

Mortality and growth of a commercial hardwood 'el cativo', *Prioria copaifera*, in Panama

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Abstract

The demography of a valuable timber tree, *Prioria copaifera*, was studied in undisturbed forest on Barro Colorado Island (BCI) in central Panama using data from a permanent, 50 ha census plot. All individuals above 10 mm diameter at breast height (dbh) in the plot were mapped and dbh measures taken in 1982, 1985, and 1990. Although *Prioria* is mainly known from swamp forest, it was abundant in the upland forest of BCI, with a mean density of 27–29 stems ha⁻¹ of 10 mm dbh or more. Mortality rates of *Prioria* were 0.5 and 0.6% year⁻¹ during the two census intervals and did not depend on dbh. Mean growth of saplings was slow, less than 1 mm year⁻¹, but larger trees grew rapidly, at 8–16 mm year⁻¹. Growth rates of medium and large trees were higher during 1982–1985 than during 1985–1990, probably because a severe drought in 1983 increased forest-wide mortality rates and opened the forest canopy, allowing more light to penetrate the forest. During both census intervals, growth was extremely variable, ranging from 0 to 40 mm year⁻¹ in different individuals. The range of variability changed little with size: across dbh values from 100 to 1000 mm, maximum growth rates were 20–40 mm year⁻¹. Unlike absolute growth rates, however, relative growth declined with size, from about 5% year⁻¹ in saplings to 1% year⁻¹ in large trees, and was much more variable among small stems than among larger.

Information about variation in growth between individuals and between census periods will be important in forest management, as it indicates how and to what extent silvicultural treatment might enhance timber production in *Prioria*. In addition, rapid growth of some stems suggests that plantation forestry might be productive in *Prioria*. Our finding that population density and performance were good in upland soils suggests that plantations of this species could be attempted in drier soils than previously thought necessary.

Introduction

Extracting goods from tropical forests on a sustainable and economically viable basis demands detailed information on the population dynamics of individual species. Basic demographic parameters of growth and survival are needed to develop precise quantitative models of harvest. Only then can pro-

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grams for sustainable harvest be developed, and the long-term value of the forest resource be assessed (Ashton and Panayotou, 1992). However, for most tree species in tropical forests, even many of the most valuable, adequate data on basic biology are lacking (Hubbell and Foster, 1992).

One valuable timber species in Panama is 'el cativo', *Prioria copaifera* Gri-seb., a large, straight-trunked legume (subfamily Caesalpinioideae) which often occurs in nearly pure stands called 'cativales' (Lamb, 1953; Holdridge and Budowski, 1956). The wood is soft and used almost exclusively for plywood, but its occurrence in pure stands near rivers has enhanced its value as a timber resource (Lamb, 1953). Indeed, many of the cativales in Panama are being clear-cut for timber at this moment. Recently, government agencies in Panama have been working on management plans that allow sustained harvests of this species, yet are finding that detailed data on its basic biology are lacking. Studies of growth have been carried out on a small scale in Colombia (Del Valle, 1979; Linares, 1987; Linares and Martinez, 1991), but little work has been done in Panama (Mayo Melendez, 1965; Rovira et al., 1987).

In 1980, a large-scale, permanent census plot was installed in tropical moist forest on Barro Colorado Island in central Panama, with the intention of gathering basic data on tropical trees (Hubbell and Foster, 1983, 1992). Complete censuses of the 50 ha plot were completed in 1982, 1985, and 1990, with all stems down to 1 cm in diameter at breast height (dbh) included. The justification for the large size of the plot and the small lower limit for the census was that solid demographic data on individual tree species were needed. With over 300 species in the 50 ha plot (Condit et al., 1992b), individual species are not common, and to gather a large sample size for most species requires a very large area. For instance, if this plot were 1 ha, it would include just seven species with over 100 individuals (in the average hectare; see Hubbell and Foster, 1990a), whereas in 50 ha, there are over 150 species with 100 stems (100 stems is a reasonable minimum sample size for collecting demographic data). Parallel 50 ha plots have now been established in peninsular Malaysia (Manokaran et al., 1990; Saw et al., 1991) and in India (Sukumar et al., 1992), with similar goals in mind for very different tropical forests, and development of additional plots is underway in Sri Lanka, Thailand, and Sarawak in Malaysia.

Based on this 50 ha plot, we now have a substantial database on a population of *Prioria copaifera*, which allows us to describe in detail patterns of its growth and mortality. Here we examine the relationship between mortality and dbh and between growth and dbh. We also focus on variability in growth rates, assessing the range of growth rates observed to see how this varies with tree size. The latter issue is particularly important from the management point of view, because understanding variation in growth can lead to clues about how to augment growth in managed forests or plantations.

Materials and methods

The study was carried out in tropical moist forest on Barro Colorado Island (BCI) in central Panama. Detailed descriptions of the climate, flora, and fauna of BCI have been given by Croat (1978) and Leigh et al. (1982). Censuses of 50 ha of forest were carried out in 1981–1983, 1985, and 1990 (Hubbell and Foster, 1983, 1986a,b, 1990a,b, 1992; Condit et al., 1992a,b; we refer to the first census, which lasted 2 years, as the 1982 census). All free-standing, woody stems of 10 mm dbh or more were identified, tagged, and mapped. The diameter of each stem was measured at breast height (1.3 m) unless there were irregularities in the trunk there, in which case the measurement was taken at the nearest higher point where the stem was cylindrical. In 1982 and 1985, a plastic plate with 0.5 cm increments was used to measure diameters of smaller stems (Manokaran et al., 1990), so that dbh of stems less than 55 mm were effectively rounded down to the next smallest 5 mm multiple. In 1990, calipers were used and dbh values recorded to the nearest millimeter. In the present study, we focus on the 1523 individuals of *Prioria copaifera* encountered in the censuses.

Mortality rates were calculated by dividing the number of dead stems in one census by the total living in the previous census. Confidence limits for this fraction were calculated using the binomial variance and *t*-statistics, which are based on a normal approximation appropriate for moderately large sample sizes (Sokal and Rohlf, 1973). To determine annual mortality rates, the mean time interval was calculated from the dates of census of each 20 m × 20 m quadrant of the plot. A standard exponential mortality model was used to calculate annual mortality, based on this mean time interval. This same procedure allows annual confidence limits to be obtained as well.

We separately recorded plants which broke their main stem below 1.3 m but which survived and resprouted. In some cases, it was not possible to tell whether the breakage occurred before or after the prior census, so we counted stem breakage only in cases where a plant had a dbh smaller than in the prior census. Rates of stem breakage were calculated exactly as were mortality rates. It should be noted that stems broken above 1.3 m were not included in this definition.

Growth rate was calculated as dbh increment, and the annual rate was obtained using the time interval for a plant's quadrant. Because dbh values were rounded down in 1982 and 1985 but not 1990, it was necessary to round 1990 dbh values below 55 mm down to the nearest 5 mm interval before calculating growth rates. Living stems which were not resprouts were included in growth calculations. Means and confidence limits were based on standard *t*-statistics, which are appropriate for normal distributions, and growth distributions were reasonably normal. We also present mean relative growth rates: the annual growth increment divided by the initial dbh (Welden et al., 1991).

Rounding dbh values of smaller stems may bias growth estimates, so we experimented with simulated growth distributions applied to a real size distribution and determined how different an estimate of growth would be if dbh values were rounded down to 5 mm intervals as opposed to not rounded. For example, we started with the real distribution in the 10–14 mm size class in 1990 (32 stems of 10 mm; 41 stems of 11 mm; 32 stems of 12 mm; 29 stems of 13 mm; 29 stems of 14 mm) and we assumed that each stem grew exactly 2 mm over 3 years, or $0.67 \text{ mm year}^{-1}$. In this imaginary scenario, if all dbh values were rounded down, we would have recorded increments of 5 mm for the 58 stems above 13 mm dbh and no increment for the other stems. This yields a mean growth of $0.59 \text{ mm year}^{-1}$, 11% below the true growth rate of $0.67 \text{ mm year}^{-1}$. We repeated this experiment using a number of more complex growth distributions (but the same size distribution) and found biases of 3–13%, usually but not always downward. These small biases hinge on the size distribution: the number of 14 mm stems is not very different from the number of 10 mm stems. If 10 mm stems greatly outnumbered 14 mm stems, then our rounding technique would greatly underestimate growth rates, whereas if 14 mm stems outnumbered 10 mm stems, it would overestimate growth rates. It is important, then, to note that size distributions were relatively flat across the five 1 mm size classes in each 5 mm size interval up to 55 mm. Thus, we conclude that rounding dbh values to 5 mm intervals had relatively little impact on our estimates of mean growth rates.

Another caution about estimates of mean growth was raised by a few instances in which trees apparently had extreme growth, including some cases of extreme shrinkage. To reduce the impact of a few erroneous dbh measures on mean growth estimates, we discarded all records of plants which shrank by more than 5% of their initial dbh per year or grew by over 75 mm year^{-1} . Decrements less than 5% were not excluded because they probably represented measurement errors on trees that did not grow; removing them would bias growth rates upward. Excluding increments above 75 mm year^{-1} eliminates truly absurd errors but probably includes the full range of legitimate growth rates in *Prioria* as it is approximately the upper limit of legitimate growth records for all trees in the 50 ha plot (Condit et al., 1993). To determine how well this approach worked, we compared mean growth rates from edited data (that is, with extremes removed) with mean and median growth rates based on unedited data, and we present the unedited distributions of growth rates for some size classes. Because of the extreme variation observed in the growth rates of saplings, we also present full records of all stems less than 40 mm dbh which grew faster than 4 mm year^{-1} . This can help indicate whether or not the few very high growth rates in saplings were legitimate measures or were caused by errors.

To assess changes in growth or mortality with size, trees were divided into dbh intervals based only on criteria of sample size. As small stems were much

more abundant than large ones, size intervals expanded with size. Changes in growth or mortality were considered statistically significant if 95% confidence limits on estimates in pre-defined size intervals did not overlap.

Recruits in the plot were defined as stems of 10 mm dbh or more in one census that were not present in the prior census (Condit et al., 1992a). Recruitment rate was standardized by dividing the total number of recruits in one census by the number of adults in the previous census, then dividing by the mean time interval. Adults were defined as trees greater than 600 mm dbh in *Prioria*, which is the approximate size at which fruit production begins.

Results

Distribution and abundance

There were 1356 trees of 10 mm dbh or more in 1982, 1408 in 1985, and 1442 in 1990, for a mean density of 27–29 ha⁻¹. The majority of these were stems of less than 80 mm dbh (Table 1). There were 125 trees above 320 mm dbh, or 2.5 ha⁻¹, and 62 above 640 mm dbh, or 1.2 ha⁻¹ (Table 1).

Prioria is common in the southwest corner of the 50 ha plot, but rare in other parts (Fig. 1). The southwest region is flat and contains well-drained soils, but other parts of the plot where *Prioria* is rare are similar (especially the high area north and east of the center). There is no obvious feature of the forest (a swampy area, moderate slopes, or a patch of young forest (Hubbell and Foster, 1986b)) that correlates with its distribution.

Mortality

Total mortality rate was 0.45% year⁻¹ from 1982 to 1985, and 0.57% year⁻¹ from 1985 to 1990 (Table 1), but this difference was not statistically significant. There was a tendency for mortality to decline with size; however, the changes were slight and no trend was statistically significant (Table 1). Of 59 trees recorded dead in the two censuses, 14 were found as fallen trunks and 17 were found standing. In the remaining 28 cases, no sign of the tree was found (tags were found on some occasions, but not all).

Stem breakage

Rates of stem loss below breast height were low, but were higher than mortality rates in the small size classes (Table 1). In larger classes, resprouting after loss of the whole main stem below 1.3 m did not occur (Table 1). Most of the resprouted stems were of less than 10 mm dbh and thus were not counted in the total population given in Table 1.

Table 1
Mortality, stem breakage, growth, and recruitment in *Prioria*

Dbh (mm)	Initial stems	Time	Mortality			Breakage			Growth			Recruits	Final stems
			<i>n</i>	Rate	CI	<i>n</i>	Rate	CI	<i>n</i>	Rate	CI		
10–19	360	2.86	7	0.69	0.51	12	1.18	0.67	331	0.62	0.14	72	385
	385	5.17	13	0.66	0.36	10	0.51	0.31	349	0.61	0.08	71	337
20–29	253	2.94	5	0.68	0.60	1	0.13	0.53	228	0.92	0.15	7	231
	231	5.20	8	0.68	0.47	4	0.34	0.33	214	0.76	0.15	7	259
30–39	136	2.98	2	0.50	0.69	1	0.25	0.49	123	1.33	0.31	2	144
	144	5.20	5	0.68	0.59	1	0.13	0.26	136	1.33	0.35	1	146
40–79	261	3.09	1	0.12	0.24	0	0.00	0.40	257	2.02	0.30	1	275
	275	5.23	6	0.42	0.33	3	0.21	0.24	262	1.57	0.27	2	297
80–159	158	3.08	1	0.21	0.41	0	0.00	0.76	157	2.96	0.43	2	176
	176	5.24	3	0.33	0.37	0	0.00	0.40	172	3.00	0.45	0	191
160–319	76	3.03	1	0.44	0.85	0	0.00	1.51	75	8.61	1.69	1	76
	76	5.21	1	0.25	0.49	0	0.00	0.93	75	6.06	1.58	0	87
320–639	55	2.99	1	0.61	1.23	0	0.00	2.24	51	15.87	2.35	0	58
	58	5.22	1	0.33	0.64	0	0.00	1.22	57	8.23	1.41	0	63
≥ 640	57	2.89	0	0.00	2.25	0	0.00	2.25	55	13.90	4.06	0	63
	63	5.25	4	1.25	1.31	0	0.00	1.12	58	3.78	2.65	0	62
Total	1356	2.97	18	0.45	0.21	14	0.35	0.18	1277	2.96	0.32	85	1408
	1408	5.21	41	0.57	0.18	18	0.25	0.12	1323	1.99	0.21	82	1442

For each size class, the first row of data is from the 1982–1985 census interval and the second row from the 1985–1990 census interval. 'Initial stems' is the total number of stems alive at the start of the census interval, and 'final stems' the number alive at the end. Under mortality and breakage, *n* is the number of stems that died (or broke) by the end of the interval, rate the annual per cent rate of mortality (or breakage), and CI the width of 95% confidence limits of the rate. Under growth, *n* is the number of stems for which growth was measured (excluding dead or broken stems and extremes of growth), rate the mean edited growth (in mm year⁻¹), and CI the width of the 95% confidence intervals. 'Recruits' gives the number of stems which entered the census for the first time in a given size class in 1985 (first row) or 1990 (second row).

Mean growth

There was a statistically significant increase in dbh increment with size, from below 1 mm year⁻¹ for saplings up to 8–16 mm year⁻¹ for 320–639 mm trees; in larger trees, growth leveled off in 1982–1985 but declined in 1985–1990 (Table 1, Fig. 2). Relative growth, on the other hand, declined with size (Fig. 2(B)), with the smallest trees growing over 5% in dbh per year and large trees growing 1% or less per year. In 1982–1985, however, there was a marginally non-significant peak in relative growth at an intermediate size class (160–319 mm trees had higher relative growth than 80–159 mm trees, but 95% confidence limits barely overlapped; Fig. 2(B)).

There were substantial differences in growth between the two census periods among trees of 320 mm dbh or more (Table 1, Figs. 2–4). The largest

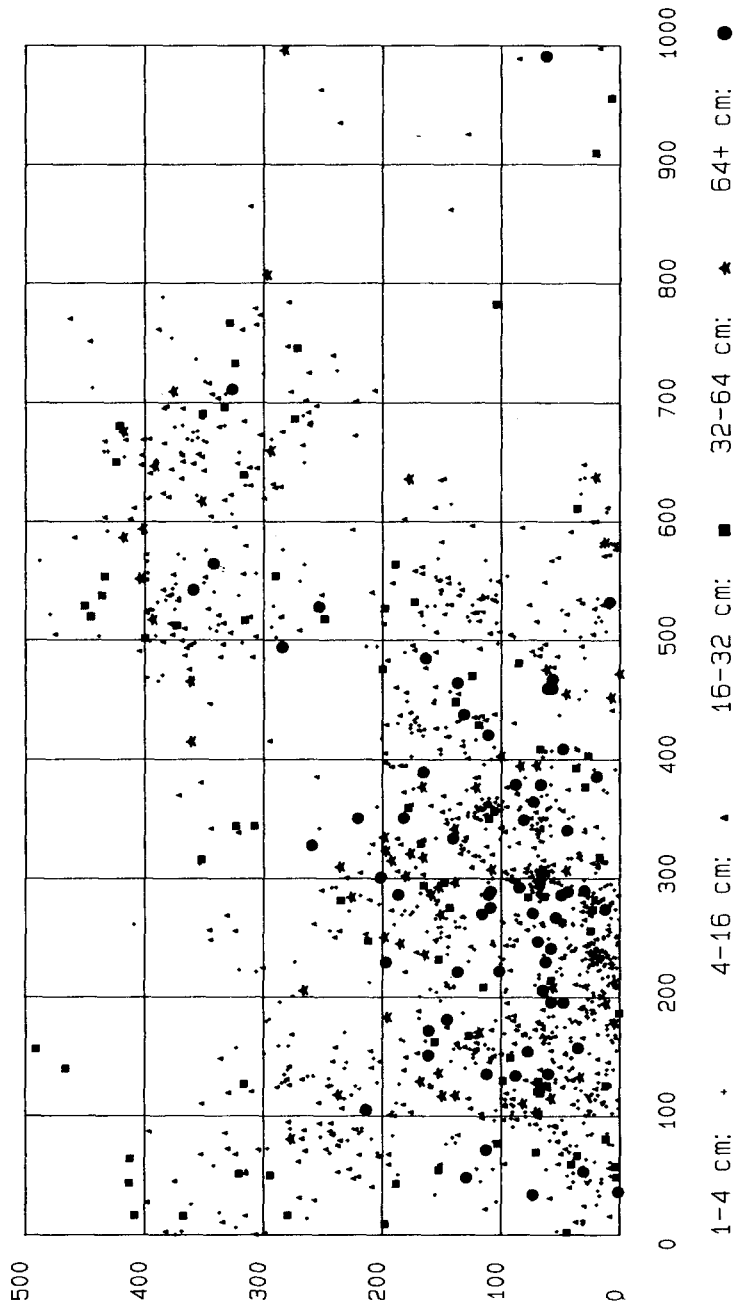


Fig. 1. Map of the distribution of *Prioria* (dbh range 10-10 000 mm) in the 50 ha plot in 1990. Dimensions are in meters, and north is upward. Size classes for 10-39 mm dbh and 40-159 mm dbh were combined in the map to improve clarity. (Note that the class limits are given in cm rather than mm.)

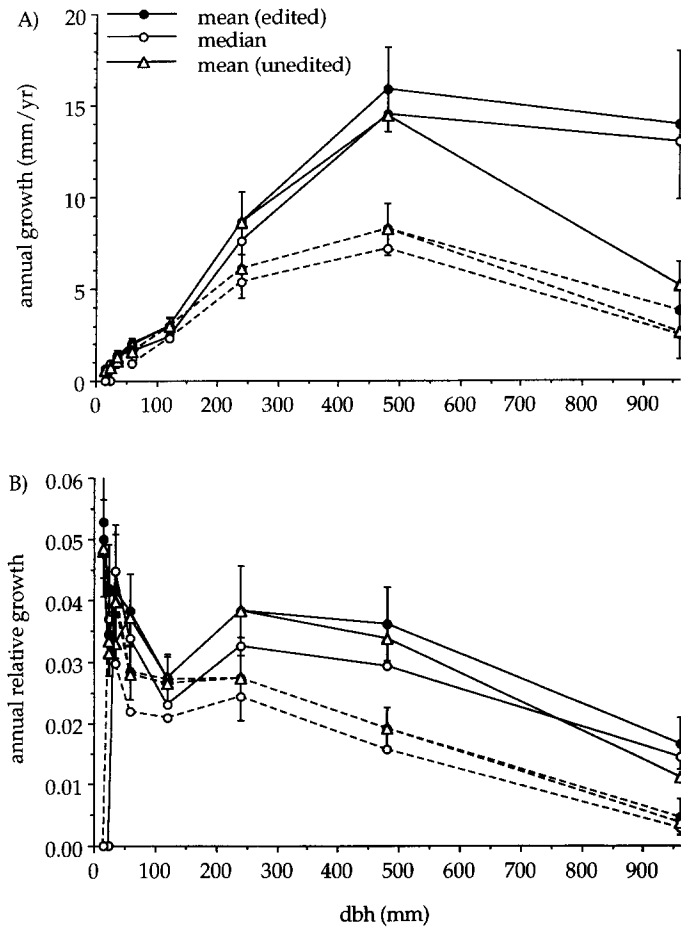


Fig. 2. Growth as a function of size in *Prioria*: mean growth with all points included ('unedited'), mean growth with extreme values removed ('edited'), and median growth. The vertical bars indicate 95% confidence limits for the edited means. (A) Absolute dbh increment; (B) relative growth increment (both given as annual values).

difference was in trees above the 640 mm size class, where mean growth was more than three times higher in 1982–1985 than in 1985–1990 (Table 1).

The growth rates discussed above and listed in Table 1 were calculated after removal of stems with extreme growth, but all the main patterns were maintained whether unedited means or medians were considered (Fig. 2). There were minor discrepancies, however, the largest being in the biggest size class in 1982–1985, where mean growth based on unedited data was much lower than the median or the mean with extremes removed. This was caused by a

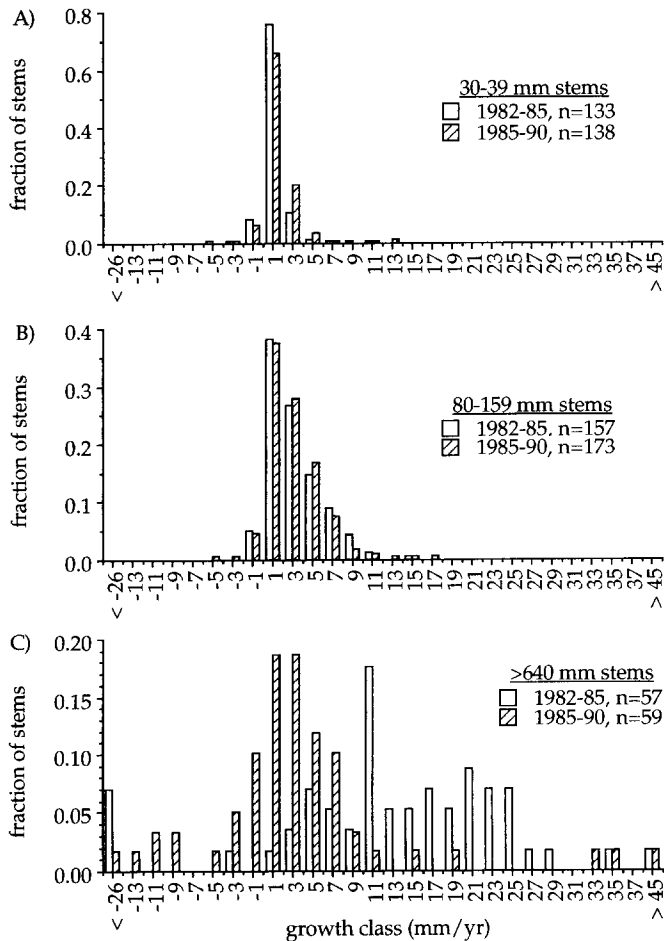


Fig. 3. Distributions of annual absolute growth rates in *Prioria*, given as the fraction of total stems in each size class. No records were excluded, but extremes are combined in terminal intervals. Growth rates are plotted in 2 mm intervals at the midpoint of the interval. (A) 30–39 mm stems; (B) 80–159 mm stems; (C) stems of 640 mm or more.

single aberrant record: a tree whose dbh was measured at 1838 mm, 905 mm, and 915 mm in consecutive censuses; the large decrement between the first two was sufficient to reduce the mean for the 57 trees in this size class from 13.9 to 5.2 mm year⁻¹. There were 55 other cases where growth rates were less than -5% year⁻¹, most of which were in trees of less than 40 mm dbh; their inclusion had little impact on mean growth estimates (Fig. 2). There was only one stem with a growth rate above 75 mm year⁻¹: it had dbh values of 330, 596, and 609 mm in consecutive censuses, yielding a growth rate of 93.3 mm year⁻¹ over the first interval. There were four other cases where

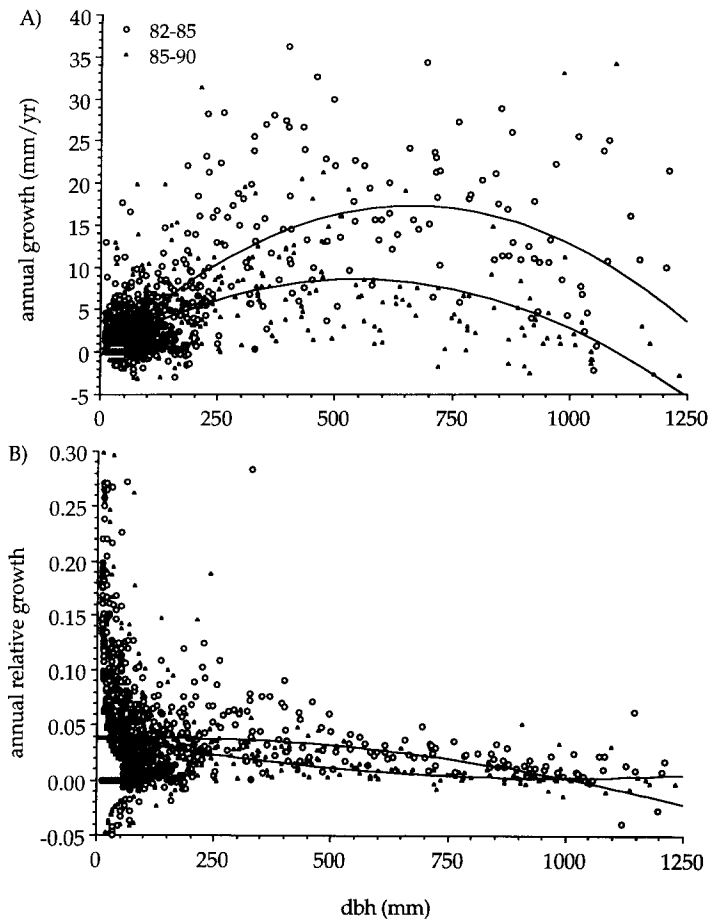


Fig. 4. Individual growth rates of *Prioria* stems in the plot for 1982–1985 and for 1985–1990, as a function of dbh. Some points are excluded, both above and below. The curves were fitted by polynomial regression and were included solely as viewing guides; the upper curve in both plots is for 1982–1985 data, the lower for 1985–1990. (A) Absolute dbh increment; (b) relative dbh increment (both given as annual values).

large stems had aberrant dbh records—one at 1144, 1333, then 938 mm; one at 1111, 907, then 1150 mm; one at 407, 242, then 470 mm; one at 388, 214, then 242 mm—but the magnitude of the errors was small enough that their impact on overall growth statistics was minor.

The other conspicuous discrepancy between median and mean growth estimates was that median growth was zero in the small size classes (Fig. 2), simply because more than half the stems did not register growth. Median relative growth thus increased from zero in the smallest size class, to a peak at 20–40 mm dbh, then declined at larger sizes.

Growth variation

Among saplings, mean growth was below 1 mm year⁻¹ but maximum growth was over 12 mm year⁻¹ (Fig. 3(A)), although very few plants achieved such high growth. Out of a total of 1428 growth records for 10–39 mm plants, including both census periods, there were 25 (1.8%) over 4 mm year⁻¹ and only five (0.4%) over 10 mm year⁻¹.

Table 2 lists growth histories of all 10–39 mm plants that had growth rates faster than 4 mm year⁻¹ in either census interval. Six plants in the list had growth rates exceeding 4 mm year⁻¹ in both census intervals and are indicated in Table 2, including the tree with tag 81842, which was 35, 78, then

Table 2

Growth rates faster than 4 mm year⁻¹ in either census interval for cativo saplings that were: (A) 10–19 mm dbh, (B) 20–29 mm dbh, or (C) 30–39 mm dbh in the census before rapid growth

Tag no.	dbh (mm) in			Growth rate in		Comment
	1982	1985	1990	1982–1985	1985–1990	
(A) 10–19 mm plants						
72244	10	60	66	13.0		
99192	15	30	31	4.1		
148136	10	25	34	4.7		
159600	15	25	33	4.6		
185860	15	40	47	8.8		
260238	15	25	55	4.0	5.9	Both
(B) 20–29 mm plants						
97990	20	35	41	4.1		
136115	20	35	71	4.4	6.8	Both
181194	20	25	57		6.2	
185661	20	35	20	5.3		Problem
205232	20	35	41	5.4		
255971	25	35	Dead	4.0		
(C) 30–39 mm plants						
81842	35	78	152	11.0	13.9	Both
97948	35	50	72	4.1	4.1	Both
133152	60	35	100		12.3	Problem
166698	30	50	88	6.8	7.1	Both
170637	35	30	59		5.6	Problem
187128	25	30	56		5.0	
205096	35	35	57		4.2	
205637	30	35	90		10.4	
227597	35	50	38	5.6		Problem
230089	35	30	96		12.9	Problem
255528	30	50	79	8.0	5.7	Both

Tag number is the individual record of each tree. Growth rate is given only for the interval where it exceeded 4 mm year⁻¹. The comment column gives the word 'both' for plants that grew faster than 4 mm year⁻¹ in both census intervals and 'problem' for cases where there were obvious discrepancies in dbh measures.

152 mm in dbh, growing consistently at more than 10 mm year^{-1} . These records cannot be attributed to error, as the chance of making two errors that led to consecutive estimates of high growth would be remote: as 1.8% of saplings grew 4 mm year^{-1} or less, the random chance of consecutive intervals of such fast growth would be $0.018^2 = 0.0003$, or one stem in 3330, and as we sampled fewer than 1000 saplings, not even one such record should have appeared. On the other hand, there are five records in the same list which can clearly be attributed to dbh mis-measures; these are indicated in Table 2.

Larger size classes had growth distributions that spread away from the origin (Figs. 3(B) and 3(C)), and the largest size classes had bell-shaped curves, with mean, mode, and median about the same (Fig. 3(C)). Figure 4 provides a comprehensive summary of growth variation in all size classes, with individual growth rates in both censuses plotted as a function of size. Above about 200 mm dbh, all variation in growth was found within any given size class; there was little difference between size classes. In fact, although mean growth rates changed dramatically with size (Table 1, Fig. 2), the range of growth rates changed little. Even the smallest stems had maximum growth of $10\text{--}15 \text{ mm year}^{-1}$, and the largest stems had maxima of $35\text{--}40 \text{ mm year}^{-1}$ (three records above 40 mm year^{-1} were omitted from Fig. 4). When growth was expressed relative to dbh, however, the pattern was different, with great variation among smaller stems and far less among larger stems (Fig. 4(B)).

Recruitment

There were 85 *Prioria* recruits in 1985 and 61 adults in 1982, and the mean census interval for all *Prioria* stems was 2.97 years. This yields a recruitment rate of 0.47 per adult per year. Similar figures for 1985–1990 were 82 recruits, 68 adults, 5.21 years, and 0.23 recruits per adult per year. Recruitment was close to double the total number of deaths in each census interval, and total recruitment exceeded the combined number of stems that died or broke (Table 1). Most recruits were of less than 30 mm dbh when first recorded (Table 1), but a few were larger. The few above 80 mm dbh (Table 1) were probably trees missed in the earlier census period, as no tree smaller than 20 mm dbh grew by as much as 80 mm during the census intervals (Table 2).

Discussion

The goal of a detailed study of the population biology of a tree species is to understand its basic ecological requirements. Some of this information can then be applied to management of the species for improved harvests. Several

of the results from the present study have direct bearing on attempts to manage cativo populations for harvest.

Cativo is generally harvested from swampy forests, where it occurs in nearly pure stands, and earlier studies of *Prioria* were carried out in swamp forests (Del Valle, 1979; Linares, 1987; Linares and Martinez, 1991). Many foresters are surprised to learn that it occurs on BCI, which consists almost entirely of well-drained upland soils (Dietrich et al., 1990). However, cativo is numerous in the 50 ha plot; indeed, in the southwest 10 ha, there are 85 trees above 400 mm dbh, a higher density than recorded in one swamp forest in eastern Panama identified for the production of cativo (8.3 ha^{-1} , J.A. Rovira et al., unpublished work, 1987); although other cativales have much higher cativo density—see Mayo Melendez (1965). Moreover, the population at BCI is flourishing—recruitment is high, mortality low, growth rates are somewhat higher than those reported for swamp forest in Colombia (Del Valle, 1979), and the population increased by 6% over 8 years. This is clearly not a remnant population. Here is one lesson for the management of cativo: plantation forestry could be attempted in upland soils. There is no need to restrict experiments with this species to swampy terrain.

Also potentially important for the management of cativo is the observation that saplings are capable of very rapid growth, although mean growth is slow. Foresters recognize cativo as slow-growing when young (Del Valle, 1979; Linares, 1987), but its potential rapid growth had not been noted before (presumably because earlier studies were based on much smaller samples). Based on mean growth of $5\text{--}8 \text{ mm year}^{-1}$ for trees above 100 mm dbh, Del Valle (1979) estimated that it would take about 100 years for a tree to reach 600 mm dbh. However, based on growth rates of 10 mm year^{-1} in saplings up to 40 mm year^{-1} in trees, the maximum that we found, it would only take 25 years to reach the same size. It would thus be extremely useful to determine the conditions that permit such rapid growth of a few trees in the native forest. A likely hypothesis to account for variation in growth is light availability, and we are currently examining the canopy structure in the vicinity of selected fast- and slow-growing trees to try to determine the optimum light regime.

Relevant to the factors that may control the cativo's growth was the huge difference in growth rates between the two census periods, with trees growing faster during the interval of the severe 1983 drought. This rather counter-intuitive result was a community-wide phenomenon presumably caused by the increased mortality rate of the forest canopy, which allowed more light to reach lower levels of the forest (Condit et al., 1992b; Smith et al., 1992). Perhaps also the increased insolation and temperatures of the drought improved growth rates. The abrupt change in growth makes a very strong case that cativo could be managed for improved growth; clearly, further under-

standing of the factors affecting growth would yield important clues for improving productivity of managed cativo stands.

Mortality rates of cativo in the BCI forest were below 1% year⁻¹ in all size classes but one. This is considerably lower than the mean mortality for the forest as a whole, which was 2% year⁻¹ between 1985 and 1990 (Condit et al., 1992b), and lower than the mean for most tropical forests (Swaine et al., 1987). Certain individual tree species have mortality as low as cativo, for example, *Gilbertiodendron dewevrei* (De Wild.) Léonard, a large caesalpioid legume whose natural history is like that of *Prioria* (Hart et al., 1989; T. Hart, personal communication, 1992). Oddly, although most of the BCI forest suffered higher mortality during 1982–1985 because of the 1983 drought (Condit et al., 1992b), cativo did not. This once again illustrates that *Prioria* is capable of surviving the relatively dry conditions of a tropical moist forest (compared, that is, with the swampy conditions where it is so abundant).

Many small stems lost their main stem but sprouted and survived. This is an important feature of a tree from the point of view of loggers or plantation foresters, as sprouts could be used to produce a generation of new trees after harvesting. We found, however, no evidence that large cativo trunks sprouted after the main trunk broke near ground level. Putz and Brokaw (1989) found decreasing frequency of sprouting with increasing size in a number of tree species, and Clark and Clark (1991) measured frequency of stem damage in tropical trees, and demonstrated the importance of litter fall in damaging stems.

Apart from providing such basic information as soil preferences and the like, another of the main values of detailed demographic data is in the development of models of timber harvest. Growth and mortality rates together allow predictions of the quantity of wood that a forest can produce and the interval between harvests (Usher, 1966; Getz and Haight, 1989). With these predictions, models of sustainable forestry can be developed, and the value of the forest resource can be estimated (Ashton and Panayotou, 1992). One controversy in Panama now centers on the length of land leases given to logging companies, and modeling studies that predict inter-harvest intervals are necessary to make adequate decisions about land tenure. We are currently working to develop such models for cativo, which we hope could have immediate impact in policy decisions on the harvest of cativo in Panama.

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