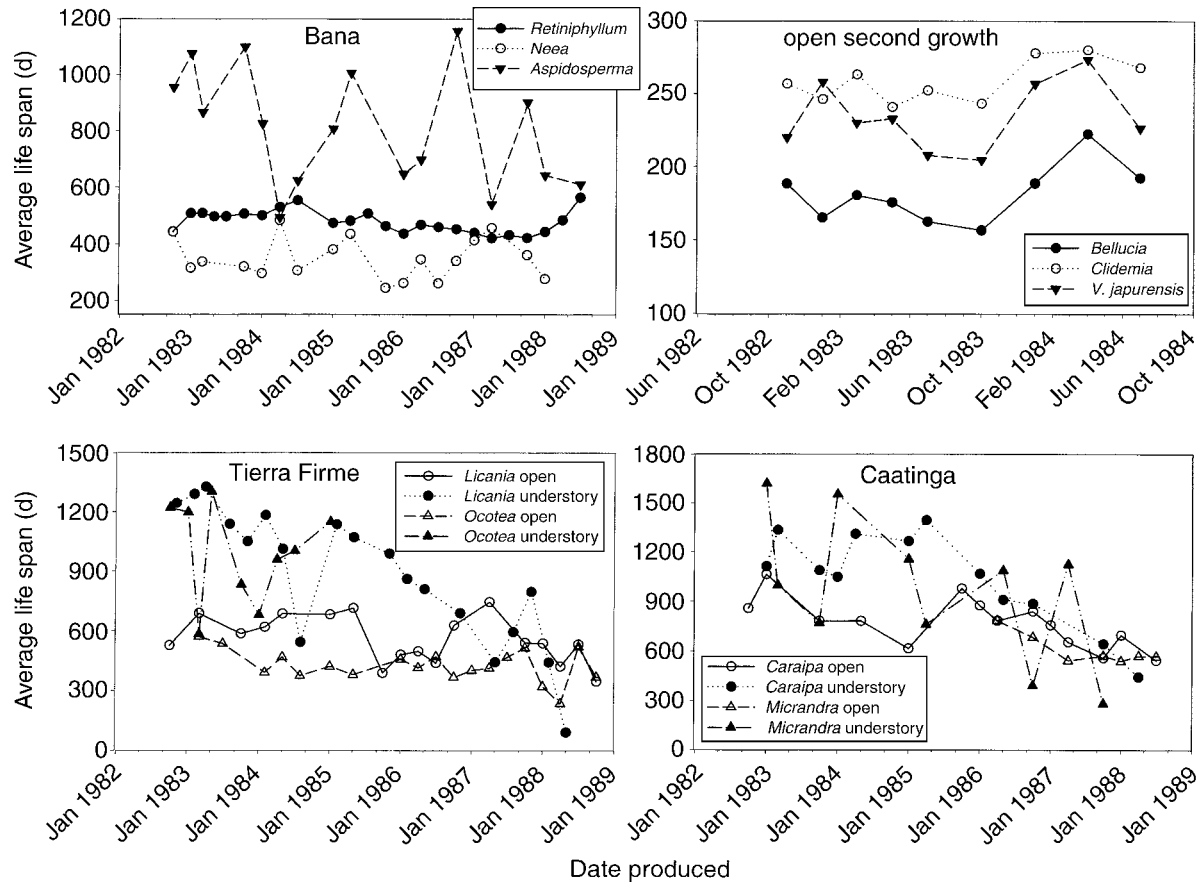


FIG. 7. Median leaf life span for leaves produced at every census date for 10 species in four communities. For the two species in each of the tall forest communities (Tierra Firme and Caatinga), trees in open canopy vs. shaded understory positions are contrasted.

terval between census dates for a 4-year period (from 1987 to 1990) for trees once the age-structure of the leaf population in the census had stabilized. Moreover, we differentiated percentage mortality by leaf age classes (expanding, young fully expanded, mature, old) to further minimize potential confounding due to variation in leaf population age structure over time. In no case was leaf production rate related to any of the available climate indices for any species. For mortality rate, in only a small number of cases (6 of 96 possible tests) were significant relationships ($P < 0.05$) found, and a similar number (5) of significant correlations would occur by chance. Moreover, even for the significant correlations, leaf mortality was sometimes positively associated with wetter and sometimes with drier time periods. We also found no correlation of mortality or production with either extreme years or months (wettest or driest). Hence, overall we conclude that for the time period of this study, there was no detectable relationship between leaf demography and any of the available climate measures.

Other sources of synchrony.—Despite the weak signal from seasons, climate, or years, phenological de-

velopment was more frequently correlated over time among age classes of leaves, among trees, among microsites and even among species than would be expected by chance (Table 4). To evaluate this, we correlated across census dates all pairwise combinations of mortality rate (mortality of each age class with mortality of every other age class) and production vs. mortality rates (i.e., mortality of each age class with new leaf production), and compared the number of significant correlations with the number that would be expected to occur by chance (if all data were random). As an example of these tests, consider correlation of mortality for different leaf age classes of a species. In essence, we are checking whether census intervals of relatively high mortality of young leaves also had relatively high mortality of old leaves. For tests within individual species at individual sites (pooled among individual trees), the correlation of mortality rates of one leaf age class with another, or of production rates with mortality rates of a given leaf age class, was greater than would be expected by chance (Table 4). Moreover, for *Retiniphyllum*, the species with the greatest database, among-tree mortality rates and production

TABLE 3. Average leaf life span (median, in days) for leaves produced in different years.

Site and species	1982	1983	1984	1985	1986	1987	1988
Bana							
<i>Aspidosperma album</i>	958	979	632	796	891	961	952
<i>Neea obobata</i>	444	328	423	386	313	396	271
<i>Protium</i> spp.	997	976	1046	1009	720	961	885
<i>Retiniphyllum truncatum</i>	444	505	532	483	453	429	496
<i>Rhodognaphalopsis humilis</i>	629	699	678	699	702	1073	
Farm plot, planted with Caatinga spp.							
<i>Caraipa heterocarpa</i>					988	869	760
<i>Eperua leucantha</i>					687	842	538
<i>Micrandra sprucei</i>					821	681	772
Caatinga canopy							
<i>Caraipa heterocarpa</i>	860	882	775	882		744	
<i>Eperua leucantha</i>	1237		1128		772	778	
<i>Micrandra sprucei</i>					733	602	778
Caatinga gap							
<i>Eperua leucantha</i>					1104	1286	806
<i>Micrandra sprucei</i>					1231	1055	
Caatinga understory							
<i>Caraipa heterocarpa</i>	1280	1222	1243	1359	1198		
<i>Eperua leucantha</i>	1383			1480	1222	1167	
<i>Micrandra sprucei</i>	1745	1398	1359		997		
<i>Micropholis maguirei</i>	1617	1496	1471	1471	1417	1049	
<i>Protium</i> spp.	1474	1678	1745	1718		1219	
Farm plot, planted with Tierra Firme spp.							
<i>Eperua purpurea</i>					620	669	775
<i>Licania heteromorpha</i>					772	869	
<i>Ocotea costulata</i>					526	377	474
<i>Protium</i> spp.					663	629	772
Tierra Firme canopy							
<i>Eperua purpurea</i>	572	514	535	575			
<i>Licania heteromorpha</i>	544	635	641	717	724	845	620
<i>Ocotea costulata</i>	523	535	435	404	444	450	477
Tierra Firme gap							
<i>Ocotea costulata</i>					590	915	
Tierra Firme understory							
<i>Eperua purpurea</i>	1292	1085	1161	1116	824	754	
<i>Licania heteromorpha</i>	1274	1198	985	1146	967	967	
<i>Ocotea costulata</i>	1222	1076	894	1186	769	1058	
<i>Protium</i> spp.	1140	912	979	1049	997	909	
<i>Cabari</i>	1708	1684	1791	1122	1195	1097	
Second-growth understory, planted with Tierra Firme spp.							
<i>Licania heteromorpha</i>			927	1520+	1520+		
<i>Ocotea costulata</i>			626	1283	1614		
<i>Protium</i> spp.			973	1256	1520+		
Early second growth							
<i>Bellucia grossularioides</i>	188	179	204				
<i>Clidemia sericea</i>	255	249	286				
<i>Goupia glabra</i>	228	377	365				
<i>Vismia japurensis</i>	219	228	264				
<i>Vismia lauriformis</i>	213	207					

rates (from tree to tree, comparing trees in the same stand) were also significantly correlated more frequently than would occur by chance (Table 4). Finally, phenological events were also correlated more significantly than would occur by chance in comparing among light microsites in the same stand for a given species; and among species in a given community (Table 4).

Although these analyses indicate that there was a significant tendency for correlation across time of phe-

nology among trees, microsites, and species in a stand, it is important to examine the frequency of these correlations. For individual species at a site, significant correlations of leaf mortality rates among leaf age classes (each class vs. another), or of production with mortality (of each leaf age class), were observed in 23% of the cases; significant correlations were observed in 17% of the cases among trees for *Retiniphyllum*; in 12% of the cases among species within a site (for com-

TABLE 4. Tests of pairwise correlations across time (typically, mean of 12–20 census dates in common) of leaf production and leaf mortality rates.

Contrast	Site	Correlations		
		No. tests	No. significant	(No. expected by chance)
Within-site, within-species	Bana	65	17	3
	Caatinga	72	17	4
	Tierra Firme	88	26	4
	Second growth	56	5	3
	Farm plot (planted)	27	5	1
Cross-site open; within species		151	9	8
Cross-microsite; within site, within species		191	17	10
Cross-trees, within site, <i>Retiniphyllum</i>		171	29	9
Cross-species, within site	Bana	313	25	15
	Caatinga	263	26	13
	Tierra Firme	220	35	11
	Second growth	224	39	11
	Farm plot (planted)	244	27	12

Notes: For mortality, rates were figured separately for leaves divided into five leaf age classes: young expanding, young fully expanded, middle-aged, old, and very old leaves (roughly by 20-percentile classes). Not all leaf age classes were available for every test. Correlations “within species, within sites” were of mortality rate of each age class with every other age class and of mortality rate of every age class with production rate of new leaves (maximum of 15 tests per species per site). Correlations “across species, within site” were made for the same variables (i.e., all combinations of new leaf production rates and mortality rates by leaf age classes), but in this case between species (for all pairwise tests). Correlations of the same variables were also made “within species across sites (but restricted to open sunlit canopy positions)” and “within species, within sites but across microsites (i.e., upper canopy, gap, and understory).” Correlations of the same variables were also made between individual *Retiniphyllum* trees in the Bana site.

mon light habitats); and in 9% of the cases within species among microsites. Thus, in the large majority of cases (77% to 91% of the examples given above), leaf production and mortality rates were unrelated among individuals within a species and among species within a site. Although the evidence indicates that there is some significant tendency for synchrony of phenology, by and large phenology is asynchronous within and among individuals and species. Several examples are given in Fig. 8 of synchronous and asynchronous behaviors.

How does the risk of mortality vary with increasing leaf age?—During the earliest months of leaf life, percentage mortality rates may be somewhat uncertain, because high herbivory pressure on very young leaves could cause new leaves to “disappear” before they are included in the census. Given this important caveat, the data show little support for the idea of much higher risk of mortality for the youngest leaves (usually <150–180 d) compared to slightly older leaf age classes (Fig. 9).

In all species and sites (Fig. 9 and data not shown), percentage mortality generally increased with increasing leaf age up to “middle age” (i.e., the median leaf life span), with the shape of the curve varying substantially among species. In many species, percentage mortality continued to increase with leaf age. However, in a substantial proportion of all cases, these curves then flattened out or declined, some steeply, and percentage mortality was often lower in very old than in middle-age leaves (Fig. 9). This deceleration of mortality refutes the hypothesis that mortality would accelerate monotonically with age. For one species

shown, *Retiniphyllum*, different individual trees showed similar patterns of percentage mortality in relation to leaf age (Fig. 10). A prolonged “tail” of low mortality risk in very old age was discernible when the leaf population was pooled among trees.

Leaf population age and life span structure.—Is the median leaf life span a good indicator of the typical life span of most leaves and a good representation of the typical leaf age of a canopy? Given that mortality rates for most species were substantial throughout most of the leaf life span and increased with age, there was a broad range in life spans among individual leaves (Fig. 11) and a broad distribution of leaf ages in the population at any one time (Fig. 11), with the most common leaf age substantially less than the average longevity.

DISCUSSION

As demonstrated in this study and elsewhere, phenology and leaf demography of tropical rain forest trees is controlled by different factors than in areas where climate variability (e.g., temperate deciduous forests, tropical dry forests) exerts a strong influence. Among the major factors observed to be important at San Carlos are species and resources (light and nutrients), whereas climate variability had negligible detectable effects.

Resource availability

The forest communities varied in leaf life span. Species common to relatively sunlit gaps and disturbed second-growth sites had shorter leaf life spans than species common to any primary communities. Species

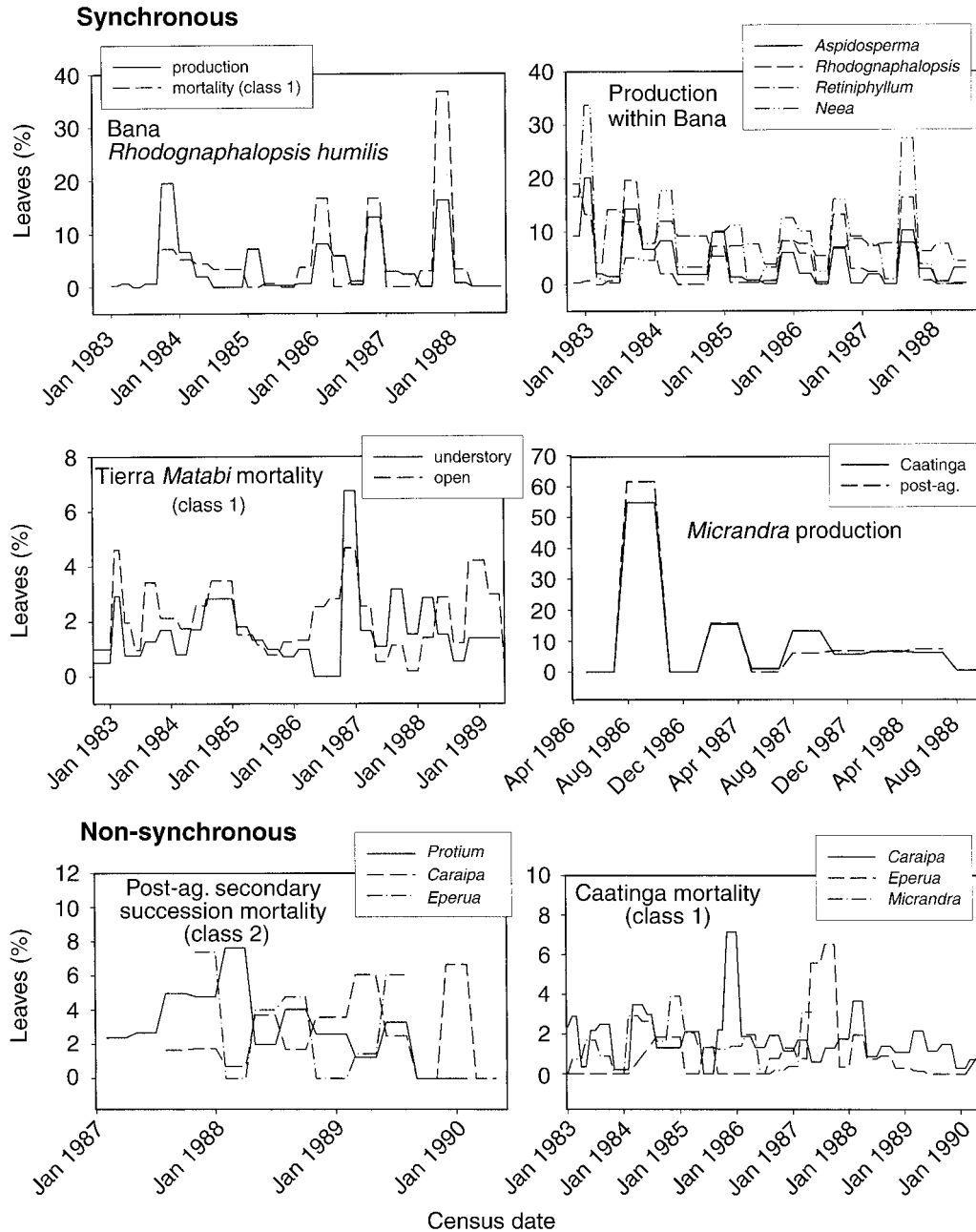


FIG. 8. Examples of synchronous and asynchronous phenology. Upper left: For all *Rhodognaphalopsis* trees in the Bana, new leaf production rates are contrasted with mortality rates of the youngest age class of leaves (all leaves less than one-third of the median leaf life span). Upper right: Leaf production rates for four different species in the Bana. Middle left: Mortality rates of the youngest leaf age class in understory and open upper canopy trees. Middle right: Leaf production rates for *Micrandra* in Caatinga vs. open postagricultural secondary sites. Lower left: Leaf mortality rates for three Caatinga species growing in postagricultural sites. Lower right: Leaf mortality rates for three Caatinga species growing in the Caatinga sites. Productivity and mortality rates are reported on a per-month basis.

from the primary communities tended to regenerate in shaded conditions (Tierra Firme and Caatinga) or in extremely nutrient-poor conditions (Bana). Given what is known about the relationship of leaf life span with other plant traits, the shorter leaf life span of earlier successional species is consistent with their faster

growth rates, greater leaf metabolic rates, and overall species strategies (Uhl 1987, Reich et al. 1991, 1995, 1999, Ellsworth and Reich 1996).

Differences among species adapted to different light habitats.—Our results showed that species that inhabit shaded understories as part of their life history have

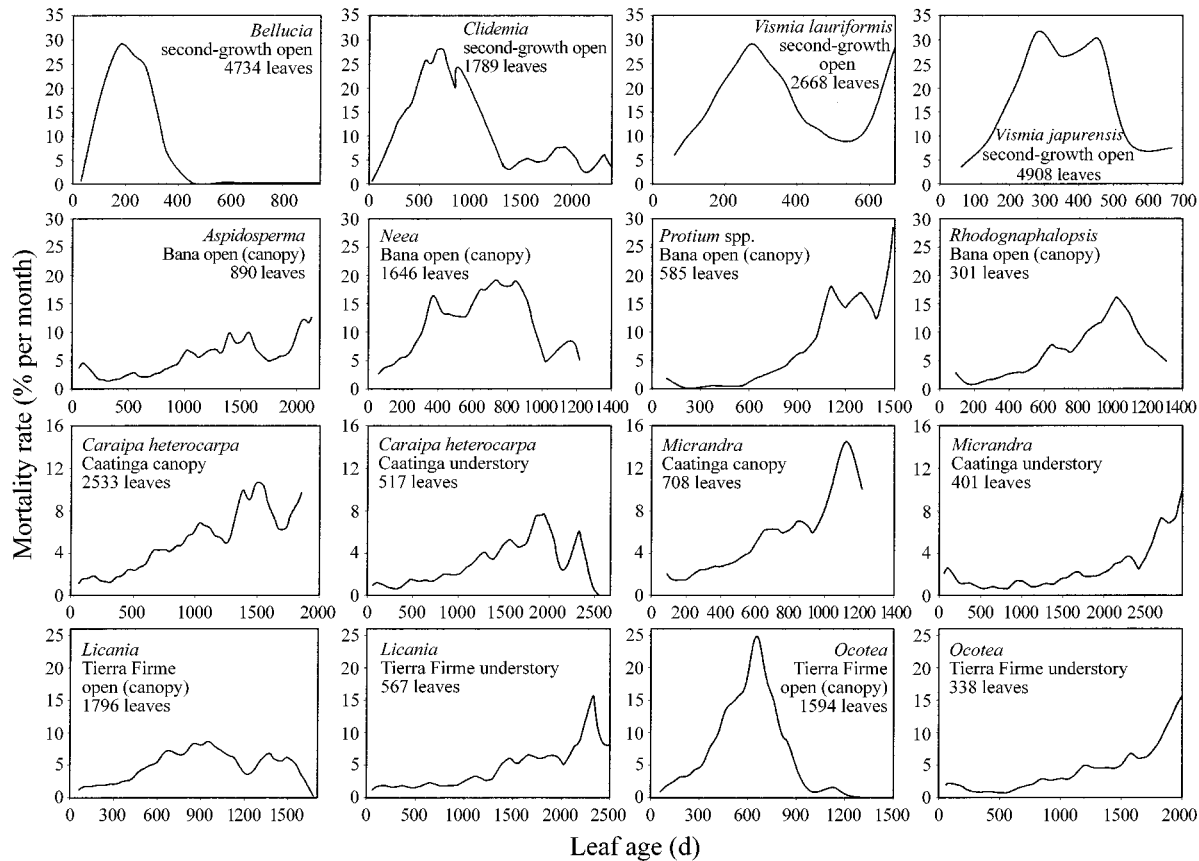


FIG. 9. Per capita mortality rates as a function of leaf age. Four species common to each of postagricultural secondary succession and Bana sites are shown (upper eight panels). Two species each from Caatinga and Tierra Firme are shown (lower eight panels), in each case contrasting upper canopy with understory leaf populations. These selected examples are shown to demonstrate typical patterns: species with slightly heightened risk of leaf mortality for immature leaves; nonlinear, progressively increasing mortality rates with increasing leaf age; and species with decelerating risk of mortality for older leaves.

longer leaf life spans (when compared under comparable light levels) than species that typically occupy higher light microhabitats. This phenomenon was found in previous studies (Coley 1988, Williams et al. 1989, Lusk and Contreras 1999) and in this one. However, Valladares et al. (2000) found only a small difference in leaf life span between six gap-demanding and 10 shade-tolerant *Psychotria* shrubs growing in their native habitats (mean of 1.25 vs. 1.5 yr, respectively), in contrast with much larger variation in leaf life span among species within each group.

Phenotypic responses to variation in light availability.—At San Carlos, all species responded with increased leaf longevity when growing in shadier microhabitats, regardless of whether trees were planted or naturally established. This agrees with some other studies (Lowman 1992a, Miyaji et al. 1997), but not all (Williams et al. 1989, Sterck 1999, Rose 2000). In our census, this response of leaf life span to shade held true regardless of tree age, since young trees planted in open clearings had leaf life spans similar to the upper canopy leaves of mature trees. It is thought that the

extended longevity of leaves in shadier conditions is physiologically affected directly by hormones (Pons and Jordi 1998) and indirectly affected by optimization strategy (Williams et al. 1989, Kikuzawa and Ackerly 1999), source-sink relations, and branch architectural considerations (Schoettle 1990, Schoettle and Smith 1991). From these perspectives, we consider increased longevity as a response to the overall slower growth rate of a plant, since: (1) remobilization of resources from older leaves is required less frequently; and (2) longevity may be modulated to maintain relatively constant foliage per unit shoot length (Schoettle and Smith 1991), and thus leaf longevity increases when shoots grow more slowly due to resource limitations.

Nutrients.—It has been proposed that a long leaf life span is advantageous in nutrient-poor habitats, because carbon and nutrient residence times are extended and the construction costs of low-productivity leaves can be amortized over a longer period (Chabot and Hicks 1982, Kikuzawa 1991, Reich et al. 1992). Consistent with these ideas is the evidence of a general and predictable tendency for species with higher leaf nutrient

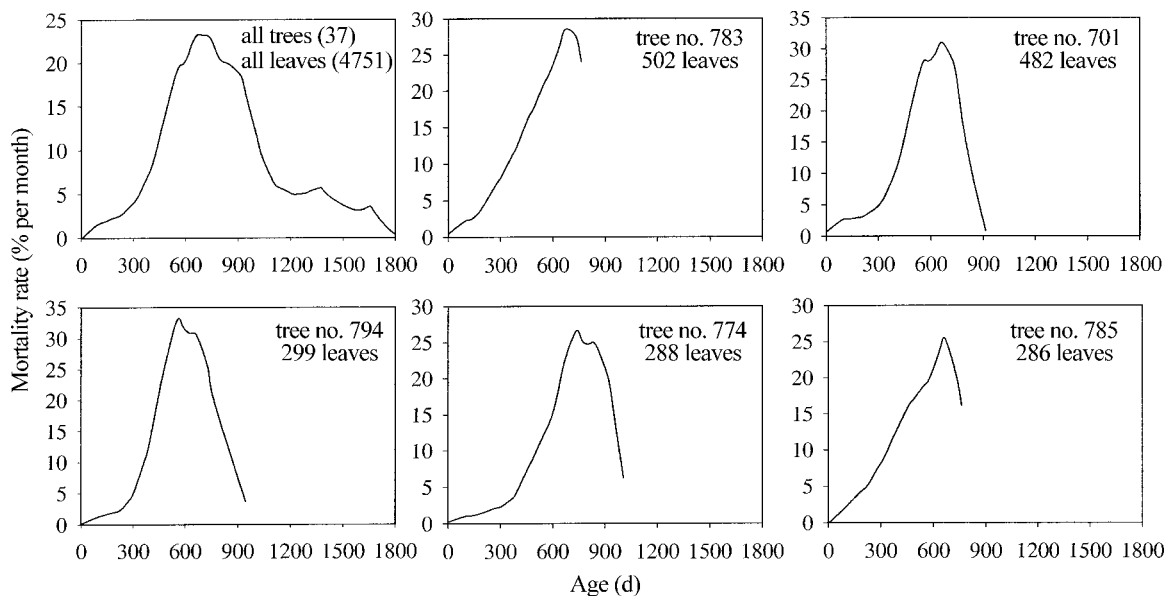


FIG. 10. Per capita mortality rates as a function of leaf age for all leaves of *Retiniphyllum* pooled from all branches and trees (upper left), and for the leaf populations on each of the five trees with the greatest censused leaf populations (all other panels). In each case, leaves from all cohorts were pooled.

concentrations to have shorter leaf life spans and vice versa (e.g., Reich et al. 1991, 1997). Several lines of data from the current study support these ideas. First, early successional species and Bana species both grow in relatively open conditions at all life stages (largely eliminating light differences as a consideration), but Bana is characterized by more severe nutrient limitation (Cuevas and Medina 1986, Reich et al. 1991). Bana species consistently have longer leaf life span than early successional species. A caveat to this must be that early successional species are also adapted to disturbed sites, and selection for disturbance adaptations likely has affected plant traits, including higher growth rates and shorter leaf life spans.

Second, Caatinga and Tierra Firme species both grow in shaded understory conditions or small gaps as seedlings and saplings, and in sunlit upper-canopy conditions as mature adults. Thus, a comparison of species from these two communities should also eliminate much of the potential for light conditions to confound a comparison of species from differing soil fertilities. Caatinga species are primarily N-limited and Tierra Firme species P-limited, but if overall levels of N and P cycling, of N and P leaf concentrations, and of photosynthetic rates are used as a collective gauge, Caatinga species appear to be more nutrient limited. They have significantly lower N concentrations, only slightly higher P concentrations, and on average, lower photosynthetic rates, and a much more pronounced limitation to photosynthesis due to low leaf N than Tierra Firme species (Reich et al. 1994). Caatinga species also have longer leaf life spans than Tierra Firme species in all four contrasts of comparable light levels, sup-

porting the idea of a linkage between nutrient limitation and species differences in leaf life span. However, in a study of *Metrosideros* in Hawaii, Cordell et al. (2001) found that N fertilization decreased leaf life span in a N-limited site, whereas neither N nor P fertilization decreased leaf life span in a P-limited site; and leaf life span in unfertilized trees was much longer in the N-than in the P-limited site. Thus, differences in leaf life span between Caatinga and Tierra Firme species may also be influenced by which nutrient is limiting, rather than the overall strength of the limitation.

Comparison of Caatinga and Tierra Firme species with Bana species, even in comparably sunlit upper canopy branches, must be made cautiously. Given that the seedling stage is an important one with respect to the selection of traits (Thomas and Bazzaz 1999), it is possible that in the tall forest species, long leaf life span is selected for because of low light conditions during the seedling and sapling stage, as well as in response to site infertility, whereas light limitation would not be a strong selective pressure for the Bana species. This may explain why Bana species, despite being recognized as growing on the most infertile site type (Cuevas and Medina 1986, Reich et al. 1994), do not have the longest leaf life span.

Plant size.—Kikuzawa and Ackerly (1999) suggested that leaf life span increases through ontogeny due to the increase in support costs associated with larger plant size, and cited evidence of much longer leaf life span in adult deciduous trees than in seedlings. It is logical that very young seedlings, with higher relative growth rate than older trees, would have higher leaf turnover rates. However, this pattern is opposite to what

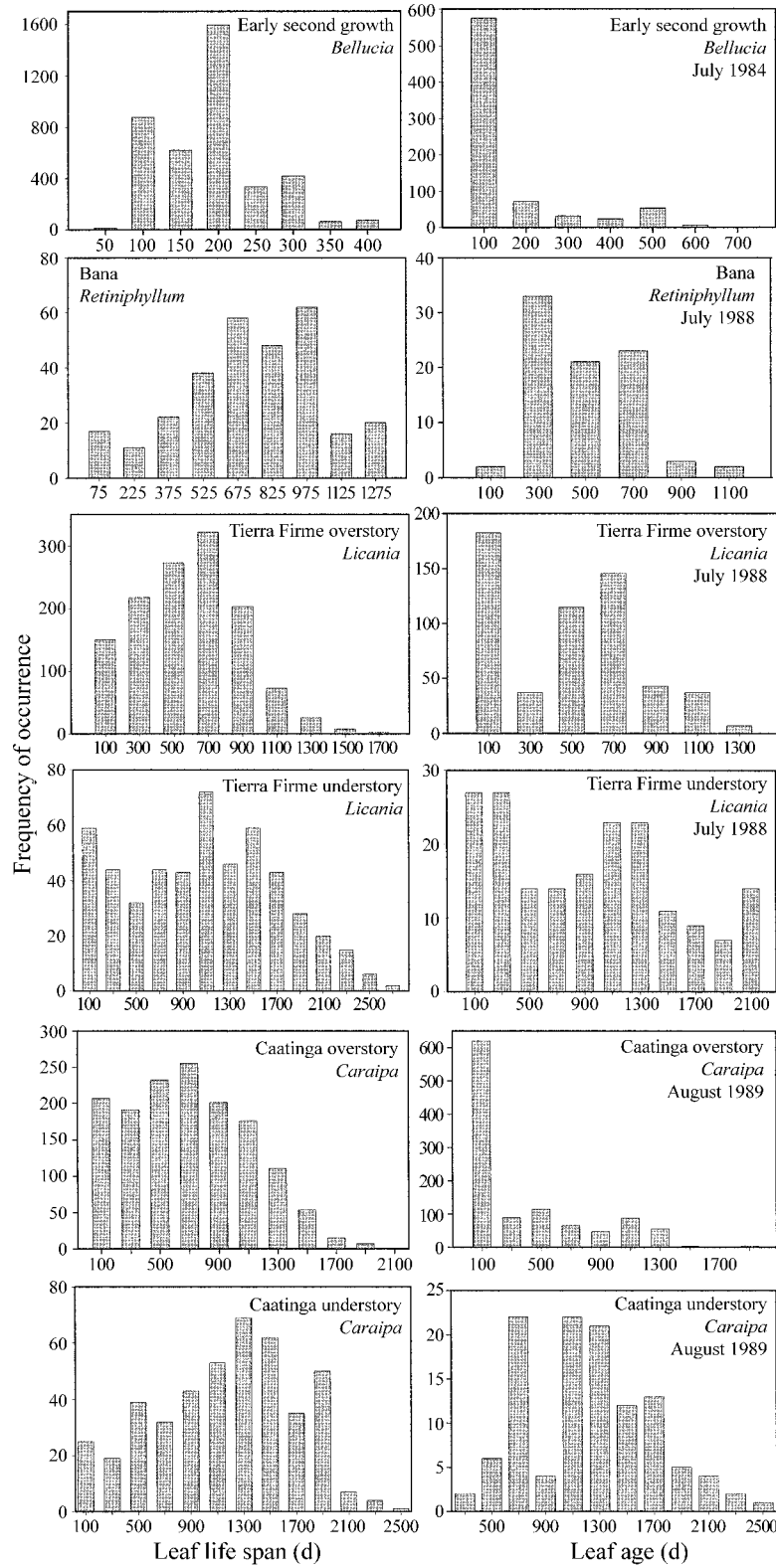


FIG. 11. The frequency distribution of leaf life span (pooled across all cohorts) and leaf age structure at a single time for populations of four species, two of which are shown in contrasting light microenvironments. Data are pooled across all individuals of each species in that habitat.

was observed intraspecifically with age in San Carlos (albeit across a light gradient), where leaves on large trees in sunlit positions lived a shorter time than leaves on younger, shorter trees in the understory in gap or shade. And regardless of tree size, leaves in open conditions had similar leaf life span. (Compare trees planted in the open to upper canopy leaves, Table 2.) Two factors may be responsible for this apparent discrepancy. First, it is possible that variation in light creates a much greater range in leaf life span than does plant size, thus obscuring whether or not tree size per se influences leaf life span. Second, variation in leaf life span with plant size may be much greater when comparing very young seedlings (in first or second year) to adult trees, than when comparing young trees (10–30 years old) to mature old trees. In essence, variation in growth rate and leaf turnover rate may be extreme, and thus plastic, early during tree development, but may be more stable once a tree is even several years old.

Interannual patterns

For leaves on branches in sunlit positions, leaf life span of different cohorts was similar. In contrast, observed leaf life span became shorter for understory trees from year to year (Table 3). No climate trends explained this shift. Hence, we ask whether this observed decline in leaf life span for understory individuals is a census design artifact that results in later cohorts representing plants in somewhat higher light environments than earlier cohorts? Just as the population of older survivors is not necessarily representative of an original population (Vaupel et al. 1998), the population of new leaves is not necessarily representative of the original branch population due to uneven branch death over time among habitats. It is likely that the initial leaf and branch population sampling in the understory was random and thus representative of the full range of light conditions therein. We did not sample new branches with each census, but continued to census old and new leaves from the original branch population. However, the branches that grew continuously with time and produced the most new leaves were often in higher than average light environments, and those that grew more slowly or had greater mortality (of the branch or tree) were often in darker environments (P. B. Reich, *personal observation*, data not shown). Hence, over time, the populations of branches contributing new leaves in each successive year would become more representative of the most actively growing and best surviving (and better lit) branches of the original pool, and less representative of the original pool overall. As shown earlier, leaves in higher light positions live for a shorter time; thus the average life span of our annual census group would decline. The lack of decline over time in observed leaf life span of plants in sunlit microhabitats is consistent with this explanation, since branch-to-branch light variation would be

much less important than for plants in low-light environments, and well-lit branches should maintain their vigor. Therefore, for the four species mentioned above as showing declines in leaf life span over time, data in the understory in the first 3–4 years (1982 to 1984 or 1985) may be more representative than the latter period.

One means to evaluate this possibility is by comparison with other studies in the literature, but few tropical rain forest studies have reported leaf demography for multiple cohorts. Lowman (1992a) focused on other issues and did not discuss intercohort patterns in detail, although she showed substantial data on multiple cohorts. Unfortunately, it is difficult to interpret those complex data directly from the materials presented. Two other studies of understory plants reported faster leaf turnover rates in cohorts that developed later in their study, similar to the pattern observed in our study. A Puerto Rican rain forest fern had markedly shorter leaf life span in late-observed cohorts, but these cohorts lived and died during an unusually dry period (Sharpe 1997). The strong interannual variation in rainfall in that study makes it impossible to deduce whether a shift in the plant population contributing to the leaf population pool was at work. Clark et al. (1992) observed a trend for later-observed cohorts to show greater mortality than early-observed cohorts in their respective years 1–4, although the overall means for these long-lived leaves were only marginally statistically different.

Trends in mortality as a function of leaf age

The risk of mortality generally increased with leaf age, as expected, with a major class of exceptions. In many species, the mortality rate decelerated at older leaf ages, and in some cases, even declined with increasing age. The deceleration of mortality with older age has been noted in a number of animal species (Vaupel et al. 1998), but as far as we are aware, has not been addressed for plant leaves. Even the trajectory for automobile mortality decelerates (Vaupel et al. 1998), suggesting the possibility that deceleration is a general property of complex systems. A number of potential arguments relevant to leaves have been raised to explain the deceleration of mortality with increasing age. One involves heterogeneity of any given population, in particular, with respect to “frailty.” The frail tend to suffer high mortality because of innate or acquired weakness, leaving a select subset of survivors and creating complexity in the patterns of aging and mortality (Vaupel et al. 1998). As a result of this compositional change in the population (in this case, of leaves), death rates increase more slowly with age than would occur in a homogeneous population (Vaupel et al. 1998). An additional factor for leaves could involve heterogeneity of growth rate and microenvironment. Individual plants, branches, or subbranches that vary in microenvironment vary in average life span (See *Results*:

Variation among trees and with season and years), such that the population of leaves of increasingly older age classes represent trees or branches in increasingly low-resource microsites, which have longer average life spans. This argument would apply both within and among individuals.

Synchrony and heterogeneity in phenology and degree of seasonality

For the 23 species assessed in this study, phenology was not related to variation or seasonality of climate variables. Perhaps our climate measures were insufficient to detect climatic events that might work to “push” individuals and species toward a degree of commonality of response if, say, such climate events included dry periods on the order of 2–3 weeks, intensive wet periods, or wind or other severe storm events. Nonetheless, examination of responses over time (e.g., see Figs. 2, 4, 7, and 8) generally show no or minimal tendency for either production or mortality to be higher or lower during the drier (e.g., December–March) or wetter (July–October) periods of the year.

Our results, showing minimal seasonality, are in stark contrast to prior reports, but at our study site, seasons and years during the study were much less variable than in these other studies. Almost all other studies that showed periodicity in phenology were either subtropical sites with marked temperature variation (e.g., Lowman 1992a), tropical sites with marked annual seasonality of precipitation (e.g., Coley 1988, Aide 1993) or had extreme dry years in their sample (e.g., Sharpe 1997). In this latter study, fern leaves had greater mortality rates during the mild dry season, in what is commonly considered a relatively aseasonal tropical rain forest (mean annual rainfall, 3400 mm) in Puerto Rico (Sharpe 1997), but the particular season in question was unusually dry. Consistent with our results, mean leaf longevity did not vary among cohorts produced during three different times of year for cacao plants in Brazil growing during a year with only modest seasonal variation in rainfall (Miyaji et al. 1997). Thus, our results suggest that in most years, aseasonal tropical rain forests do not have appreciable seasonality of leaf phenologic or demographic processes. Sharpe (1997) and Frankie et al. (1974) observed more seasonality of phenology and/or demography than seen in our study. This contrast may reflect the fact that in tropical rain forests, periodic dry periods occur, but not necessarily within the time frame of any given study. Thus, differences among rain forests in the mean seasonality of climate and its interannual variability are probably the critical factors determining whether or not phenology and demography are essentially aseasonal or not. In the upper Rio Negro region, it appears that these processes are typically aseasonal. Examining precipitation records from 1979 to 1995 (17 years), there was only one 3-month period drier than the driest 3-month period during our study.

CONCLUSIONS

Tropical rain forest trees produce leaves with widely variable phenology and longevity. In the absence of strong climatic control on these processes, plants appear to internally regulate these processes on temporally independent schedules, but with predictable differences related to evolutionary adaptation to resource availability and phenotypic acclimation to resource availability.

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